Review Article

GROWTH OF FOLIOSE LICHENS: A REVIEW

R.A. ARMSTRONG* and T. BRADWELL**

**Dept. of Vision Sciences, Aston University, Birmingham B4 7ET, United Kingdom,*
*** British Geological Survey, Edinburgh, United Kingdom*

Running Title: Foliose lichen growth

Corresponding author: R.A. Armstrong Tel. +44-121-204-4102, Fax. +44-121-204-4048, Email. R.A.Armstrong@aston.ac.uk;

Abstract

This review considers various aspects of the growth of foliose lichens including early growth and development, variation in radial growth rate (RaGR) of different species, growth to maturity, lobe growth variation, senescence and fragmentation, growth models, the influence of environmental variables, and the maintenance of thallus symmetry. The data suggest that a foliose lichen thallus is essentially a 'colony' in which the individual lobes exhibit a considerable degree of autonomy in their growth processes. During development, recognisable juvenile thalli are usually formed by 15 months to 4 years while most mature thalli exhibit RaGR between 1 and 5 mm yr^{-1}. RaGR within a species is highly variable. The growth rate-size curve of a foliose lichen thallus may result from growth processes that take place at the tips of individual lobes together with size-related changes in the intensity of competition for space between the marginal lobes. Radial growth and growth in mass is influenced by climatic and microclimatic factors and also by substratum factors such as rock and bark texture, chemistry, and nutrient enrichment. Possible future research topics include: (1) measuring fast growing foliose species through life, (2) the three dimensional changes that occur during lobe growth, (3) the cellular changes that occur during regeneration, growth, and division of lobes, and (4) the distribution and allocation of the major lichen carbohydrates within lobes.

Key Words: Radial growth rate (RaGR), Dry weight gain, Growth models, Aging and regeneration, Thallus symmetry

Introduction

The foliose lichen symbiosis has a highly structured growth form with a distinct lower cortex attached to the substratum usually by thread-like rhizinae. The margins of many thalli consist of individual leaf-like lobes that exhibit radial growth and periodically branch and divide (Armstrong 1991a). The result is a complex marginal structure in which the individual lobes may vary in size, shape, stage of division, and in radial growth rate (RaGR) (Aplin and Hill 1979, Hooker 1980, Hill 1984, Armstrong 1991a, 1993a). Foliose lichens, however, vary in the maximum size of thallus achieved and in the nature and shape of the margin, some species comprising an entire or crenate margin rather than distinct lobes. Hence, among lichens with a distinct dorsi-ventral type of thallus, a foliose growth form allows for a much greater range of morphological diversity at the margin than is possible in crustose or squamulose lichens (Hale 1967, Armstrong and Bradwell 2010). Fruticose lichens differ significantly from foliose species but also exhibit a wide diversity of form from hair-like, shrubby, finger-like, or strap-shaped structures of varying size.

The growth of foliose lichens has been reviewed previously by Hale (1973), Hill (1981), and by Lawrey (1984). Research over the last four decades has been concerned with several aspects of foliose lichen growth. First, the growth and development of thalli from vegetative diaspores such as isidia, soredia, or thallus fragments has been studied (Kershaw and Milbank 1970). Second, the RaGR of the marginal lobes changes with size, increasing significantly with size in smaller thalli but approaching a more constant (asymptotic) rate in larger thalli (Aplin and Hill 1979, Hill 1981, Armstrong and Smith 1996). Hence, there have been attempts to construct models which may explain the growth rate-size curve (Aplin and Hill 1979). Third, individual marginal lobes often show marked variations in RaGR (Philips 1969, Lawrey and Hale 1977, Topham 1977, Benedict and Nash 1990, Armstrong and Smith 1992). Consequently, there is the question of how foliose lichen thalli achieve and maintain the degree of thallus integration and symmetry observed in the field (Armstrong and Smith 1992). Fourth, using measurement of growth in mass such as dry weight gain (DWG), it has been possible to study the effects of nutrient enrichment and forestry management on foliose lichen growth.

This review considers eight main topics: (1) early growth and development, (2) variation in RaGR of different species, (3) growth to maturity, (4) lobe growth variation, (5) senescence and fragmentation, (6) growth models, (7) the influence of environmental variables, and (8) the maintenance of thallus symmetry.

Early growth and development

Many foliose lichen species have evolved vegetative diaspores to disperse the fungal and algal symbionts together (Bailey 1976). The most common methods of vegetative reproduction employed by foliose lichen thalli include isidia (Armstrong 1981), soredia (Armstrong 1991b), and thallus fragments (Armstrong 1990a).

Soredia and isidia

One of the earliest studies of the development of foliose thalli from vegetative diaspores was by Kershaw and Millbank (1970). They studied the growth of *Peltigera leucophlebia* (Nyl.) Gyelnik from individual isidia over seven months in a growth cabinet. A sigmoid pattern of growth was apparent, a slow period of initial growth being followed by a phase in which thallus area increased more or less linearly, and which was succeeded by a slower phase of growth. Subsequent studies have found varying rates of development from soredia and isidia in different species. For example, in *Peltigera didactyla* (With.) Laund. and *Peltigera praetextata* (Florke ex Sommerf.) Zopf (Stocker-Wörgötter 1991), mature thalli developed from soredia within 5 to 6 months. The size and growth form of the resulting thallus was dependent on the number of soredia involved in their formation since these are frequently dispersed in clusters of varying size (Armstrong 1990b). During development, the individual soredia within a cluster formed lobe ‘primordia’ that were then amalgamated into a single thallus. The early development of *Lobaria pulmonaria* (L.) Hoffm. from ‘isidioid’ soredia was studied by Scheidegger (1995) who found that anchored hyphae developed within 2 to 4 months after germination. After 15 months, growth zones had differentiated and lobes 0.5 mm in width were present. By contrast, in *Lobaria scrobiculata* (Scop.) DC. and in species of *Platismatia*, there was a much slower development of thalli from vegetative diaspores, and at least 4 years were required for the development of recognisable juvenile thalli in the field (Hilmo and Ott 2002). In *Lobaria scrobiculata*, for example, the first distinct lobules were observed 29 months after the start of the experiment while at 4 years, the largest lobules present were in the size range 0.4 to 1.3 mm (Hilmo and Ott 2002).

Thallus fragments

Some foliose species develop from fragments that may break off from the senescent parts of older thalli (Armstrong and Smith 1997). Hence, growth of fragments of *Parmotrema tinctorum* (Delise ex Nyl.) Hale was studied in growth cabinets in which relative humidity, temperature, light regime, pH, mineral status, and length of soaking could all be varied (Bando and Sugino 1995a,b). An area increase of approximately 20% per month was achieved if the fragments were soaked in culture medium for 90 minutes every four days and grown at 20°C and 100% relative humidity. In addition, brief periods of low, alternating with high, relative humidity resulted in particularly significant increases in surface area (Bando and Sugino 1995a,b).

There have also been studies of the radial growth of small ‘fragment-sized’ foliose thalli. Armstrong (1974), for example, measured the growth of small thalli (<1.5cm in diam.) of *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale and observed that RaGR could be described as a logarithmic function of fragment size ($r = 0.61$, $P < 0.01$, $r^2 = 0.37$) (Fig 1), i.e., a constant increase in RaGR with logarithm of size. In addition, relative growth rate (RGR), in which radial growth is expressed in relation to the total area of thallus ($cm^2\ cm^{-2}\ yr^{-1}$), increased rapidly up to a diameter of approximately 3 mm and then declined (Armstrong 1974). Hence, there may be only a short period early in the life of a thallus in which the whole of the thallus area supplies carbohydrate for growth at the margin. In a more detailed study, thallus fragments of *Xanthoparmelia conspersa*, with two or three developing lobes, were cut from mature thalli and glued to pieces of slate; their growth and development being studied over 4.5 years (Armstrong 1992, 2010). New lobe primordia were established rapidly over the cut surfaces of the fragments and, together with the number of mature lobes, increased over time. Moreover, there was an initial increase in RaGR followed by a more constant phase of growth beginning at a thallus radius of approximately 6 to 8 mm (Fig 2). Subsequently, there was a decline in RGR corresponding to the establishment of a more constant phase of radial growth.

Growth rates of foliose lichens

After initial development, the thallus grows to maturity by radial extension of the perimeter. Two of the earliest authors to measure foliose lichen growth were Linkola (1918) and Paulson (1918) and measurements have continued to be made up to the present (Armstrong 2009). One of the first authors to systematically review and compare lichen growth rates of different species was Hale (1967), who reported a range of RaGR measurements for foliose species of between 0.01 and 27.0 mm yr^{-1}. A selection of the published RaGR of foliose species is shown in Table 1. Various methods have been used to measure the RaGR reported in this table (Hale, 1967) including measurement of diameter growth, area growth, direct measurement of radial extension using a magnifying lens, and measurements using digital photography which may have contributed to growth rate variability.

The majority of studies of growth have been made on representatives of the genera *Parmelia*, *Flavoparmelia*, *Melanelia*, *Pseudoparmelia*, and *Xanthoparmelia* and to a lesser extent on *Physcia*, *Phaeophyscia*, and *Physconia*. Hence, there are very few recorded measurements for the majority of foliose species. Nevertheless, some generalizations can be made from these data. First, where RaGR has been measured on a sample of thalli from the same location, the range of RaGR is usually large. A major factor determining this growth variation is thallus size (Hale 1967), but variation in the RaGR of thalli of the same size can also be considerable. Measurement of RGR rather than RaGR can compensate for these variations in thallus size to some extent by scaling growth to thallus area. Measurements of thallus size is usually carried out be recording greatest diameter, averaging the greatest and smallest diameter, or averaging several diameters (Hale, 1967). Second, the slowest growth rates have been recorded in dry, continental Arctic and Alpine environments. Of these, possibly the lowest RaGR yet measured for a ‘mature’ foliose lichen with marginal lobes is by McCarthy and Smith (1995) in a study of *Xanthoria elegans* (Link) Th.Fr. in the Canadian Rockies (range 0.50 – 0.90 mm yr^{-1}). Third, where the same species has been measured under different climatic conditions or on different substrates, e.g., *Xanthoparmelia conspersa* and *Flavoparmelia caperata* (L.) Hale there are large differences in RaGR. Fourth, some foliose species may have extremely high RaGR, e.g., species of *Peltigera* (up to 64 mm yr^{-1}) (Frey 1959, Webster and Brown 1997) and to a lesser extent *Parmelia* (up to 13 mm yr^{-1}) (Paulson 1918).

Growth to maturity

That there are changes in RaGR during the life of a foliose lichen thallus is well documented. Because most foliose lichens may live for 30 to 60 years (Hale, 1959; Armstrong 1976a), investigation of such changes has been conducted using 'cross-sectional' studies, i.e., by measuring the growth of lichen thalli of different size and constructing a growth rate-size curve (Armstrong 1992). This type of study has three limitations. First, the method assumes a direct relationship between size and age. The degree of variation in RaGR between thalli of the same size, however, means that the range of possible age estimates for a thallus of a specific size is large (Armstrong 1976a). Second, the growth curve derived from a population of thalli of different size does not reflect the actual growth of any individual observed throughout its life. Third, variations in RaGR between thalli of similar size may obscure changes that are attributable to size so that only major trends in growth are detectable.

One of the earliest cross-sectional studies of foliose lichens reported a sigmoid pattern of growth in *Xanthoparmelia conspersa* (Hale 1959). There was a phase of slow but increasing RaGR until a thallus diameter of 1 to 1.5 cm was reached, radial growth was then relatively constant resulting in a linear increase in radius until a diameter of 10 to 12 cm, after which growth slowed. These three growth phases, viz., 'pre-linear', 'linear', and 'post-linear', occurred over a total lifespan of 39 years. The early part of this growth curve was also shown by *Melanelia fuliginosa ssp. fuliginosa* (Fr. ex Duby) Essl. in North Wales in which RaGR was constant over much of the life of the lichen, thallus radius increasing linearly as a result (Fig 3) (Armstrong 1976a). Preceding the linear phase, there was a phase in which RaGR increased with time while thallus radius increased logarithmically. There was no evidence, however, for a significant decline in RaGR (post-linear phase) in the largest thalli of *Melanelia fuliginosa ssp. fuliginosa* at the site. Several later studies have confirmed these results. Hence, the phase of increasing RaGR in smaller thalli was demonstrated in a study of *Pseudocyphellaria homeophylla* (Nyl.) Dodge and *Sticta caperata* Bory ex Nyl. (Snelgar and Green 1980). In addition, Benedict and Nash (1990) found that the growth of *Xanthoparmelia lineola* (Berry) Hale, became linear at a diameter of 25 mm and *Xanthoparmelia subdecipiens* (Vainio) Hale, at 20 mm.

Early studies of the growth curves of crustose lichens often assumed that they mirrored the relationship between RaGR and thallus size established for foliose lichens (Aplin and Hill 1979). Hence, Proctor (1977) studied the growth curve of the placodioid species (crustose lichens but with lobed margins) *Diploicia canescens* (Dicks.) Massal. It was assumed that RaGR was proportional to an area of thallus in an annulus of constant width within the growing margin and that the shape of the growth curve was essentially asymptotic similar to that of foliose lichens. However, although there is good evidence that placodioid species may grow similarly to 'true' foliose species (Hill 1981, Benedict, 2008), this may not be the case for many areolate crustose lichens such as species of *Rhizocarpon* (see review by Armstrong and Bradwell 2010).

Lobe growth variation

In a mature thallus, there is often a significant degree of variation in RaGR of different lobes (Phillips 1969, Lawrey and Hale 1977, Topham 1977, Armstrong and Smith 1992, Webster and Brown 1997). Lawrey and Hale (1977), for example, found variations of up to 50% in *Pseudoparmelia* species. In addition, in *Menegazzia terebrata* (Hoffm.) Massal. and *Lobaria pulmonaria*, some lobes grew two and a half time the average for the species while other lobes did not appear to grow at all (Phillips 1969). Moreover, in the latter study, rapid growth of a lobe was succeeded by a phase of slower growth and phases of slower growth did not appear to occur in succeeding years (Phillips 1969). A similar phenomenon was observed in *Xanthoparmelia. conspersa* and *Melanelia fuliginosa ssp. fuliginosa* in which individual lobes showed fluctuating patterns of growth from month to month with alternating periods of faster and slower growth (Armstrong and Smith 1992, Armstrong 2009).

Several factors may contribute to lobe growth variation. First, in species of *Xanthoparmelia* (Benedict and Nash 1990), RaGR varied markedly from lobe to lobe within a thallus and this variation appeared to be related to lobe width, wider lobes growing faster than narrower lobes. Second, significant variations in the concentration of soluble carbohydrates were found within individual lobes of *Xanthoparmelia conspersa* suggesting that differences in the production, allocation, and metabolism of carbohydrates between lobes might explain lobe growth variation (Armstrong and Smith 1994). Third, in an experimental study, Armstrong (1984a) 'reconstructed' thalli of *Xanthoparmelia conspersa* by cutting up the thalli into individual lobes, and gluing the lobes back to form a thallus either in their original or in a different configuration. Lobe growth variation within a reconstructed thallus was similar to that of randomly chosen intact thalli suggesting it may reflect the genetic origin of the lobes. In addition, gluing the lobes in a different configuration from the original or constructing thalli in which each lobe was removed from a different 'parent' thallus did not affect the degree of lobe growth variation. These results support the hypothesis that lobe growth variation is a property of individual lobes and not of the thallus as a whole.

Subsequently, the pattern of connections of adjacent lobes and the intensity of competition between them were shown to contribute to lobe growth variation (Armstrong 2003). Within the thallus margin, lobes vary in their degree of physical 'connectivity' to their neighbours. Some lobes are not physically connected to their neighbours before merging into the centre of the thallus. The majority of lobes, however, are connected in groups of two, three, or more, a pattern reflecting the past history of growth and lobe branching patterns (Hill 1992). The degree to which individual lobes are connected within the thallus margin, however, varies considerably from thallus to thallus and even within the same individual (Armstrong 2003). Hence, some thalli consist mainly of 'individual' lobes, without connections to their neighbours, whereas others consist of more interconnected lobes. In a study of lobe 'connectivity', the degree of 'connectivity' between lobes in a thallus was positively correlated with lobe growth variation (Armstrong 2003). In addition, a study of the interactions between adjacent lobes within the margin in species of *Xanthoparmelia* suggested that competition within the crowded thallus margin could also increase lobe growth variation (Armstrong 1995). Hence, although growth processes of neighbouring lobes are relatively autonomous, lobes also 'interact' with their neighbours by competing for space at the margin.

Senescence and regeneration

Studies of the division and turnover of algal cells in foliose lichen thalli suggest that algae divide more frequently at the lobe tips and especially in their terminal segments (Greenhalgh and Anglesea 1979, Hill 1985). By contrast, turnover of algal cells is slower away from the growing tips (Hill 1985), the central segments in particular having a high proportion of dead and dying cells (Greenhalgh and Anglesea 1979). In addition, there is a marked decrease in chlorophyll content coincident with thickening of the thallus from edge to centre (Valledares et al 1994). The activity of algal cells in the non-growing regions may be slowed by the production of fungal-derived inhibitory phenolic compounds (Honegger 1987).

Associated with the formation of a thickened, less productive area in the centre, is the appearance of fruiting bodies, most frequently apothecia (Pentecost and Rose 1985), a development that often precedes the degeneration and fragmentation of the thallus centre (Armstrong and Smith 1997). In *Xanthoparmelia conspersa*, for example, the number of apothecia present increases linearly with thallus diameter ($r = 0.75$, $P < 0.001$, $r^2 = 0.56$) while the mean diameter of apothecia is best fitted by a second-order polynomial ($r = 0.79$, $P < 0.001$, $r^2 = 0.62$) suggesting size of apothecia increases less rapidly in larger thalli (Fig 4). Pentecost and Rose (1985) demonstrated that the production of central apothecia in *Xanthoria parietina* (L.) Th. Fr. was not associated with a change in marginal RaGR. In addition, Armstrong (1974) showed that the RaGR of intact thalli was similar to that of fragmenting thalli of similar size confirming that degeneration of the thallus centre was not associated with a decline in RaGR. In further experiments, removal of the centres of *Xanthoparmelia conspersa* thalli, either with isidia alone or with a mixture of isidia and apothecia, did not influence RaGR (Armstrong 1979). These results support the hypothesis that the growth rate-size curve of a foliose lichen thallus is essentially asymptotic, a phase of increasing RaGR leading to a phase of more constant RaGR, the more constant linear phase continuing even after degeneration of a sizeable portion of the thallus centre (Armstrong and Smith 1997, Benedict and Nash 1990).

Fragmentation of the centre of a mature thallus also results in the regeneration of new lobes along the wound margins. Honegger et al (1996) transplanted thalli of *Xanthoria parietina* to a sandstone block for a five-year period. The oldest parts of the thalli developed apothecia and lost contact with the substratum but these areas were rapidly colonised by new thallus lobes that regenerated along the wound margins. In further experiments, it was demonstrated that *Xanthoria parietina* could regenerate from any cut part of the thallus including the thalline margins of the apothecial discs (Honegger 1996, et al 1996). It is likely that small islets of actively growing or dividing fungal and algal cells are initiated after wounding of the surface and that these develop into lobe primordia and then into mature lobes. Similar results were obtained by Armstrong (2010) in which fragments of the centre and perimeter of *Xanthoparmelia conspersa* thalli also regenerated new lobe primordia.

Growth models

Studies suggest that the growth rate-size curve of a foliose thallus is essentially asymptotic (Armstrong 1976a, Topham 1977, Aplin and Hill 1979). Given this pattern of growth, there have been several attempts to derive a growth model, based on morphological and physiological attributes of lichens and their symbionts, which can explain the shape of the curve.

Models based on translocation within the thallus

The earliest growth models were based on assumed analogies between lichen growth and that of fungal hyphae on artificial media (Righelato 1975). The growth of a fungus is essentially ‘autocatalytic’ resulting in exponential growth within a relatively unrestricted system. Exponential growth implies that all or a constant proportion of the hyphal length contributes to new growth by branching. The main cause of slowing of growth rates is a decrease in the concentration of one or more substrates leading to growth limiting conditions at the margin. The relevance of this type of growth model to lichens is questionable as there may be only a very short period in which lichen growth is truly exponential (Armstrong 1974). In the model developed by Trinci (1971), however, only the initial growth of the fungal colony is exponential. Once a size has been reached so that diffusion into the centre is less than demand, exponential growth in the centre ceases. Nevertheless, hyphae in an ‘annulus’ of constant width at the margin continue to grow at maximum specific growth rates, growth of the colony as a whole being proportional to that in the annulus. Radial growth is then a function of ‘w’ the width of the peripheral zone of mycelium in which nutrients can be easily translocated and the result is approximately linear growth. This type of model is attractive as it predicts the change in foliose lichens from a phase of increasing to one of more constant RaGR. Crustose lichens, with the exception of the placodioid type, exhibit a different growth curve, and growth of these lichens is discussed by Armstrong and Bradwell (2010).

The most sophisticated and useful models of this type, applied specifically to lichens, were developed by Aplin and Hill (1979) and Childress and Keller (1980). Both models are essentially similar and are based on the translocation of carbohydrate between different parts of the thallus. In Aplin and Hill’s (1979) model (Fig 5), two growth constants, viz., α and β, describing the extent of lateral movement of carbohydrate and the rate of carbohydrate production respectively are important variables. Similarly, Childress and Keller’s (1980) model is based on the production of carbohydrate, the consumption of substances to thicken the thallus, translocation towards the outer edge, and consumption at the edge for radial growth. Both models provide a mathematical description of the change in lichen radius as a function of time and both predict the essentially asymptotic growth rate-size curve. However, the model provides a poor fit to data from *Melanelia fuliginosa ssp. fuliginosa* (Fig 3) ($r = -0.46$, $P > 0.05$, $r^2 = 0.21$) but does fit the growth curve of *Xanthoparmelia conspersa* more closely ($r = -0.67$, $P < 0.05$, $r^2 = 0.45$).

In both the Aplin and Hill (1979) and Childress and Keller (1980) models, lateral translocation of carbohydrate within the thallus is an important variable. Nevertheless, experimental data have questioned whether there is translocation of carbohydrate within a foliose lichen thallus other than over very short distances. For example, in ‘lobe painting experiments’, a treatment that reduces algal numbers beneath segments of lobes which have been over painted with acrylic paint, painting the whole of the surface of a lobe virtually eliminates radial growth while partially painted lobes do grow but at slower rates than unpainted control lobes (Armstrong

1991a). In addition, the radial growth of a lobe is unaffected by either completely painting or removing its neighbours (Armstrong 1991a).

A prediction of the Aplin and Hill (1979) model is that if the level of carbohydrate in part of the perimeter is too low to sustain growth, RaGR would decline resulting in an indentation. As a consequence, carbohydrate would be translocated from adjacent regions to increase growth and maintain thallus symmetry. Experimental data, however, suggest that adjacent lobes have a considerable degree of autonomy in their growth processes with little transport of carbohydrate between them. In a subsequent experiment (Armstrong and Smith 1998), individual lobes were cut from thalli of *Xanthoparmelia conspersa* and portions of the base of the lobe excised with a scalpel to varying distances from the tip. RaGR was unaffected until less than 2 mm of the lobe tip remained. Similarly, painting the surfaces of the base of lobes only resulted in a reduction in RaGR if the paint extended to within 0.5 mm and 1 mm from the lobe tip (Armstrong and Smith 1998). These results suggest that radial growth is dependent on processes that occur only within a very short distance from the tip and not on translocation from elsewhere in the lobe. Moreover, there is a distinct gradient of carbohydrate concentration within individual lobes, the levels of arabitol, ribitol, and mannitol being greatest at the tip and declining markedly with distance from the tip towards the base of the lobe (Armstrong and Smith 1998). As a consequence, any translocation towards the lobe tip would be against a significant concentration gradient. More direct studies of translocation employing C-14/C ratios in radial transects across lichens (Bench et al 2002) also suggest that significant internal recycling and translocation of carbon is unlikely. Hence, factors other than the movement of carbohydrate may be necessary to explain the growth rate-size curves of foliose lichens. As there may be limited movement of carbohydrate even within individual lobes it is unlikely that there is significant transport in foliose lichens with less distinct lobes at the margin.

Models based on lobe morphology

In a cross-sectional study of *Xanthoparmelia conspersa* (Armstrong and Smith 1996), a growth rate-size curve derived by taking growth data from a single lobe only from each of a sample of thalli, e.g., the fastest-growing lobe, was similar to that derived by averaging the growth of several lobes from each thallus. Hence, the growth rate-size curve is a property of individual lobes rather than of the thallus as a whole. One of the first lichenologists to study the growth of individual lobes in detail was Hale (1970). He found that in *Flavoparmelia caperata,* each major lobe produced new lobes from two or more marginal bulges. At maturity, the lateral bulges atrophied and only two or three apical lobes continued growth. Most vertical growth occurred within 1 mm of the tip with cessation 1.5 to 2.0 mm back from the tip. In addition, horizontal growth was not as rapid as vertical growth and ceased when the lobe reached an approximate width of 2.5 cm. These studies were extended by Hill (1992) who photographed lobes of thalli of *Parmelia saxatilis* (L.) Ach. two years apart and found that the RaGR of the thallus was directly related to lobe width. Positive correlations between RaGR, lobe width, and the degree of bifurcation of the lobe were also observed by Armstrong (1995) (Fig 6) but although statistically significant the correlation is relatively weak ($r = 0.49$, $P < 0.05$, $r^2 = 0.24$). Since mean lobe width increases non-linearly with thallus size in *Xanthoparmelia conspersa* (Armstrong 1991a), increasing more rapidly in smaller thalli and less rapidly in larger thalli, changes in lobe width with thallus size could be a factor determining the growth rate-size curve (Armstrong and Smith 1996). Obviously, lobe width will be of considerable less importance in some tropical foliose lichens which have less distinct lobes and therefore, a more integrated margin and in species with crenate margins.

Models based on lobe competition

Lateral competition between adjacent lobes for space can be intense and changes in the intensity of this competition with thallus size could also be important in determining the growth curve. One of the first demonstrations of marginal competition was by Hooker (1980) who found that in *Xanthoria elegans,* few lobes in small thalli were overgrown by their neighbours, but in larger thalli, many lobes were overgrown, with one in four lobes unable to keep up with the advancing margin. Hooker (1980) also found that lateral growth ceased when lobes of adjacent thalli met. That the intensity of marginal competition between adjacent lobes could increase with thallus size was demonstrated by Armstrong (1991a). In addition, a complex pattern of correlations between the growth of adjacent lobes in various foliose species was observed (Armstrong 1993a). The RaGR of a single lobe, for example, was correlated with the length and radial growth of its neighbouring lobes while the pattern of lobe branching and division was related to lobe width and to a lesser extent to the length and width of its adjacent lobes. More recently, Armstrong (2003) developed a ‘crowding index’ to describe the density and degree of overcrowding of lobes at the margin and found that the index increased non-linearly with size ($r = 0.78$, $P < 0.001$, $r^2 = 0.61$), the degree of crowding increasing rapidly with size at first and then less rapidly in larger thalli as a more constant number of lobes is established (Fig 7). Hence, changes in lobe density with size and as a result, in the intensity of lateral competition, could also be a factor determining the growth rate-size curve. Hence, although the growth rate-size curve may be determined primarily by processes within individual lobes, these processes are also influenced by the general thallus environment, e.g., the degree of lobe overcrowding.

The influence of environmental variables on growth

Studies of the effects of environmental factors on foliose lichen growth have been limited by the few facilities available for culturing whole thalli in the laboratory for long periods of time. Few ‘factorial-type’ experiments, in which the synergistic effects of different variables are studied, have consequently been undertaken (Jones and Platt 1969, Armstrong 1994). As a result, many studies of lichen growth have been carried out in the field and therefore, lack the control of environmental factors possible in a laboratory experiment. In addition, variation in RaGR is usually so great under field conditions that large numbers of replicate thalli are often required for growth experiments to have sufficient statistical ‘power’ to detect the effects of environmental factors. As a consequence, many recent studies have used measurements of growth in mass such as DWG or thallus specific weight (TSW) as measures of growth performance.

Climate

Evidence for the influence of climate on growth has been obtained mainly from studies of seasonal variation (Rydzak 1961, Hale 1970, Armstrong 1973, 1993b, Showman 1976, Lawrey and Hale 1977, Fisher and Proctor 1978, Moxham 1981, Benedict 1990). Seasonal fluctuations in growth measured as RaGR per month, often correlate best with average or total rainfall (Karenlampi 1971, Armstrong 1973, Golm et al 1993), but linear regressions fitted to radial growth increments measured per month against total rainfall often account for relatively small amounts of the total variance (usually <40%) (Armstrong 1988). In a study of *Cetraria*, Paterson et al (1983) found that moisture was the most important factor governing growth. In addition, assimilation gains during rainy days were sufficient to offset carbon losses over five dry days. Mean daily rainfall in summer was found to be the controlling factor determining growth in *Flavocetraria nivalis* (L.) Kärnefelt & A. Thell. although temperature was also considered to be a factor (Karenlampi 1971). Similarly, in the high Arctic, low light intensity did not depress the RGR of *Cetraria* species; the frequency of watering being the most important factor determining growth (Cooper et al 2001).

Stepwise multiple regression is a useful statistical method of analysing seasonal trends (Armstrong, 1991b). For example, Lawrey and Hale (1977) found that a multiple regression equation that included the variables maximum temperature, total rainfall, and percent cloudy days explained 22% of the variation in the growth of *Flavoparmelia baltimorensis* (Gyeln. & Fóriss) Hale. An example of the use of this method to study the monthly radial growth of single lobes of *Xanthoparmelia conspersa* in North Wales over 22 months is shown in Table 2 (Armstrong 2009). Of eight climatic variables included in the regression analysis, three, viz., the frequency of rainy days, average wind speed, and the frequency of ground frosts each month were selected as important variables and accounted in total for 49% of the total variance. Of the three variables, stepwise multiple regression suggested that the frequency of rainy days was the most important.

The affect of climate and microclimate on lichen growth performance on tree bark has frequently been studied using reciprocal transplants (Gaio-Oliveira et al 2004). Hence, the relationship between thallus size and growth was studied in three successional forest stands across three boreal climate zones using transplants of *Lobaria pulmonaria* (Gauslaa et al 2009). Stand specific water availability was the most important factor increasing thallus area consistent with its role in fungal expansion. In a further transplant experiment, the influence of canopy cover on growth was studied along a regional forest gradient in the boreal forest (Gauslaa et al

2007). Growth was greatest in the Atlantic rainforest with a DMG of 36-38% but was reduced by low light levels even in old forests and in most semi-exposed clear-cuts. The relationship between irradiance and lichen growth was also studied in five macrolichens in Sweden (Palmqvist and Sundberg 2000) and a strong correlation observed especially when the lichens were wet. Hence, clear-cutting, which often creates an abrupt edge to forest stands, may affect foliose lichen growth. The affect of 'hard edges' and a less abrupt edge to the forest on the growth was studied in British Columbia using transplants of *Lobaria retigera* (Bory) Trevis. (Stevenson and Coxson 2008). There was a high mortality of thalli and loss of biomass over three years at 'hard' edge sites with significantly less losses when a less abrupt edge was present suggesting that leaving a substantial number of residual trees at the margin would reduce the impact of forest clearing on lichen diversity.

Considerable regional variation in the response to climatic variables has also been observed between different isolates of the lichen-forming fungus *Xanthoria elegans* (Murtagh et al 2002). Hence, temperature had a significant effect on RGR such that isolates from sites with a lower mean annual temperature had significantly higher RGR at all test temperatures between 2 – 18 ºC. Hence, enhanced metabolic activity may be an adaptation for growth in cold climates in this species.

Microclimate

Physiological experiments have suggested that interactions between microclimatic factors and especially light intensity, temperature, and moisture are the most important in determining local growth rates. In a transplant experiment designed to evaluate growth responses of *L. pulmonaria* to canopy structure, for example, DWG was strongly correlated with canopy light transmission, DWG over 2 years being <5% under canopies and rising to 20% on branches under canopy gaps (Coxson and Stevenson 2007). The net assimilation rate (NCAR) is influenced by the moisture content of the thallus (Harris 1971a,b,c, Kershaw 1972), reaching a peak between 65% and 90% saturation and falling at water contents near to saturation. In addition, at least for some species of temperate lichens, wetting the thallus results in losses of carbon by a release of carbon dioxide gas and resaturation respiration (Smith and Molesworth 1973, Farrar 1973, 1976). Hence, to grow, thalli have to be wet sufficiently long in the light to overcome the carbon lost on rewetting (Armstrong 1976b). The interactions between light, temperature, and rate of drying of the thallus are therefore, likely to be particularly important for lichen growth and may vary with aspect (Armstrong 1975), slope (Sletvold and Hestmark 1998), rock and bark texture (Moxham 1981, Armstrong 1993c), and vertical location on the substratum (Harris 1971a, Armstrong 1978). Computer simulation methods have also been used in an attempt to unravel the effects of different microclimatic variables. Hence, Harris (1971a, 1971b, 1972) constructed a model to test the hypothesis that the vertical distribution of epiphytic lichens in south Devon was a function of light intensity and water availability. He found that the predicted vertical NCAR compared not unfavourably with the observed distributions of the lichens with height on the tree.

Substratum

The physical and chemical nature of the substratum has a profound influence on the growth of foliose lichens (Brodo 1973). Nutritional elements may influence growth by being in limited supply or in excess, although it is generally believed that the concentration of chemical ions in the field is sufficient to satisfy the demands of slow-growing lichens (Farrar 1976).

The relationship between mechanical, chemical, and mineralogical soil properties and the types of substratum chosen by lichens was studied by Garty et al (1974). They found that *Squamarina* species were located on soils with low shrinkage rates. When the shrinkage rate was above 5%, however, the lichens colonized rock and moss instead. Hence, the effects of texture, porosity, rate of drying, and the physical changes of the substratum on growth are likely to influence lichen distributions. *Xanthoria parietina* is also influenced by the texture of the substratum, thalli on rock and smooth-barked surfaces having a higher RaGR than those on rough bark; a phenomenon that particularly affects small thalli (Moxham 1981). In addition, a combination of high water absorbing power and a high base content of the substratum favoured growth of lichens on roofs in a London suburb (Brightman 1959).

Several studies suggest that nutrient enrichment by bird droppings has a significant influence on the lichen flora (Hale 1967). Bird droppings may influence growth and survival by smothering the thalli, altering the pH, or adding inhibitory and stimulatory compounds. Droppings from a variety of birds were applied as a thick paste (12 applications in one year) and as a suspension in deionized water (24 applications in one year) to a range of foliose lichens with different distributions on and off bird perching stones (Armstrong 1984b). Treatment with bird droppings was essential for the survival of *Xanthoria parietina* thalli on siliceous rock away from the sea and increased the growth of *Xanthoparmelia conspersa*, a species common on well-lit nutrient enriched rocks. The paste, however, inhibited the growth of *Melanelia fuliginosa ssp. fuliginosa* and this species is rarer on bird perching stones. Uric acid, the most abundant nitrogenous component of bird droppings, did not influence growth when applied as a suspension (Armstrong 1984b). Hence, the growth responses may be attributable to either increased pH or to levels of inorganic chemicals in the bird droppings.

The response of *Xanthoria parietina* to varying nitrogen concentrations was studied by Gaio-Oliveira et al (2005). TSW was similar in all thalli without any significant effect of added nitrogen suggesting that *Xanthoria parietina* may respond more to changes in pH than to nitrogen (Armstrong 1990b). The relationship between nitrogen concentration and growth was also studied in *Nephroma arcticum* (L.) Torss. and *Peltigera aphthosa* (L.) Willd. (Sundberg et al 2001). After 4 months, control and nitrogen-fertilized thalli of *Nephroma arcticum* increased in area by 0.2 m^2 m^{-2} (mean RGR 3.8 mg gm^{-1} d^{-1}) and *Peltigera aphthosa* by 0.4 m^2 m^{-2} (mean RGR 8.4 mg gm^{-1} d^{-1}). Slower growth in *Nephroma arcticum* was explained by lower nitrogen and chlorophyll A concentration and as a consequence, substantially lower light energy conversion efficiency. The interaction between nitrogen availability and light exposure was studied in *Platismatia glauca* (L.) WL Culb. & CF Culb. (Palmqvist and Dahlman 2006). DWG was significantly enhanced by nitrogen supply, variations in DWG being most significantly accounted for by Chlorophyll A concentration. Hence, *Platismatia glauca* may respond to increasing nitrogen concentration by increasing growth rate and carbon assimilation capacity through investment in algal cells. Phosphorus may also be important in some cyanobacteria lichens such as *Lobaria pulmonaria* (McCune et al 2007). Hence, this species doubled in annual biomass after a single 20-minute immersion in a phosphorus solution suggesting that phosphorus may as important a stimulant in caynobacteria-rich lichen communities as it is to cyanobacteria in aquatic environments.

In a factorial growth experiment (Armstrong 2000), the interaction between nutrient status of the substratum and competitive ability was demonstrated in four foliose species by growing them in monoculture and in competitive mixtures in well-lit plots with and without nutrient enrichment by bird droppings. In monoculture, addition of bird droppings increased the growth of *Xanthoparmelia conspersa*, decreased that of *Parmelia saxatilis* and *Melanelia fuliginosa ssp. fuliginosa* while the growth of *Phaeophyscia orbicularis* (Neck.) Moberg was unaffected. In untreated plots, *Xanthoparmelia conspersa* had a strong influence on all three competitors and especially on *Phaeophyscia orbicularis*. There was also mutual competition between *Phaeophyscia orbicularis* and *Parmelia saxatilis* and between *Melanelia fuliginosa ssp. fuliginosa* and *Parmelia saxatilis*. Under conditions of nutrient enrichment, *Xanthoparmelia conspersa* was a stronger competitor against *Parmelia saxatilis* but a weaker competitor against *Phaeophyscia orbicularis*. Hence, nutrient enrichment appeared to alter the competitive balance between the four species suggesting that a different combination of species would occur on nutrient rich and poor rocks (Armstrong 2007).

Chemical factors may also be important in the growth of lichens on maritime rocks. Fletcher (1976) suggested that although calcium was an important ion, salinity exerted little effect, the species responding more to periods of immersion. By contrast, Ramkaer (1978) found that the response of four different mycobionts to salinity correlated well with location of the lichens with reference to the zonation on maritime rocks. No studies appear to have been published on the influence of chemical treatments on the growth of species on maritime rocks. Nevertheless, the radial growth of *Xanthoria parietina*, a common species of the submesic zone of the suppralittoral (Fletcher 1976) and many nutrient enriched sites inland (Brodo 1973), was inhibited when transplanted to inland sites (Armstrong 1990b). Nevertheless, the transplanted thalli grew successfully when calcium carbonate was added to the thalli at intervals during the year; treatment with a 0.250 mM solution of calcium chloride at similar intervals having less effect. Hence, a relatively constant supply of calcium may be necessary for the growth of this species. This hypothesis is also supported by experiments carried out by Fletcher (1976). He found that *Xanthoria parietina* thalli lost potassium ions when treated with distilled water and an application of a 0.250 mM solution of calcium to the medium prevented this loss in the light.

A requirement for calcium may also explain the distribution of *Xanthoria parietina* on limestone rocks and walls, wall mortar, asbestos, tree bark where stemflow is enriched with calcium, and siliceous rocks near the sea. By contrast, *Parmelia saxatilis* is virtually restricted to acid substrata. Thalli of this species adopt a ‘crescent-shaped’ form after treatment with calcium carbonate and then fragment and disappear after about 10 months (Armstrong 1990). Treatment with a 0.250 mM solution of calcium as calcium chloride had little effect on growth of *Parmelia saxatilis* suggesting that this species could occur at more mildly alkaline sites. Gilbert (1971) found, for example, that *Parmelia saxatilis* could occur at more alkaline sites in polluted environments. Zinc, copper, and mercury may also be important in lichen growth as they have been shown to affect the chlorophyll content of lichen algae (Backor and Djubai 2004).

Element concentrations may also be involved in speciation. Hence, six species of foliose lichen were studied in eleven protected areas of the northern Great Lakes in regions not greatly influenced by pollution (Bennett 2008). Concentrations of elements in the different species were useful in discriminating between the various taxa.

Discussion and conclusions

Lichen growth rate-size curve

Studies of foliose lichens have concluded that aspects of the biology of individual lobes are important in determining the pattern of growth of the thallus as a whole. A characteristic feature of foliose species is the asymptotic growth rate-size curve (Aplin and Hill 1979, Armstrong and Smith 1996) in which an early increasing phase of RaGR in smaller thalli gives way to a more constant growth phase. Apart from the very earliest phases of growth, when thalli are less than a few millimetres in size, it is unlikely that the shape of this curve is determined by changes in the lateral translocation of carbohydrates. Instead, change in RaGR with thallus size appears to be determined more by the properties of the lobes themselves (Armstrong and Smith 1996, 1999). In *Xanthoparmelia conspersa*, marginal growth is determined by processes that take place immediately behind the lobe tip (Armstrong and Smith 1998) although the degree of involvement of the rest of the lobe may vary with species (Hill 1981). An important feature is the change in lobe width with thallus size. In small thalli, the lobes are less crowded than in larger thalli and this allows for more lateral growth and an increase in lobe width. These developments increase the photosynthetic area immediately behind the tip and, as a consequence, result in increasing RaGR with size. As the thallus continues to grow, however, an increase in lobe width results in faster rates of lobe division and an increased density of lobes at the margin (Armstrong 1991a). The inevitable overcrowding of lobes at the margin and increased competition for space may then restrict further increases in lobe width and this may result in more constant or asymptotic growth.

Lobe growth variation

A number of factors may contribute to lobe growth variation including the degree of connectivity of lobes within a thallus (Armstrong 2003), and variations in lobe morphology (Armstrong and Smith 1992), algal cell density (Slocum et al 1980), hyphal elongation (Slocum et al 1980), and carbohydrate concentration (Armstrong and Smith 1994). A recently identified factor is variation in the degree of connectivity of lobes (Armstrong 2003); a greater degree of growth variation being present in thalli where there are more physical connections between the lobes. Each group of connected lobes within a thallus may be derived from a different diaspore. A previous study (Armstrong 1984a) demonstrated that an individual thallus could be made up of lobes which originate from several different genetically distinct ‘parents’ as a result of the aggregation of diaspores in cracks or fissures on the substratum(Armstrong 1984a). Hence, lobes sharing the same genotype may show less variation than lobes that have a mixed genetic origin. Second, lobe competition may be more intense in thalli in which all the lobes originate by branching from a single diaspore (Armstrong 1995). Studies suggest that lobe competition could decrease the degree of lobe growth variation, e.g., a strong faster-growing competitor could overgrow and reduce the growth of weaker slower-growing neighbours (Armstrong 1995). The consequence of this competition could be a population of marginal lobes with a rapid but more uniform RaGR.

Thallus symmetry

Given the degree of lobe growth variation often observed in foliose lichens, how is thallus symmetry maintained in a lobed foliose thallus? The data suggest that although an obvious integrating mechanism appears to be absent, a number of factors contribute to thallus symmetry. First, in many thalli, lobes show a non-synchronised pattern of fluctuating radial growth from month to month (Phillips 1963, Armstrong and Smith 1992, Armstrong, 2009). This pattern of growth, although highly variable over short intervals of time, results in more constant lobe growth over longer periods because the effect of the monthly fluctuations is essentially cancelled out. Second, in some thalli, there are positive correlations between the growth of different lobes as a consequence of either the lobes having the same genetic origin or mutual correlations with climatic factors (Armstrong and Smith 1992). Third, despite these compensating factors, some individual lobes may still grow consistently more slowly than the average for the thallus. The data suggest that a slower growing lobe would be overgrown by faster growing neighbours and eliminated as suggested by Hooker (1980). In addition, if indentations develop in the perimeter then they would be removed as a result of a rapid increase in width of the neighbouring lobes (Hale 1970). Nevertheless, the experimental data fail to demonstrate that a rapidly growing lobe would slow down when it grows beyond the perimeter at least over short periods of time. It is possible that when such a lobe divides its growth would be slowed sufficiently to allow neighbours to catch up, thus preventing the development of frequent outgrowths or ‘buds’ on the thallus perimeter (Armstrong 2009). Hence, a relatively undifferentiated lichen thallus, which shows more or less independent growth at any point on the colony, can achieve a degree of symmetry without an obvious integrating mechanism. There are parallels between foliose lichen growth and lobe branching with growth of vascular plants. Hence, simulation models based on tree or vascular plant branching may be useful in understanding foliose lichen growth. Sumner (2001), for example, developed a model of lichen morphogenesis which can be used to generate images and animations of lichen growth.

Future research

There is a great deal still to be learned concerning the growth of foliose lichens and several areas of future research could be profitable pursued. First, some foliose lichens have a very rapid RaGR (Webster and Brown 1997) and therefore, direct study of at least part of the lichen growth curve is feasible, e.g., the transition from a phase of increasing RaGR to one of more constant growth (Armstrong 1992). Second, more detailed studies are needed of the concentration, distribution, and allocation of the major lichen carbohydrates within different lobes (Armstrong and Smith 1994). Third, studies of changes in lobe thickness with distance from the lobe tip and with time would enable a three-dimensional perspective of lobe growth to be achieved. Fourth, the stages involved in lobe branching, division, and regeneration (Armstrong and Smith 1998) need to be investigated together with light and electron microscope studies of the cellular changes accompanying these processes. Fifth, studies on the processes of decay and rejuvenation in the thallus centre (Armstrong and Smith 1997) would be valuable both in determining not only whether degeneration ultimately affects growth at the margin but also to establish the factors determining thallus regeneration. Sixth, factorial experiments are needed to investigate the influence of environmental factors on growth and would lead to a more realistic understanding of the interactive processes influencing lichen growth in the field.

References

Aplin PS, Hill DJ (1979) Growth analysis of circular lichen thalli. J Theor Biol 78:347

Armstrong RA (1973) Seasonal growth and growth rate colony size relationships in six species of saxicolous lichens. New Phytol 72:1023-1030

Armstrong RA (1974) Growth phases in the life of a lichen thallus. New Phytol 73:913

Armstrong RA (1975) The influence of aspect on the pattern of seasonal growth in the lichen *Parmelia glabratula* ssp. *fuliginosa*. New Phytol **75**:245-251

Armstrong RA (1976a) Studies on the growth rate of lichens. In: Brown DH, Bailey RH and Hawksworth DL (ed.) Progress and Problems in Lichenology, Academic Press, London, 309-322

Armstrong RA (1976b) The influence of the frequency of wetting and drying on the radial growth of three saxicolous lichens in the field. New Phytol **77**:719-724

Armstrong RA (1978) The colonization of a slate rock surface by a lichen. New Phytol 81:85-88

Armstrong RA (1979) Growth and regeneration of lichen thalli with the central portions artificially removed. Env Exp Bot 19:175-178

Armstrong RA (1981) Field experiments on the dispersal, establishment and colonization of lichens on a slate rock surface. Env Exp Bot 21:116-120

Armstrong RA (1984a) Growth of experimentally reconstructed thalli of the lichen *Parmelia conspersa.* New Phytol 98:497-502

Armstrong RA (1984b) The influence of bird droppings and uric acid on the growth of five species of saxicolous lichens. Env Exp Bot 24:95-99

Armstrong RA (1988) Substrate colonization, Growth and Competition. In: Galun M (ed) Handbook of Lichenology, CRC Press, Cleveland, pp 3-16

Armstrong RA (1990a) Dispersal, establishment and survival of soredia and fragments of the lichen *Hypogymnia physodes* (L.). New Phytol 114:239-245

Armstrong RA (1990b) The influence of calcium and magnesium on the growth of the lichens. *Xanthoria parietina* and *Parmelia saxatilis*. Env Exp Bot 30:51-57

Armstrong RA (1991a) Experimental studies of lobe growth in the lichen *Parmelia conspersa* (Ehrh. ex Ach.) Ach. New Phytol 119:315-319

Armstrong RA (1991b) The influence of climate on the dispersal of lichen soredia. Env Exp Bot 31:239-245

Armstrong RA (1992) A comparison of the growth curves of the foliose lichen *Parmelia conspersa* determined by a cross-sectional study and by direct measurement. Env Exp Bot 32:221-227

Armstrong RA (1993a) Factors determining lobe growth in foliose lichen thalli. New Phytol 124: 675-679

Armstrong RA (1993b) Seasonal growth of foliose lichens in successive years in South Gwynedd, Wales. Env Exp Bot 33:225-232

Armstrong RA (1993c) The growth of six saxicolous lichens transplanted to lime-rich and lime-poor substrates in South Gwynedd, Wales. Symbiosis 15:257-267

Armstrong RA (1994) The influence of bird droppings on the growth of lichen fragments transplanted to slate and cement substrates. Symbiosis 17:75-86

Armstrong RA (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 RA (2000) Competitive interactions between four foliose lichen species with and without nutrient enrichment. Symbiosis 28:323-335

Armstrong RA (2003) Lobe connections and lobe crowding are associated with growth rate in the lichen *Xanthoparmelia conspersa*. Symbiosis 34:133-143

Armstrong RA (2007) Competition in lichen communities. Symbiosis 43: 1-12.

Armstrong RA (2009) Monthly fluctuations in radial growth of individual lobes of the lichen *Parmelia conspersa* (Ehrh. Ex Ach.) Ach. Symbiosis 47:9-16

Armstrong RA (2010) Lobe formation and division in the foliose lichen *Xanthoparmelia conspersa*. Symbiosis 51:227-232

Armstrong RA, Smith SN (1992) Lobe growth variation and the maintenance of symmetry in foliose lichen thalli. Symbiosis 12:145-158

Armstrong RA, Smith SN (1994) The levels of ribitol, arabitol and mannitol in individual lobes of the lichen *Parmelia conspersa* (Ehrh. ex Ach.)Ach. Env Exp Bot 34:253-260

Armstrong RA, Smith SN (1996) Factors determining the growth curve of the foliose lichen *Parmelia conspersa*. New Phytol 134:517-522

Armstrong RA, Smith SN (1997) Factors associated with degeneration of the thallus center in foliose lichens. Symbiosis 22:293-302

Armstrong RA, Smith SN (1998) Does radial growth of the lichen *Parmelia conspersa* depend exclusively on growth processes at the lobe tip? Env Exp Bot 39:263-269

Armstrong RA, Smith SN (1999) Factors associated with lobe division in the lichen *Parmelia conspersa* (Ehrh. ex. Ach.)Ach. Symbiosis 26:265-277

Armstrong RA, Bradwell T (2010) Growth of crustose lichens: A review. Geografiska Ann, Series A, Phys Geog 92A: 3-17

Backor M, Djubai A (2004) Short-term and chronic effects of copper, zinc and mercury on the chlorophyll content of four lichen photobionts and related algae. J Hatt Bot lab 95: 271-284

Bailey RH (1976) Ecological aspects of dispersal and establishment in lichens. In: Brown DH, Bailey RH and Hawksworth DL (ed) Progress and Problems in Lichenology, Academic Press, London, 215-247

Bando M, Sugino M (1995a) Cultivation of the lichen *Parmotrema tinctorum* in growth cabinets. J Plant Res 108:53-57

Bando M, Sugino M (1995b) Effect of low-humidity treatment on growth of the lichen *Parmotrema tinctorum* in a growth cabinet. J Plant Res 108:527-529

Bench G, Clark BM, Mangelson NF, St Clair LL, Rees LB, Grant PG, Southon JR (2002) Use of 14C/C ratios to provide insights into the magnitude of carbon turnover in the crustose saxicolous lichen *Caloplaca trachyphylla*. Lichenologist 34:169-180

Benedict JB (1990) Experiments on lichen growth. I. Seasonal patterns and environmental controls. Arct Alp Res 22:244-254

Benedict JB (1991) Experiments on lichen growth II. Effects of a seasonal snow cover. Arc Alp Res 23:189-199

Benedict JB (2008) Experiments on lichen growth III. The shape of the age-size curve. Arc Ant Alp Res 40:15-26

Benedict JB, Nash TH (1990) Radial growth and habitat selection by morphologically similar chemotypes of *Xanthoparmelia*. Bryologist 93:319-327

Bennett JP (2008) Discrimination of lichen genera and species using element concentrations. Lichenologist 40: 135-151

Brightman FH (1959) Some factors influencing lichen growth in towns. Lichenologist 1:104-108

Brodo IM (1965) Studies of growth rates of corticolous lichens on Long Island, New York. Bryologist 68:451-456

Brodo IM (1973) Substrate ecology. In: Ahmadjian V and Hale ME (ed) The Lichens, Academic Press, London and New York

Childress S, Keller JB (1980) Lichen growth. J Theor Biol 82:157-165

Cooper EJ, Smith FM, Wookey PA (2001) Increased rainfall ameliorates the negative effect of trampling in the growth of high Arctic forage lichens. Symbiosis 31:153-171

Coxson DS, Stevenson SK (2007) Growth rate responses of *Lobaria pulmonaria* to canopy structure in even-aged and old-growth cedar-hemlock forests of central-interior British Columbia, Canada. For Ecol Man 242: 5-16

Degelius G (1964) Biological studies of the epiphytic vegetation on twigs of *Fraxinus excelsior.* Acta Horti Gotoburg 27:11-55

Farrar JF (1973) Lichen Physiology. In: Ferry BW, Baddeley MS and Hawksworth DL (ed) Progress and Problems in Lichenology. Athlone Press, University of London, pp 238-282

Farrar JF (1976) The lichen as an ecosystem: observation and experiment. In: Brown DH, Bailey RH and Hawksworth DL (ed) Progress and Problems in Lichenology, Academic Press, London, pp 385-406

Fisher PJ, Proctor MCF (1978) Observations on a season's growth of *Parmelia caperata* and *P. sulcata* in South Devon. Lichenologist 10:81-89

Fletcher A (1976) Nutritional aspects of marine and maritime lichen ecology. In: Brown DH, Bailey RH and Hawksworth DL (ed) Progress and Problems in Lichenology, Academic Press, London, 359-384

Frey ED (1959) Die Flechtemflora und –vegetation des Nationalparks im Unterengadin. Erg Wiss Untersuch Schweizer Nationalparks 6:1–319

Gaio-Oliveira G, Dahlman, Maguas C, Palmqvist K (2004) Growth in relation to micoclimatic conditions and physiological of four *Lobaria pulmonaria* populations in two contrasting habitats. Ecography 27: 13-28

Gaio-Oliveira G, Dahlman, Palmqvist K, Maguas C (2005) Responses of the lichen *Xanthoria parietina* (L.) Th. Fr. to varying nitrogen concentrations. Lichenologist 37: 171-179

Garty J, Gal M, Galun M (1974) The relationship between physiochemical soil properties and substrate choice of ‘multisubstrate’ lichen species. Lichenologist 6:146- 150

Gauslaa Y, Palmqvist K, Solhaug KA, Holien H, Hilmo O, Nybakken L, Myhre LC, Ohlson M (2007) Growth of epiphytic old forest lichens across climatic and successional gradients. Can J For Res – Rev 37: 1832-1845

Gauslaa Y, Palmqvist K, Solhaug KA, Hilmo O, Holien H, Nybakken L, Ohlson M (2009) Size-dependent growth of two old-growth associated macrolichen species. New Phytol 181: 583-692

Gilbert OL (1971) Studies along the edge of a lichen desert. Lichenologist 5:11-17

Golm GT, Hill PS, Wells H (1993) Life expectancy in a Tulsa cemetery: growth and population structure of the lichen *Xanthoparmelia cumberlandia*. Am Mid Nat 129:373-383

Greenhalgh GN, Anglesea D (1979) The distribution of algal cells in lichen thalli. Lichenologist 11:283- 292

Hakulinen R (1966) Über die Wachstumgeschwindigheit einerger Laubflechten. Ann Bot Fenici 3: 167-179.

Hale ME (1959) Studies on lichen growth rate and succession. Bull Torrey Bot Club 66:126

Hale ME (1967) The Biology of Lichens. Edward Arnold, London

Hale ME (1970) Single-lobe growth-rate patterns in the lichen *Parmelia caperata*. Bryologist, 73:72-81

Hale ME (1973) Growth. In: Ahmadjian V and Hale ME (ed) The lichens, Academic Press, New York, pp 473-492

Harris GP (1971a) The ecology of corticolous lichens. I. The zonation on oak and birch in south Devon. J Ecol 59:431-439

Harris GP (1971b) The ecology of corticolous lichens II. The relationship between physiology and the environment. J Ecol 59:441-452

Harris GP (1972) The ecology of corticolous lichens III. A simulation model of productivity as a function of light intensity and water availability. J Ecol 60:19-40

Hill DJ (1981) The growth of lichens with special reference to the modelling of circular thalli. Lichenologist 13:265-287

Hill DJ (1984) Studies on the growth of lichens. 1. Lobe formation and the maintenance of circularity in crustose species. Lichenologist 16:273-278

Hill DJ (1985) Changes in photobiont dimensions and numbers during co-development of lichen symbionts. In Brown DH (ed) Lichen physiology and cell biology. Plenum Press, New York and London, pp 303-317

Hill DJ (1992) Lobe growth in lichen thalli. Symbiosis 12:43-48

Hilmo O, Ott S (2002) Juvenile development of the cyanolichen *Lobaria scrobiculat*a and the green algal lichens *Platismatia glauca* and *P. norvegico* in a boreal *Picea abies* forest. Plant Biol 4:273-280

Honegger R (1987) Questions about pattern formation in the algal layer of lichens with stratified (heteromerous) thalli. In: Peveling E (ed) Progress and Problems in

Lichenology in the eighties. Biblio Lichenol No 25 J. Cramer, Berlin-Stuttgart, pp 59-71

Honegger R (1996) Experimental studies of growth and regenerative capacity in the foliose lichen *Xanthoria parietina*. New Phytol 133:573-581

Honegger, Conconi S, Kutasi V (1996) Field studies on growth and regeneration capacity in the foliose macrolichen *Xanthoria parietina* (teloschistales, Ascomycotina). Bot Acta 109:187-193

Hooker TN (1980) Lobe growth and marginal zonation in crustose lichens. Lichenologist 12:313-323

Jones JM, Platt RB (1969) Effects of ionizing radiation, climate and nutrition on growth and structure of a lichen *Parmelia conspersa* (Ach.)Ach. Radioecology Symposium 2:111- 119

Karenlampi L (1971) Studies on the relative growth rate of some fruticose lichens. Rep Kevo Subarct Res 7:33-39

Kershaw KA (1972) The relationship between moisture content and net assimilation rate of lichen thalli and its ecological significance. Can J Bot 50:543-555

Kershaw KA, Millbank JW (1970) Isidia as vegetative propagules in *Peltigera apthosa* var *variolosa* (Massal.)Thoms. Lichenologist 4:214-217

Lawrey JD (1984) Biology of Lichenized Fungi. Praeger Publishers, New York.

Lawrey JD, Hale ME (1977) Studies on lichen growth rates at Plummers Island, Maryland. Proc Biol Soc Wash 90:698-725

Linkola K (1918) Über die jahrlichen Längenzuwachs einiger *Parmelia* and *Parmeliopsis* Arten. Meddn Soc Fauna Flora fenn 44:153-158

McCarthy DP, Smith DJ (1995) Growth curves for calcium tolerant lichens in the Canadian Rocky Mountains. Arc Alp Res 27:290-297

McCune B, Caldwell BA (2009) A single phosphorus treatment doubles growth of cyanobacterial lichen transplants. Ecology 90:567-570

Moxham TH (1981) Growth rates of *Xanthoria parietina* and their relationship to substrate texture. Cryp Bryol Lichenol 2:171-180

Murtagh GJ, Dyer PS, Furneaux PA, Crittenden PD (2002) Molecular and physiological diversity in the bipolar lichen-forming fungus *Xanthoria elegans*. Mycol Res 106:1277-1286

Palmqvist K, Sundberg B (2000) Light use efficiency of dry matter gain in five macro-lichens: relative impact of microclimate conditions and species-specific traits. Plant Cell Environ 23:1-14.

Palmqvist K, Dahlman L (2006) Responses of the green algal foliose lichen *Platismatia glauca* to increased nitrogen supply. New Phytol 171:343-356

Paterson DR, Paterson EW, Kenworthy JB (1983) Physiological studies on temperate lichen species. I. A mathematical model to predict assimilation in the field based on laboratory responses. New Phytol 94:605-618

Paulson R (1918) Notes on the ecology of lichens with special reference to Epping Forest. Essex Nat 18:276-286

Pentecost A, Rose CI (1985) Apothecium production in *Xanthoria parietina.* Lichenologist 17:33-38

Phillips HC (1963) Growth rate of *Parmelia isidiosa* (Mull. Arg.) Hale. J Tenn Acad Sci 38:95-96

Phillips HC (1969) Annual growth rates of three species of foliose lichens determined photographically. Bull Torr Bot Cl 96:202-206

Porter L (1927) The rate of growth of lichens. Transactions of the British Mycological Society 12:149-152

Proctor MCF (1977) The growth curve of the crustose lichen *Buellia canescens* (Dicks) De Not. New Phytol 79:659-663

Ramkaer K (1978) The influence of salinity on the establishment phase of rocky shore lichens. Bot Tidsskr 72:119-123

Righelato RC (1975) Growth of mycelial fungi. In: Smith JE, Berry DR (ed) The filamentous fungi Vol 1. Industrial Mycology. Arnold, London

Rhoades FM (1977) Growth rates of the lichen *Lobaria oregano* as determined from sequential photographs. Can J Bot 55:2226-2233

Rydzak J (1961) Investigations on the growth rate of lichens. Annales Universitatis Mariae Curie-Sklodowska (Lublin, Poland) sec C 16:1-15

Scheidegger C (1995) Early development of transplanted isiodiod soredia of *Lobaria pulmonaria* in an endangered population. Lichenologist 27:361-371

Showman RE (1976) Seasonal growth of *Parmelia caperata*. Bryologist 79:360-363

Sletvold N, Hestmark G (1998) Thallus growth asymmetry and habitat inclination in *Lasallia pustulata*. Bryologist 100:465-466

Slocum RD, Ahmadjian V, Hildreth KC (1980) Zoosporogenesis in *Trebouxia gelatinosa*: ultrastructure potential for zoospore release and implications for the lichen association. Lichenologist 12:173-187

Smith DC, Molesworth S (1973) Lichen physiology XIII. Effects of rewetting dry lichens. New Phytol 72:525

Snelgar WP, Green TGA (1982) Growth rates of Stictaceae lichens in New Zealand beech forests. Bryologist 85:301-306

Stevenson SK, Coxon DS (2008) Growth responses of Lobaria retigera to forest edge and canopy structure in the inland temperate rainforest, British Columbia. For Ecol Man 256: 618-623

Stocker-Wörgötter E (1991) Thallus formation of two cyanobacterial lichens: *Peltigera didactyla* and *P. praetextata*, under laboratory conditions. Bull Soc Bot France Let Botaniq 138:179-187

Størmer P (1934) Remarks on the growth of *Parmelia pulla*. Ach. Nyt Mag Naturv 74: 295-298

Sumner RW (2001) Pattern formation in lichens. MSc Thesis, Massachusetts Institute of technology, pp 1-76.

Topham PB (1977) Colonisation, growth, succession and competition. In: Lichen Ecology, MRD Seaward (ed), London, Academic Press, London, pp 31-68.

Trinci APJ (1971) Influence of the width of the peripheral growth zone on the radial growth rate of fungal colonies on solid media. J Gen Mic 67:325-344

Valladares F, Ascaso C, Sancho LG (1994) Intrathalline variability of some structural and physical parameters in the lichen genus *Lasallia*. Can J Bot 72:415-428

Webster M, Brown DH (1997) Preliminary observations on the growth of transplanted *Peltigera canina* under semi-natural conditions. Lichenologist 29:91-96

Table 1. A selection of annual radial growth rates (RaGR, mm yr^{-1}) of foliose lichen species from various geographical locations. (C = corticolous, S = saxicolous)

Species	Site	RaGR	Reference
Flavoparmelia baltimorensis	Maryland (S)	5.09	Lawrey & Hale (1977)
Flavoparmelia caperata	Cork (C)	3.5	Porter (1927)
Flavoparmelia caperata	Washington, DC	4.0	Hale (1967)
Flavoparmelia caperata	Long Island, NY (C)	0.46 – 2.48	Brodo (1965)
Flavoparmelia caperata	Devon (UK) (C)	4.73	Fisher & Proctor (1978)
Flavoparmelia caperata	Essex (UK) (C)	11.20	Paulson (1918)
Hypogymnia. physodes	Essex (C)	5.5	Paulson (1918)
Lobaria oregana	Washington State (C)	9.4	Rhoades (1977)
Lobaria pulmonaria	Tennessee (C)	4.82	Phillips (1969)
Lobaria quercizans	Tennessee (C)	5.62	Phillips (1969)
Melanelia aurulenta	Maryland (S)	4.80	Lawrey & Hale (1977)
Melanelia exasperata	Scandinavia (C)	2.08	Degelius (1964)
Melanelia exasperatula	Scandinavia (C)	3.12	Degelius (1964)
Melanelia fuliginosa ssp. fuliginosa	North Wales (S)	0.09 – 3.31	Armstrong (1976)
Melanelia fuliginosa ssp. glabratula	Essex (UK) (C)	4.3	Paulson (1918)
Melanellia fuliginosa ssp. glabratula	Finland	0.70	Linkola (1918)
Melanelia subaurifera	Cork (C)	2.1	Porter (1927)
Melanelia subaurifera	Scandinavia (C)	3.57	Degelius (1964)
Menegazzia terebrata	Tennessee (C)	2.54	Phillips (1969)
Neofuscelia pulla	Norway	1.0 – 1.2	Størmer (1934)
Parmelia rudecta	Maryland (S)	5.29	Lawrey & Hale (1977)

Parmelia saxatilis	North Wales (S)	0.59 – 2.79	Armstrong (1973)
Parmelia saxatilis	Germany (S)	0.5 – 4.0	Frey (1959)
Parmelia saxatilis	Long Island, NY (C)	1.42 – 2.09	Brodo (1965)
Parmelia saxatilis	Durham, UK (S)	3.6	Gilbert (1971)
Parmelia saxatilis	Essex, UK (C)	13.0	Paulson (1918)
Parmelia sulcata	Cork (C)	1.4	Porter (1927)
Parmelia sulcata	Long Island, NY (C)	0.09 – 3.00	Brodo (1965)
Parmelia sulcata	Scandinavia (C)	2.22	Degelius (1964)
Parmelia sulcata	Washington, DC	1.2	Hale (1967)
Parmelia sulcata	Finland	1.2	Linkola (1918)
Parmelia sulcata	Devon (UK) (C)	4.73	Fisher & Proctor (1978)
Parmeliopsis ambigua	Finland	0.70	Linkola (1918)
Parmotrema perlata	Cork (C)	2.8 – 3.5	Porter (1927)
Peltigera canina	South UK	64.0	Webster & Brown (1997)
Peltigera canina	Germany	3.0 – 7.0	Frey (1959)
Peltigera praetextata	Germany	25.0 – 27.0	Frey (1959)
Phaeophyscia orbicularis	North Wales (S)	0.50 – 3.34	Armstrong (1973)
Physcia aipolia	Cork	2.0	Porter (1927)
Physcia aipolia	Finland	1.30	Hakulinen (1966)
Physcia dubia	Scandinavia (C)	2.50	Degelius (1964)
Physcia millegrana	Long Island, NY (C)	0.24 – 2.48	Brodo (1965)
Physcia millegrana	Maryland (S)	1.72	Lawrey & Hale (1977)
Physcia tenella	Scandinavia (C)	1.25	Degelius (1964)
Physcia stellaris	Washington, DC	1.1	Hale (1967)
Physcia stellaris	Scandinavia (C)	2.86	Degelius (1964)
Physconia grisea	North Wales (C)	0.75	Armstrong (1984)
Pleurosticta acetabulum	Scandinavia (C)	0.66	Degelius (1964)
Pseudocyphellaria homeophylla	New Zealand (C)	2.0 – 27.0	Snelgar & Green (1982)
Sticta caperata	New Zealand (C)	3.0 – 16.70	Snelgar & Green (1982)

Umbilicaria cylindrica	Germany (S)	0.01 – 0.04	Frey (1959)
Vulpicida pinastri	Finland	1.15	Hakulinen (1966)
Xanthoparmelia coloradoensis	Colorado (S)	2.01	Benedict (2008)
Xanthoparmelia conspersa	North Wales (S)	0.55 – 4.95	Armstrong (1973)
Xanthoparmelia conspersa	Washington, DC (S)	1.6	Hale (1959)
Xanthoparmelia conspersa	Washington DC (S)	7.6	Hale (1967)
Xanthoparmelia conspersa	Tennessee (S)	5.3	Phillips (1963)
Xanthoparmelia conspersa	Maryland (S)	3.28	Lawrey & Hale (1977)
Xanthoparmelia conspersa	Atlanta, Georgia (S)	3.84	Jones & Platt (1969)
Xanthoria elegans	Canadian Rockies (S)	0.5 – 0.9	McCarthy& Smith (1995)
Xanthoria lineola	Colorado (S)	0.98 – 2.39	Benedict (1991)
Xanthoria parietina	Germany (S)	6.0	Honegger et al (1996)
Xanthoria parietina	Scandinavia (C)	2.5	Degelius (1964)
Xanthoria polycarpa	Scandinavia (C)	0.70	Degelius (1964)
Xanthoria subdecipiens	Colorado (S)	1.15 – 1.67	Benedict (1991)

Table 2. Multiple regression analysis of the monthly radial growth of a single lobe of *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale in North Wales over 22 months in relation to climatic variables (X = independent variable, β = regression coefficient, SE = Standard error of β, 't' = Students 't', P = probability, R = multiple regression coefficient, R^2 = Coefficient of determination (Data from Armstrong 2009)

Multiple regression statistics

X variable selected	β	SE	t	P	R	% change in R^2
Number of rainy days	0.81	0.19	4.34	< 0.001	0.58	34%
Average wind speed	-0.43	0.17	-2.52	< 0.05	0.66	10%
Frequency of ground frosts	0.55	0.24	2.28	< 0.05	0.84	5%

Legends to figures

Fig 1 Growth of small fragment-sized thalli of *Xanthoarmelia conspersa* (Ehrh. ex Ach.) Hale. A logarithmic curve was fitted to these data ($Y= 0.358 + 1.819\mathrm{Log}_{10} X$) (Goodness of fit: $r = 0.61$, $P < 0.01$, $r^2 = 0.37$) (Data from Armstrong 1974)

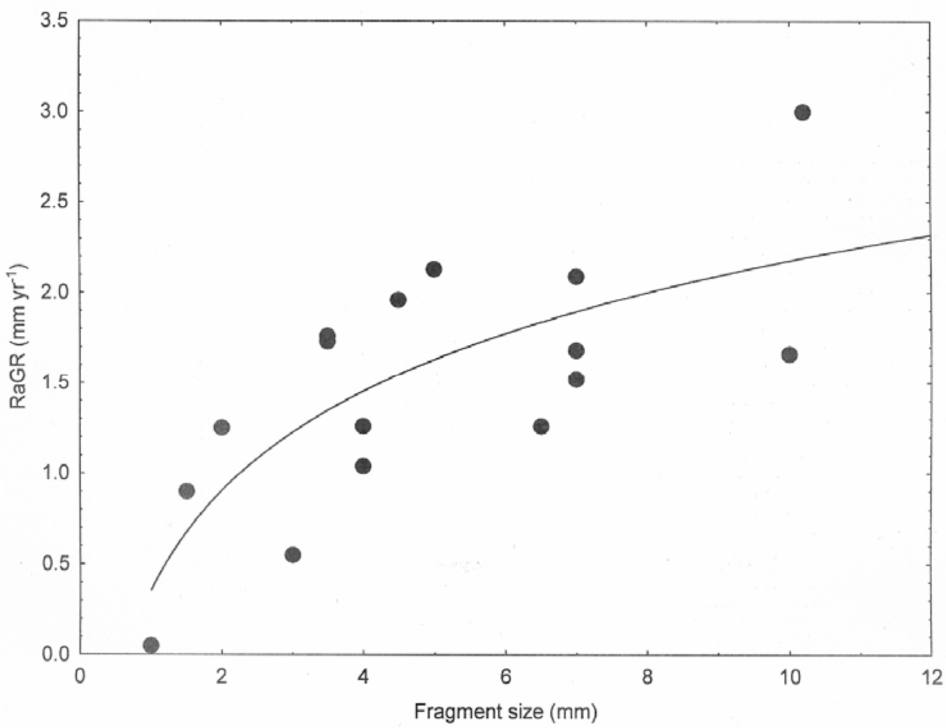

Fig 2 Direct observation of the growth of *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale thalli developing from small fragments over a period of 54 months (Data from Armstrong 1992)

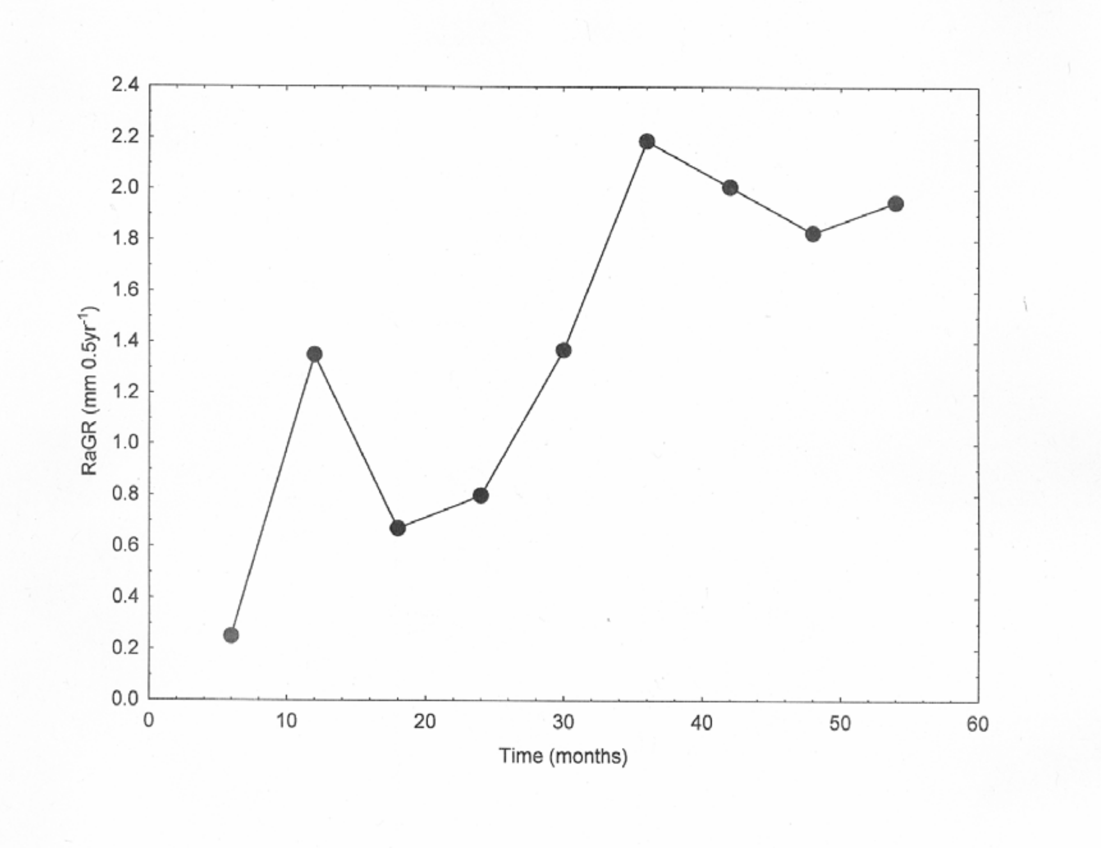

Fig 3 Growth rate-size curve of the foliose lichen *Melanelia fuliginosa ssp. fuliginosa* (Fr. ex Duby) Essl. determined by a cross-sectional study. The fitted curve is derived from the Aplin and Hill (1979) model (Goodness of fit: $r = -0.46$, $P > 0.05$, $r^2 = 0.21$) (Data from Armstrong 1976a)

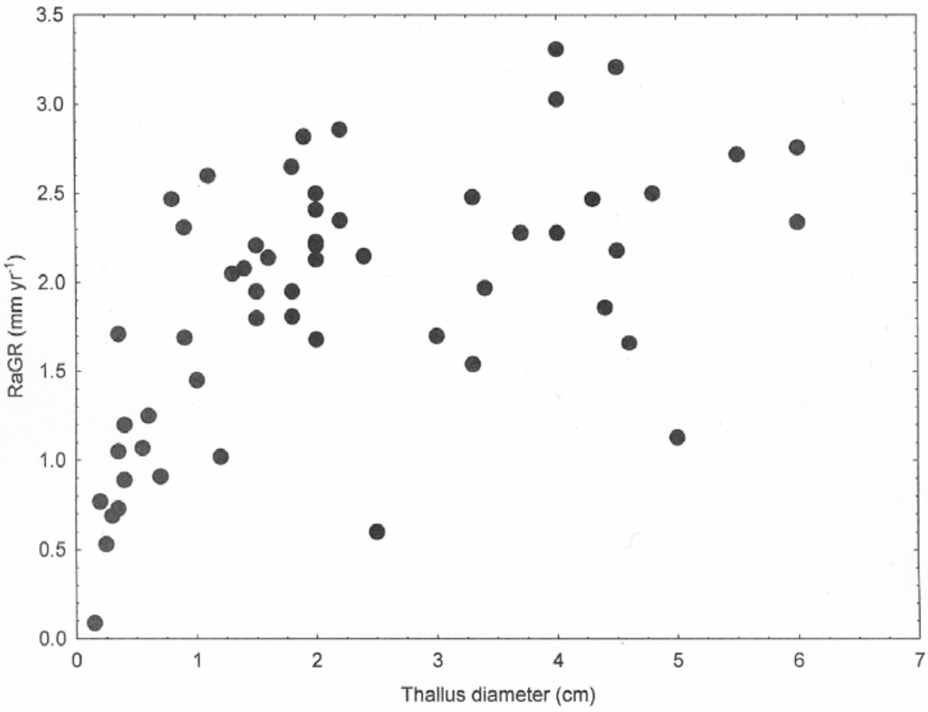

Fig 4 The numbers of apothecia and mean diameter of apothecia (mm) in thalli of *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale of different size. The fitted regressions are: Total number of apothecia Y = 12.62 + 1.10X (Goodness of fit: r = 0.75, $P < 0.001$, $r^2 = 0.56$); Mean diameter of apothecia Y = =-0.68 + 0.45X – $0.0145X^2$) (Goodness of fit: r = 0.79, $P < 0.001$, $r^2 = 0.62$) (R.A.Armstrong, unpublished data)

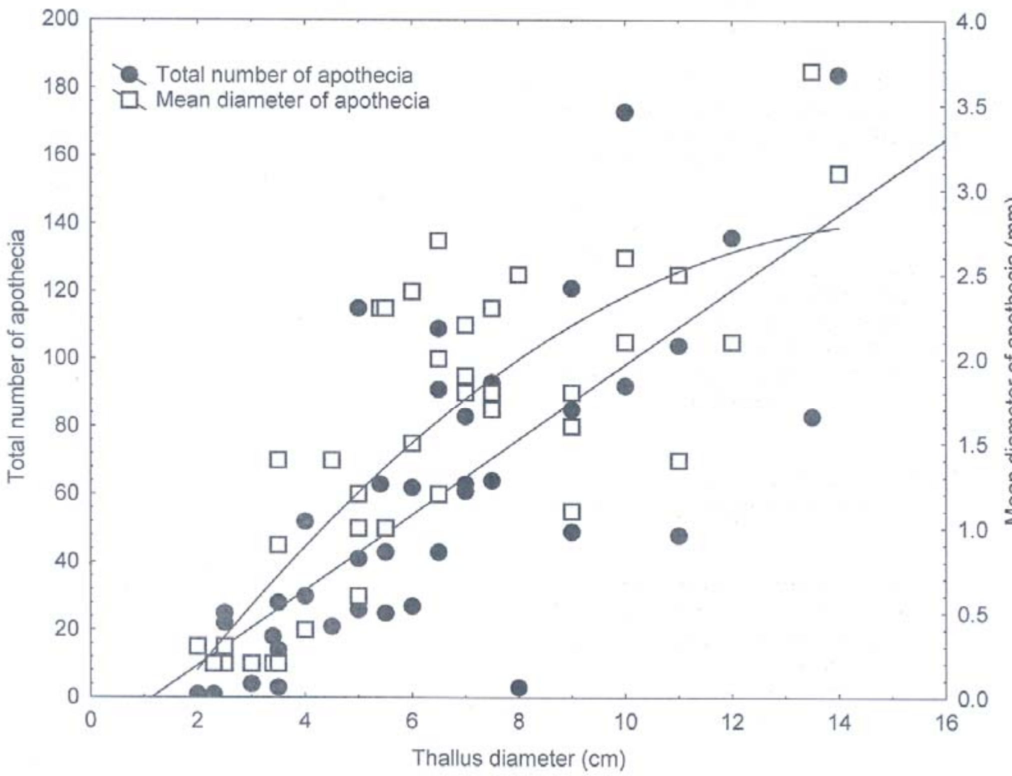

Fig 5 Fitting the Aplin and Hill (1979) growth model to growth rate-size data obtained from *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale: 1) the data were grouped into size classes, 2) mean RaGR in each size class (r_2 - r_1) was plotted as a function of $\log_e r_2 - \log_e r_1$, and 3) the degree of linearity in the relationship was tested using Pearson's correlation coefficient (Goodness of fit: $r = -0.67$, $P < 0.05$, $r^2 = 0.45$). The fitted line is $r_2 - r_1 = 3.2513 - 3.878 (\log_e r_2 - \log_e r_1)$

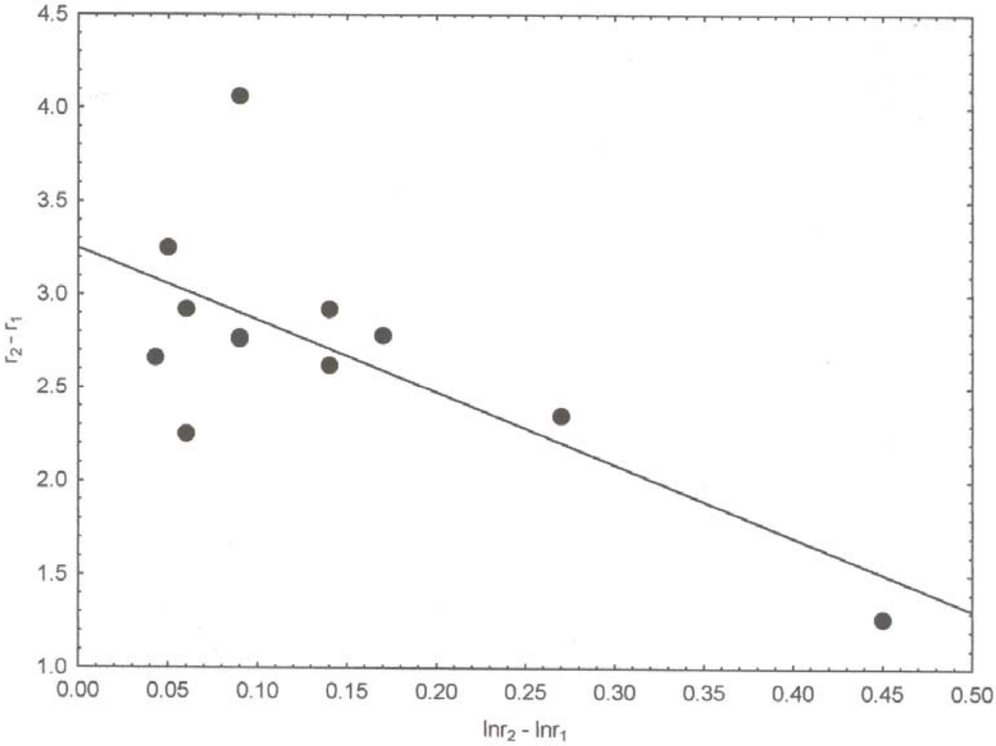

Fig 6 The relationship between radial growth rate (RaGR) and mean lobe width in thalli of *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale. The fitted line is Y = 0.804 + 0.704 X with 95% confidence intervals (Goodness of fit: $r = 0.49$, $P < 0.05$, $r^2 = 0.24$) (Data from Armstrong 1995)

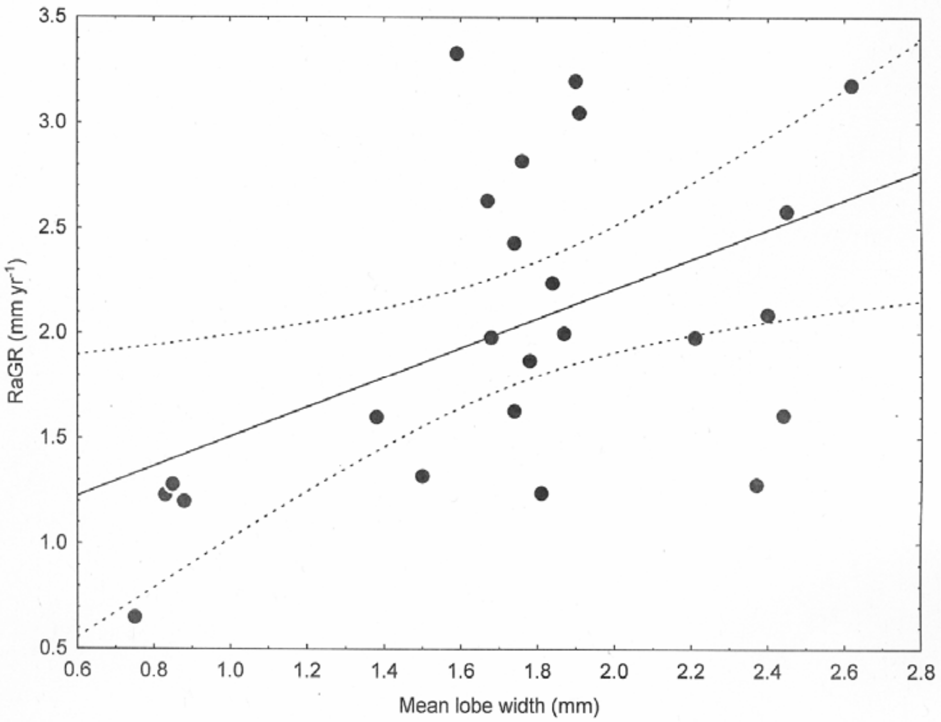

Fig 7 Relationship between lobe crowding (crowding index) and thallus diameter in thalli of *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale. The fitted curve is Y = 0.32 + 0.086 – $0.0029X^2$ with 95% confidence intervals (Goodness of fit: $r = 0.78$, $P < 0.001$, $r^2 = 0.61$) (Data from Armstrong 2003)