

The Influence of Environmental Factors on the Growth of Lichens in the Field

Richard A. Armstrong

Contents

1.1	Introduction	2
1.2	Measuring Lichen Growth	2
1.3	The Influence of Climate on Growth	3
1.3.1	Rainfall.....	3
1.3.2	Temperature	5
1.3.3	Frost Injury and Snowfall	6
1.3.4	Light Intensity.....	6
1.3.5	Interactions Between Factors.....	7
1.4	The Influence of Microclimate on Growth	7
1.4.1	Aspect and Slope.....	7
1.4.2	Vertical Height on Trees	8
1.5	The Influence of the Substratum on Growth	9
1.5.1	Physical Properties.....	9
1.5.2	Rock Chemistry	10
1.6	The Effect of Nutrient Enrichment on Growth	10
1.6.1	Bird Droppings	10
1.6.2	Nitrogen and Phosphorus	11
1.6.3	Salinity	12
1.6.4	Pollution.....	12
1.7	Ecological Significance of Growth Effects	12
1.8	Conclusions	14
	References	15

Abstract

The majority of studies of the effects of environmental factors on lichen growth have been carried out in the field. Growth of lichens in the field has been measured as absolute growth rate (e.g. length growth, radial growth, diameter growth, area growth, or dry weight gain per unit of time) or as a relative growth rate, expressed per unit of thallus area or weight, e.g. thallus specific weight. Seasonal fluctuations in growth in the field often correlate best with changes in average or total rainfall or frequency of rain events through the year. In some regions of the world, temperature is also an important climatic factor influencing growth. Interactions between microclimatic factors such as light intensity, temperature, and moisture are particularly important in determining local differences in growth especially in relation to aspect and slope of rock surface, or height on a tree. Factors associated with the substratum including type, chemistry, texture, and porosity can all influence growth. In addition, growth can be influenced by the degree of nutrient enrichment of the substratum associated with bird droppings, nitrogen, phosphate, salinity, or pollution. Effects of environmental factors on growth can act directly to restrict species distribution or indirectly by altering the competitive balance among different species in a community.

R.A. Armstrong (✉)
Department of Vision Sciences, Aston University,
Birmingham, B4 7ET, UK
e-mail: r.a.armstrong@aston.ac.uk

Keywords

Lichen · Radial growth rate · Dry weight gain · Relative growth rate · Climate · Substratum · Nutrient enrichment · Competition

1.1 Introduction

Lichens are influenced by many environmental factors including the long-term effects of climate, local changes in microclimate, and a variety of factors associated with the substratum such as type of rock, bark, or soil, substrate chemistry, and the degree of nutrient enrichment by birds, salinity, or pollution (Armstrong 1974; James et al. 1977). Studies of the effects of environmental factors on lichen growth are important for several reasons. First is to understand the factors determining the distribution of rare or interesting species and the structure of important lichen communities. Hence, a change in the environment to a less than optimal condition may inhibit lichen growth to such an extent that thalli rapidly fragment and disappear from a substratum. In addition, the environment can act more indirectly, subtle changes altering the competitive balance among different species in a community (Armstrong and Welch 2007). Second, knowledge of environmental growth effects is important in ‘lichenometry’, a technique which uses lichens to estimate the surface age of a substratum (Locke et al. 1979; Innes 1985; Matthews 1994; Benedict 2009). Third, it may be important to separate out growth effects due to natural factors, such as climate or microclimate, from those attributable to human activity, such as grazing by herbivores, pollution, or woodland management.

Two major problems have been encountered in studying lichen growth. First, studies have been limited by the relatively few facilities available for culturing whole lichen thalli in the

laboratory for long periods of time. Hence, few ‘factorial-type’ experiments have been undertaken, in which the synergistic effects of different variables have been studied (Jones and Platt 1969; Armstrong 1994). As a result, most studies have been carried out in the field and therefore lack the control of the environment possible in a laboratory. Second, lichens are morphologically diverse consisting of crustose, foliose, placodioid, and fruticose forms, and they also grow on different substrata with contrasting properties such as rock, tree bark, and soil. Hence, different methods have been devised to measure growth, making it difficult to compare the results of different studies. This review considers various aspects of the influence of the environment on the growth of lichens as measured in the field including: (1) methods of measuring and expressing growth, (2) the influence of climate, microclimate, substratum factors, and nutrient enrichment on growth, and (3) the importance of the influence of growth on competition as a factor determining distribution and community structure (Armstrong and Welch 2007).

1.2 Measuring Lichen Growth

Different methods have been employed to measure lichen growth in the field depending on growth form and substratum type. Hence, foliose and crustose lichens both exhibit a flat dorsal-ventral thallus and when growing on relatively flat substrata such as rock and tree bark, similar methods can be used to measure their growth (Armstrong and Bradwell 2011). Current techniques enable measurements of foliose lichen growth to be made over relatively short-time intervals such as weeks and months (Hale 1970; Armstrong 1973) and are based on the original method described by Hale (1970, 1973). This involves measuring the advance of the thallus perimeter, either the tip of a lobe in foliose species

or the edge of the hypothallus in many crustose species, with reference to fixed markers on the rock. Digital photography (Hooker 1980) and an image analysis system (Image-J) (Armstrong 2013) can then be used to measure growth increments. Measurements can be made over various time scales, viz. one month for faster-growing foliose (Armstrong and Bradwell 2011) and three months for slower-growing crustose species (Armstrong and Bradwell 2010).

Many studies have employed an absolute measure of growth such as radial growth, diameter growth, area growth, or dry weight gain. The most popular measure in many studies of foliose lichens has been rate of radial extension or radial growth rate (e.g. mm year^{-1}). A limitation of radial growth rate, however, is that it is strongly correlated with thallus size and exhibits a high degree of variability both within and between thalli (Armstrong and Bradwell 2010, 2011). As a consequence, measurement of relative growth rate has been used to compensate for these variations in size, growth being scaled to an existing thallus measure such as increase in area per unit of area in unit time ($\text{mm}^2 \text{mm}^{-2}, \text{time}^{-1}$) (Armstrong 1973, 1976a).

Fruticose lichens have a much more complex-branched morphology and different methods necessary to study their growth. Methods of quantifying growth of fruticose species have usually involved measuring length, internode length, diameter, thallus dry weight, or biomass (Karenlampi 1971). Karenlampi (1970) measured growth of thalli of *Cladonia alpestris* (L.) Rabenh. by dividing up thalli and weighing the various parts. The major growth zone was at the tip of the podetia, and relative growth values for length, diameter, and dry weight suggesting significantly higher values for younger than older portions of thalli. More recently, a non-destructive method of estimating biomass of *Usnea* species by harvesting a sample of sites and measuring dry weight gain, ratio of chlorophyll 'a' to 'b', and thallus area have been described, regression methods then being applied to calibrate biomass against the non-destructive measures (Bohuslavova et al. 2012).

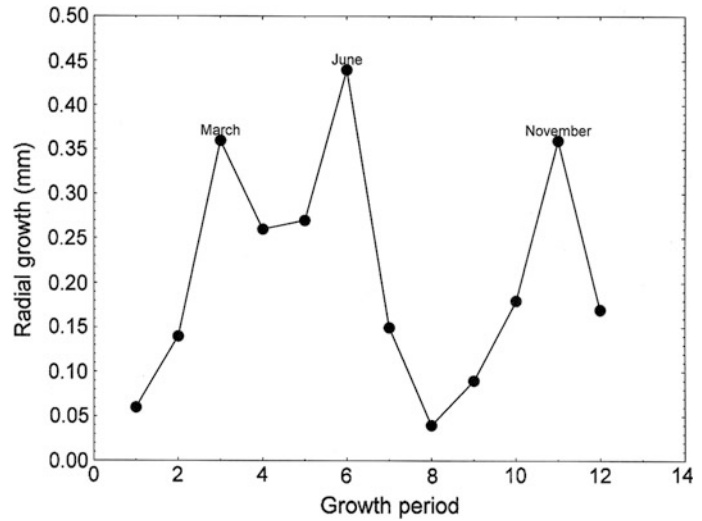
1.3 The Influence of Climate on Growth

Beschel's detailed lichenometric studies in the 1950s and 1960s were some of the first to demonstrate the important role played by climate on lichen growth (Beschel 1958, 1961). Beschel found that the same species of the crustose genus *Rhizocarpon* grew considerably more slowly in Greenland than in the Swiss Alps (Beschel 1958, 1961). Re-measurement at Beschel's sites, 12 years after the original study (Tenbrink 1973), confirmed that growth of *Rhizocarpon geographicum* (L.) DC. was more than 50 % slower at those sites in Greenland furthest from the sea (6–7 mm/100 year compared with 17–18 mm/100 year). Subsequently, many lichenometric studies from the northern hemisphere have reported similar trends. Hence, Innes (1983) found a general decrease in growth rate of thalli of *Rhizocarpon* section *Rhizocarpon* from west to east in Scotland, UK. In addition, Bradwell (2001a) and Mathews (2005) found growth rate gradients across Iceland and southern Norway, respectively, probably reflecting reduced moisture availability associated with a diminishing maritime influence. Not all such studies, however, have found significant growth effects. For example, growth of transplanted specimens of *Dolicousnea longissima* (Ach.) Articus was studied in four contrasting habitats (Keon and Myer 2002), length growth or dry weight gain being measured after one year. Growth was similar at all sites studied including those in which the habitat was not predicted to be suitable for growth of this species. Similarly, dry weight gain of *Cladonia portentosa* (Dufour) Coem. was studied at five heathland sites differing in precipitation acidity, nitrogen deposition, and annual rainfall (Hyvarinen and Crittenden 1998), but no regional differences in growth were evident.

1.3.1 Rainfall

Evidence for the influence of climate on lichen growth has usually been obtained from studies of

Fig. 1.1 Radial growth (RaG, mm) of the foliose lichen *Melanelia fuliginosa* ssp. *fuliginosa* (Fr. ex Duby) Essl. at a site in north Wales, UK, over 12 months. A large peak of growth occurred in June with smaller growth peaks in March and November corresponding to periods of maximum rainfall (data from Armstrong 1973)



annual or seasonal variations in growth (Rydzak 1961; Hale 1970; Armstrong 1973, 1993a; Showman 1976; Lawrey and Hale 1977; Fisher and Proctor 1978; Moxham 1981; Benedict 1990a). Hence, monthly relative growth rate of *Melanelia fuliginosa* ssp. *fuliginosa* (Fr. ex Duby) Essl. was measured over a period of one year in north Wales (Armstrong 1973, 1993a) (Fig. 1.1). A large peak of growth occurred in June with smaller growth peaks in March and November corresponding to periods of maximum rainfall. In general, monthly fluctuations in growth 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 account for relatively small amounts of the total variance in growth (usually <40 %) (Armstrong 1988). For example, growth of *Xanthoparmelia conspersa* (Ehrh. Ex Ach.) Hale in each of 22 successive months in north Wales in relation to total monthly rainfall was studied by Armstrong (1988). A significant positive correlation between growth and rainfall over this period was evident ($r = 0.61$, $P < 0.001$), but the proportion of the variance accounted for by rainfall alone was low ($r^2 = 0.37$). In a study of *Cetraria* species, Paterson et al. (1983) found that moisture was the most important factor influencing growth, assimilation gains achieved

during rainy days being sufficient to offset any carbon losses accrued over five dry days. In addition, mean daily rainfall in summer was an important determiner of growth in *Flavocetraria nivalis* (L.) Kärnefelt & A. Thell. although temperature was also considered an important factor (Karenlampi 1971). Similarly, in the high Arctic, the frequency of watering was the most important factor determining the relative growth rate of *Cetraria* species (Cooper et al. 2001). The effect of climate on growth on tree bark has frequently been studied using reciprocal transplants (Gai-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* (L.) Hoffm. (Gauslaa et al. 2009). Stand-specific water availability was the most important factor increasing thallus area.

Because of significantly lower radial growth rates, fewer studies of the seasonal growth of crustose species have been carried out. Nevertheless, seasonal growth over three-month growth periods was studied in *R. reductum* Th. Fr. and *Lecidea tumida* Massal. growing on rocks in north Wales (Armstrong 1973). Both showed maximum growth between May and July, relatively little growth in November to January, and slow growth in August to October suggesting that a combination of higher rainfall

and lower temperatures was not conducive to growth of these species.

One of the first lichenologists to study the relationship between growth and climate in fruticose lichens was Karenlampi (1971). At sites in Finland, relative growth rate of a number of fruticose species, measured as increase in weight or length, was correlated with mean daily rainfall in summer while temperature was inversely related to growth. In addition, growth of *Ramalina menziesii* (Taylor) was studied in California at coastal and inland sites (Boucher and Nash 1990), the primary determinant of growth appearing to be rainfall. However, the growth of a second species, viz. *R. farinacea*, (L.) Ach. was not be explained by any of the climatic variables.

1.3.2 Temperature

Although rainfall is the predominant variable in many regions, other climatic factors have also been identified as affecting lichen growth. Hence, Brodo (1965) studied annual variations in radial growth of the corticolous lichens *Lecanora chlarotera* Nyl. and *L. caesiorubella* Ach. and

observed significantly greater growth during 1959–1961 compared with 1961–1962 largely attributable to differences in mean temperature. In addition, diameter growth of *R. geographicum* was studied at 47 sites covering 18 glaciers in south Norway. Annual growth was correlated with mean temperature and winter mean temperature but not with summer temperature and less correlation with rainfall was evident compared with other studies (Trenbirth and Mathews 2010).

In a study of the seasonal growth of *R. geographicum* (Armstrong 2006), radial growth rate of a sample of 20 thalli was measured in situ on a southeast-facing rock surface at three-month intervals over 51 months (Fig. 1.2). There were five periods of significant growth: July–September of 1993, 1994, and 1995, in January–March of 1996, and in April–June of 1997. In four of these periods, growth coincided with a mean temperature maximum over a three-month period exceeding 15 °C and three of the maxima also coincided with greater than 450 sunshine hours. In addition, two of the growth maxima coincided with three-month periods of total rainfall exceeding 300 mm and one with greater than 50 rain days.

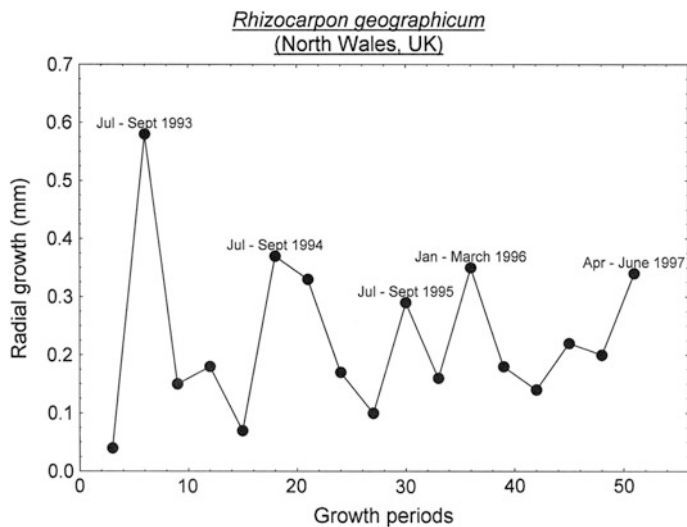


Fig. 1.2 Mean radial growth of thalli of *Rhizocarpon geographicum* measured in 17 three-month periods from 1993 to 1997 in south Gwynedd, Wales, UK. There were five periods of significant growth: July–September of

1993, 1994, and 1995, in January–March of 1996, and in April–June of 1997. Analysis of variance (two-way), between thalli, $F = 0.03$ ($P > 0.05$), between growth periods, $F = 3.86$ ($P < 0.001$) (data from Armstrong 2006)

There were no significant linear correlations between growth and individual climatic variables but significant nonlinear relationships were evident between growth and maximum temperature, mean temperature minimum, total number of air and ground frosts, and number of rain days, maximum temperature being the most significant (Armstrong 2006). Hence, in north Wales, maximum growth of *R. geographicum* may occur in any season, although July–September appeared the most favourable. Coxon and Kershaw (1983) studied changes in photosynthetic capacity in *R. superficiale* (Schaer.) Vain. through the season. This species showed a broad response to temperature and a high resistance to heat stress, characteristic of species living in ‘boundary-layer’ habitats, but there were no significant seasonal changes in photosynthetic capacity.

1.3.3 Frost Injury and Snowfall

At higher altitudes, the degree of winter frost injury and snowfall are important factors. Hence, Innes (1985) found that thalli of *Rhizocarpon* were smaller close to snow patches due to reduced growing season and ground instability. At some sites, however, the effects of increasing moisture balanced the negative influence of snow. In the Colorado Front Range (Benedict 1990b), frost damage, including ‘spalling’ of the upper cortex and algal layers, was evident especially in foliose species. Crustose species such as *R. riparium* Räsänen were less affected but some spalling did occur affecting the surface of areolae. Benedict (1990b) also demonstrated that, under snow, photosynthesis was limited due to impaired light penetration but thalli did continue to respire. To demonstrate this effect, lines of lichen-covered rocks were installed in two semi-permanent snow patches in the Colorado Front Range. Thalli of *R. geographicum* survived 5–8 years after transplanting when average duration of snow cover in the year exceeded 40–43 weeks. By contrast, *R. riparium* thalli survived the duration of the study and were clearly more snow tolerant than *R. geographicum*.

The effect of snow on long-term lichen growth at high elevations has also been studied by measuring the size of *R. geographicum* along a transect traversing snow-free and snow-accumulation areas (Benedict 1991). No differences in maximum thallus diameter were observed despite large differences in duration of snow cover. Hence, zoned lichen communities, which are often observed adjacent to snow patches, are more likely to be attributable to episodic snow kill rather than to slow growth under seasonal cover.

1.3.4 Light Intensity

The influence of light on lichen growth in the field has been studied most frequently in woodland. Hence, in a transplant experiment, in which the influence of canopy structure on *L. pulmonaria* was studied, growth was strongly correlated with canopy light transmission, dry weight gain over 2 years being less than 5 % under canopies and rising to 20 % on branches associated with canopy gaps (Coxson and Stevenson 2007). 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). Dry weight gain was greatest in the Atlantic rainforest (36–38 %) but was reduced by low-light levels even in old forests and in most semi-exposed clear-cuts. The relationship between light intensity and growth of five macrolichens was studied in Sweden (Palmqvist and Sundberg 2000), a strong correlation being observed when thalli were moist. Hence, clear-cutting, which often creates an abrupt edge to forest stands, may affect foliose lichen growth. The effect of ‘hard edges’ and a less abrupt edge to the forest on 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 3 years at ‘hard’ edge sites but a significantly reduced loss when a less abrupt edge was present, suggesting that residual trees at the margin could reduce the impact of forest clearing on lichen diversity.

1.3.5 Interactions Between Factors

Factorial experimental designs have been relatively little used to study the synergistic effects of climatic and other factors on lichen growth. However, Jones and Platt (1969) studied the growth of *X. conspersa* using a three-factor experimental design incorporating four levels of radiation exposure, two contrasting climates, and two nutrient addition conditions. All factors significantly influenced radial growth, but climate had the most substantial effect. There were also significant interactions between climate, radiation exposure, and nutrient levels.

Stepwise multiple regression has also been used to analyse the various climatic factors determining seasonal trends in growth. Hence, Lawrey and Hale (1977) found that a multiple linear regression, which included maximum temperature, total rainfall, and per cent cloudy days as independent variables, explained 22 % of the variation in the growth of *Flavoparmelia baltimorensis* (Gyeln. & F6riss) Hale. This method was also used to study the monthly radial growth of single lobes of *X. conspersa* in North Wales over 22 months (Armstrong 2009). Of eight climatic variables studied, the frequency of rain days, ground frosts per month, and average wind speed were selected as significant variables in total accounting for 49 % of the variance in the data.

1.4 The Influence of Microclimate on Growth

Investigation of lichen physiology suggests that interactions between light intensity, temperature, and moisture are likely to be important in determining local growth rates (Farrar 1973). Hence, the growth of the fruticose species *Cetrariella delisei* (Bory ex Schaer.) K6rnefelt & A. Thell. was measured in the high Arctic (Uchida et al. 2006). Positive net photosynthesis was recorded when thallus water contents were high, photosynthetic rates being lower on clearer days due to low thallus water contents. Net assimilation rate is influenced by the moisture content of the thallus (Harris 1971a, b, 1972;

Kershaw 1972), reaching a peak between 65 and 90 % saturation, and falling at water contents near to saturation. In addition, in some species of temperate lichens, wetting the thallus results in losses of carbon by a release of carbon dioxide gas and re-saturation 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, but not to be continuously saturated. An experimental demonstration of this effect was reported by Armstrong (1976b) who wetted thalli of three foliose species at different frequencies (Fig. 1.3). The radial growth of *M. fuliginosa* ssp. *fuliginosa* and *Phaeophyscia orbicularis* thalli (Neck.) Moberg declined with increased wetting frequency, while growth of *X. conspersa* increased with wetting frequency until 10 experimental wettings per month, declining at 15 wettings per month. Brown and Webster (1997) studied the growth of *Peltigera canina* (L.) Willd. transplanted onto garden soil. They found considerable linear growth of the transplants, especially when the soil was kept permanently watered, suggesting that a more continuous moisture regime may be beneficial in some species. Similarly, intact lichens grew most rapidly during periods of sustained moisture in the high Arctic (Cooper et al. 2001).

1.4.1 Aspect and Slope

Light, temperature, and rate of drying of the thallus may all vary with aspect (Armstrong 1975), slope (Sletvold and Hestmark 1998), rock and bark texture (Moxham 1981; Armstrong 1993b), and vertical location on a substratum (Harris 1971a; Armstrong 1978). The influence of aspect on the radial growth of *M. fuliginosa* ssp. *fuliginosa* at a site in north Wales was investigated by Armstrong (1975). In the periods September–October and March–July, growth of thalli on a northwest-facing rock surface was greater than on a south-facing rock surface. However, in the period January/February, growth on the south face was greater than on the northwest face. A physiological model which involved interactions between the levels of light, wetting

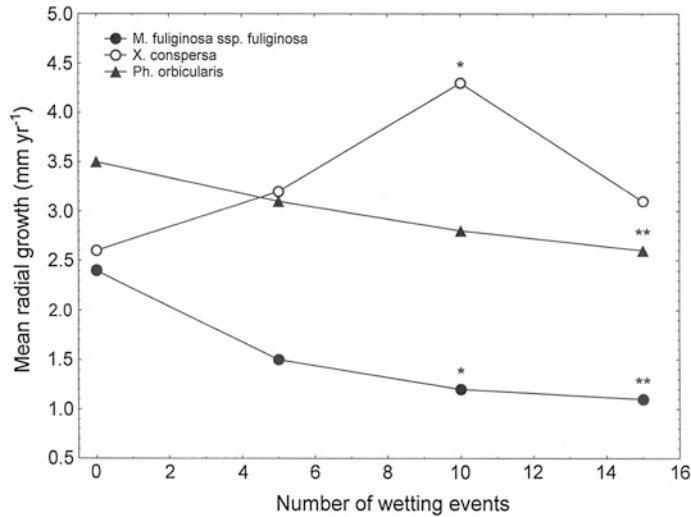


Fig. 1.3 The effect of frequency of wetting events on the radial growth (*RaG*) of three foliose lichens in south Gwynedd, Wales, UK. The radial growth of *Melanelia fuliginosa* ssp. *fuliginosa* and *Phaeophyscia orbicularis* thalli declined with increased wetting frequency while

growth of *Xanthoparmelia conspersa* increased with wetting frequency until 10 experimental wettings per month, declining at 15 wettings per month. Asterisk indicates treatments significantly different from control (0) (data from Armstrong 1975)

regime, and rates of drying of the thalli was necessary to explain growth on the two surfaces (Armstrong 1975).

A number of studies have reported the effects of aspect on growth of crustose species. Hence, in the Brooks Range, Alaska, for example, radial growth of *R. geographicum* at sites with high to moderate light intensities was twice those at shaded locations (Haworth et al. 1986). Similarly, Bradwell (2001b) found that in Iceland, the largest thalli of *R. geographicum* were generally found on south-facing surfaces of boulders and are possibly a consequence of the longer thermal operating period and higher temperatures on southern surfaces. In the Cascade Mountains, Washington State, radial growth of *R. geographicum* on boulders was significantly greater on east-southeast and south-southeast facets compared with north-facing facets suggesting that at sites in the northern hemisphere, well-lit, southern facing surfaces are optimal for the growth of *R. geographicum* (Armstrong 2005) (Fig. 1.4). By contrast, variation in the slope of the facet appeared to have less influence on growth.

1.4.2 Vertical Height on Trees

Microclimatic differences also influence lichen growth with height on trees thus influencing vertical zonation. Hence, *Parmelia olivacea* (L.) Ach. em. Nyl. and *Parmeliopsis ambigua* (Wulf.) Nyl. differ in abundance and in vertical distribution especially on birch trees (Sonesson et al. 2011). During the cold season, *P. ambigua*, which was largely distributed on the lower trunk, was covered much of the time by snow, whereas *P. olivacea* occurred well above the snowline. The radial growth of *P. olivacea* was approximately twice that of *P. ambigua* but *P. ambigua* avoided competition by being adapted to the environment at the base of trees where snow accumulated and where *P. olivacea* could not survive. In addition, Harris (1971a, b, 1972) constructed a mathematical model to test the hypothesis that the vertical distribution of foliose lichens on trees in south Devon, UK, was a function of light intensity and water availability. Predicted vertical net carbon assimilation rates compared not unfavourably with the observed vertical distribution of the lichens (Harris 1972).

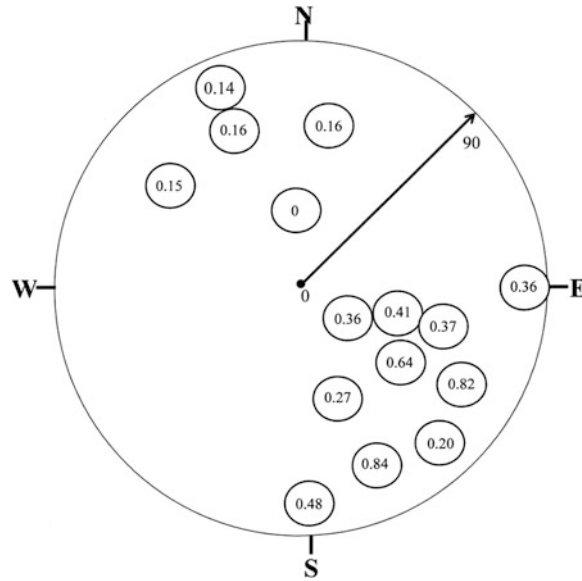


Fig. 1.4 Polar graph showing the influence of aspect and slope of the boulder facet on the radial growth (mm in 6 years) of *Rhizocarpon geographicum* in the north cascades, Washington State. Radial growth was significantly greater on east-southeast and south-southeast facets

compared with north-facing facets suggesting that at sites in the northern hemisphere, well-lit, southern facing surfaces are optimal for growth. By contrast, variation in the slope of the facet appeared to have less influence on growth (data from Armstrong 2005)

1.5 The Influence of the Substratum on Growth

1.5.1 Physical Properties

The substratum may have several different effects on lichen growth and many of these factors could also interact with climate and microclimate. Hence, the relationship between the mechanical, chemical, and mineralogical properties of soil and the types of substratum chosen by terricolous lichens was studied by Garty et al. (1974). Species of *Squamarina* were found to be located on soils with the lowest shrinkage rates. When the shrinkage rate was above 5 %, however, the lichens grew on rock and moss instead suggesting that interactions between texture, porosity, rate of drying, and the physical attributes of the substratum on growth could have been responsible. In addition, *Xanthoria parietina* (L.) Th. Fr. can be affected by the texture of the substratum, thalli on rock, and smooth-barked surfaces having a higher radial growth than those on rough bark (Moxham 1981).

Moreover, a combination of high water absorbing power and a high base content of the substratum favoured growth of lichens on roofs in suburban London (Brightman 1959). In addition, many lichens grow on moss which creates a very specific environment. In *Peltigera rufescens* (Weiss) Humb., for example, moss-associated thalli have a different morphology, have a 66 % higher net photosynthetic rate, and have a carbon dioxide concentration measured beneath the thalli more than 25 % greater than thalli growing on non-moss substrata (Colosie et al. 2012).

Relatively few studies of the growth of crustose lichens have been carried out on different types of substrata. *R. geographicum*, however, appears to be able to grow on a wide variety of siliceous rocks (Innes 1985). In addition, observations suggest *R. geographicum* may exhibit faster radial growth on sandstone than gneiss (Belloni 1973) and on andesite compared with granodiorite (Porter 1981).

The growth of the fruticose *Cladonia alpestris* (L.) Rabenh. and *C. rangiferina* (L.) Web. was studied by Kershaw and Rouse (Kershaw and

Rouse 1971). A strong correlation was observed between podetial length, diameter, internode length, and soil moisture; the level of soil moisture essentially integrating the effects of net radiation and drying rates of the lichen canopy as well as the relative metabolic activity of the lichen.

1.5.2 Rock Chemistry

The lichen flora of lime-rich rocks substantially differs from that of lime-poor, siliceous rocks and relatively few species are able to grow successfully on both types of substrata (James et al. 1977). To test the hypothesis that rock chemistry has a substantial effect on growth, fragments were cut from the perimeters of foliose lichens and glued onto different substrata, slate, granite, cement, and asbestos (Armstrong 1993b). The data for two foliose species are shown in Fig. 1.5. Radial growth of *X. conspersa* was inhibited on the calcium-rich compared with the siliceous substrates, while *X. parietina* would only grow successfully on a calcium-rich substratum, the fragments becoming discoloured and fragmented on lime-poor substrates.

A requirement for calcium may explain many aspects of the distribution of *Xanthoria parietina* in the UK. Hence, this species occurs on limestone rocks and walls, wall mortar, asbestos, tree bark where stemflow is enriched with calcium, and siliceous rocks near the sea (Armstrong 1990). By contrast, *Parmelia saxatilis* (L.) Ach. is virtually restricted to acid substrata, thalli of this species adopting a ‘crescent-shaped’ form after treatment with calcium carbonate, after which the thalli fragment and disappear (Armstrong 1990). Treatment with a 0.250 mM solution of calcium as calcium chloride, however, had little effect on growth of *P. saxatilis* (Fig. 1.5) suggesting that this species may tolerate mildly alkaline conditions. Gilbert (1971) found, for example, that *P. saxatilis* could occur at more alkaline sites in polluted environments. Zinc, copper, and mercury in rocks may also influence lichen growth as they have been shown to affect the chlorophyll content of lichen algae (Backor and Djubai 2004).

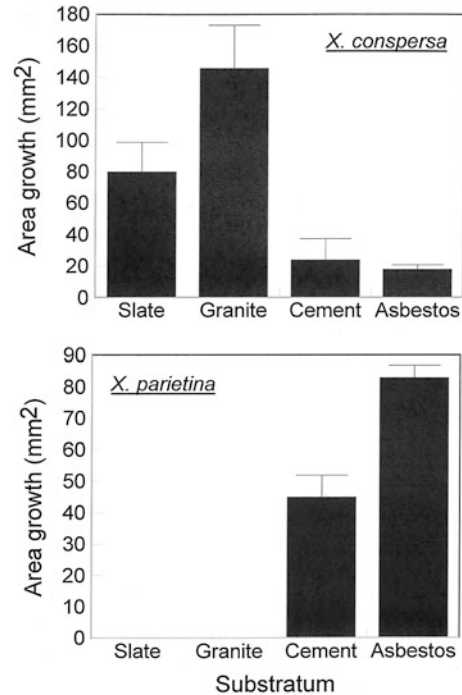


Fig. 1.5 The influence of the substratum on the radial growth (RaG mm year^{-1}) of two foliose saxicolous lichens in north Wales, UK. Analysis of variance (ANOVA): Radial growth of *Xanthoparmelia conspersa* was inhibited on the calcium-rich compared with the siliceous substrates while *Xanthoria parietina* would only grow successfully on a calcium-rich substratum. Between substrates $F = 11.09^{***}$, *post hoc*: Asbestos = cement, Slate/Granite > Asbestos/Cement; *Xanthoria parietina*, Asbestos versus Cement $t = 4.71^{**}$, $^{***}P < 0.001$, $^{**}P < 0.01$ (data from Armstrong 1993b)

1.6 The Effect of Nutrient Enrichment on Growth

1.6.1 Bird Droppings

Several studies suggest that the degree of nutrient enrichment of a substratum especially by bird droppings can have a significant influence on lichen growth and community composition (Hale 1967). Bird droppings may influence growth by smothering the thalli, altering pH, or adding inhibitory and stimulatory compounds (Armstrong 1984). Hence, 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 several foliose lichens with differing distributions on and off bird perching stones (Armstrong 1984). Treatment with bird droppings increased the radial growth of *X. conspersa*, a species common on well-lit nutrient-enriched rocks. The paste and to a lesser extent the suspension inhibited growth of *P. saxatilis* (L.) Ach. a species which is relatively rare on bird perching stones. Uric acid, the most abundant nitrogenous component of bird droppings, did not influence growth when applied as a suspension to either species (Armstrong 1984). Hence, growth response to bird droppings was likely to be attributable to either increased pH or inorganic chemicals in the bird droppings.

Few direct studies of the influence of nutrient enrichment on growth of crustose species have been carried out. In a long-term study at Signy Island (Maritime Antarctic), however, growth of lichens at sites enriched by nitrogenous compounds derived from seabirds was rapid, especially that of *Acarospora macrocyclos* Vain. and species of *Buellia* and *Caloplaca* (Smith 1995). In addition, Wootton (1991) compared different maritime lichen communities with and without overhead seabird colonies. When guano was present, the 'orange' zone dominated by *Caloplaca marina* Wedd. was elevated further up the shore, and the grey *Physcia* zone eliminated in the supralittoral zone. Moreover, in the splash zone, *Verrucaria maura* Wahlenb. Ex Ach. decreased as a result of enhanced competition with the green alga *Prasiola*.

1.6.2 Nitrogen and Phosphorus

The response of *X. parietina* to varying nitrogen concentrations was studied by Gaio-Oliveira et al. (2005). Thallus specific weight was similar in all thalli without any significant effect of added nitrogen suggesting that this species may respond more to changes in pH than to nitrogen consistent with previous data (Armstrong 1990). 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-month growth, control and nitrogen-fertilised thalli of *Nephroma arcticum* increased in area by $0.2 \text{ m}^2 \text{ m}^{-2}$ (mean relative growth rate = $3.8 \text{ mg gm}^{-1} \text{ d}^{-1}$) and *Peltigera aphthosa* by $0.4 \text{ m}^2 \text{ m}^{-2}$ (mean relative growth rate = $8.4 \text{ mg gm}^{-1} \text{ d}^{-1}$). 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 also studied in *Platismatia glauca* (L.) WL Culb. & CF Culb. (Palmqvist and Dahlman 2006). Dry weight gain was significantly enhanced by nitrogen supply, variations in growth 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 encouraging the production of algal cells. Phosphorus may also be important in some cyanobacteria lichens such as *Lobaria pulmonaria* (McCune and Caldwell 2009). Hence, this species doubled its annual biomass after a single 20-min immersion in a phosphorus solution suggesting that phosphorus is an important stimulant to growth.

Growth of the fruticose lichen *Cladonia stellaris* (Opiz) Brodo was studied in relation to levels of fertilisation, and growth not responding to nutrient additions suggesting that some fruticose species may not respond to short-term changes in the availability of nutrients (Hyvarinen et al. 2003). In a further study of *C. stellaris*, Makkonen et al. (2007) found that both nitrogen and phosphate could limit the growth of fruticose lichens with phosphate having a greater effect than nitrogen. Moreover, nitrogen and phosphorus enrichment may have differential effects on the algal and fungal partners (Makkonen et al. 2007). In addition, nitrogen was added to two lichen communities in south-west Norway dominated by species of *Cladonia* and *Cetraria*, respectively, (Fremstad et al. 2005). There was a decrease in lichen size and overall cover, and later, thalli became discoloured, the most sensitive species being *Alectoria nigricans* (Ach.) Nyl. and *Cetraria ericitorum*.

1.6.3 Salinity

Additional chemical factors may be important in determining growth at maritime sites (Fletcher 1976). Although calcium was shown experimentally to be an important ion in these environments, salinity exerted little effect, the species responding more to periods of immersion (Fletcher 1976). By contrast, Ramkaer (1978) found that the response of four different lichen fungi to salinity correlated well with the zonation on maritime rocks. No studies appear to have been published on the influence of chemical treatments on the radial growth of species in situ on maritime rocks. The radial growth of *X. parietina*, a common species of the submesic zone of the supralittoral (Fletcher 1976) and many nutrient-enriched sites inland (Brodo 1973), however, was inhibited when transplanted to an inland site (Armstrong 1990). In addition, the transplanted thalli grew successfully inland when calcium carbonate was added as a paste to the thalli at intervals over a year, treatment with a 0.250 mM solution of calcium chloride at similar intervals having less effect. A relatively constant supply of calcium may therefore be necessary for successful growth of this species. This hypothesis is also supported by experiments showing that *X. 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 (Fletcher 1976). By contrast, addition of calcium carbonate to the calcifuge species *P. saxatilis* inhibited its growth which may explain its absence from lime-rich rocks.

1.6.4 Pollution

Despite the reinvasion of many urban sites by lichens in the last 20 years, polluted sites have significantly lower lichen diversity than rural sites, a testament to the powerful effect of air pollution on growth. Samples of foliose and crustose species were transplanted on rock fragments from north Wales to a city centre site in Birmingham, UK; no measurable growth was recorded, all thalli exhibiting evidence of

fragmentation within 7 days of transplantation and all had disappeared completely within one month (Armstrong unpublished data). Gilbert (1971) directly measured the effects of air pollution on the growth of *Parmelia saxatilis*. As the level of sulphur dioxide increased, thalli became crescent-shaped, the thalli persisting for several years before flaking off the substratum. During this period, however, actively growing lobes were found on the outside margin and radial growth did not appear to be affected. In addition, both *P. saxatilis* and *X. parietina* developed an intense orange or green colour within the medulla, respectively, representing the breakdown of lichen acids (Gilbert 1971). In the West Riding of Yorkshire, UK, there was greater uniformity in radial growth of *Lecanora muralis* (Schreb.) Rabenh. as measured from year to year, than observed in rural environments (Seaward 1976). In addition, at nine sites within the WNW to NNE quadrant of Leeds, radial growth varied from 2.84 to 6.5 mm year⁻¹ increasing with distance from the city centre. The study also suggested that urban environmental factors have a greater detrimental effect on growth during winter months suggesting that toxicity, due to air pollution, rather than drought was the most important factor.

1.7 Ecological Significance of Growth Effects

Ecological consequences may result from direct or indirect action of environmental factors on growth. A direct effect results from a significant change in an environmental factor which has such a detrimental effect on lichen physiology so as to completely inhibit growth. In such a circumstance, lichen thalli often exhibit the characteristic signs of degeneration, i.e. they become discoloured, crescent-shaped, or exhibit fragmentation of the thallus centre, ultimately disappearing from a substratum (Armstrong and Smith 1997). In many situations, however, growth effects are more subtle and indirect, changes in growth being manifest as alterations in the competitive balance among different

species in a complex community (Armstrong and Welch 2007).

Few studies have examined the interaction between growth and competition in determining the composition of lichen communities (Armstrong and Welch 2007). In north Wales, for example, a complex relationship exists between growth and aspect of *R. geographicum* (Armstrong 1974, 2002). Hence, *R. geographicum* is abundant on south-facing surfaces at these sites but exhibits significantly greater growth on some northwest-facing surfaces (Armstrong 2002). The size frequency distributions of the thalli also differed between these two habitats, a higher percentage of thalli in the smallest size classes and a more restricted range of size being observed on the north-west surfaces. The rate of mortality of the thalli also appeared to be greater on north-west surfaces. It was concluded that the radial growth of *R. geographicum* did not predict its aspect distribution in north Wales but that the differing competitive environments on the two surfaces could explain its aspect distribution rather than the direct effects of environmental factors. In addition, Bradwell (2010) studied the radial growth of *R. geographicum* in a maritime subpolar environment in northern Scotland. The fastest radial growth of thalli greater than 10 mm in diameter at the two sites was 0.67 and 0.29 mm year⁻¹, the difference being attributable to the level of competition.

Armstrong (1991) studied the influence of rock surface aspect on competition between four foliose lichen species in experimental plots. In south-facing plots, the growth of *X. conspersa* was not reduced by the presence of any of its competitors and, *X. conspersa* is frequently found on well-lit, south-facing rock surfaces at the site (Armstrong 1974). By contrast, in north-facing plots, the growth of *X. conspersa* was reduced by *P. saxatilis*, thus reducing its competitiveness and possibly allowing *M. fuliginosa* ssp. *fuliginosa* to coexist with *X. conspersa*.

In a further experiment (Armstrong 2000), four foliose species were grown in well-lit plots with and without nutrient enrichment by added bird droppings. The results of the experiment for one of the species, *M. fuliginosa* ssp. *fuliginosa*,

are shown in Fig. 1.6. Without addition of bird droppings, area growth of *M. fuliginosa* ssp. *fuliginosa* was reduced by each of the other three species, most notably by *X. conspersa*. In addition, performance in the 3-species mixture was not predictable from the 2-species mixture. Hence, *M. fuliginosa* ssp. *fuliginosa* survived better in the *Ph. orbicularis*/*P. saxatilis* and *X. conspersa*/*Ph. orbicularis* mixtures than predicted but was completely eliminated in the *X. conspersa*/*P. saxatilis* mixture. In addition, the performance of *M. fuliginosa* ssp. *fuliginosa* in the 4-species mixture was not predictable from the 3-species mixture, this species surviving better than expected. In plots with bird droppings added, however, *M. fuliginosa* ssp. *fuliginosa* was not significantly reduced by *P. saxatilis* but was substantially reduced by *Ph. orbicularis* and *X. conspersa* and eliminated completely in the *X. conspersa*/*P. saxatilis*, *X. conspersa*/*Ph. orbicularis*, and *X. conspersa*/*P. saxatilis*/*Ph. orbicularis* mixtures. Hence, addition of bird droppings altered the competitive balance between the species, reducing the effectiveness of *P. saxatilis* as a competitor, but increasing the competitive effect of *X. conspersa*. Hence, *M. fuliginosa* ssp. *fuliginosa* survives better in more complex mixtures but only under conditions where there is little nutrient enrichment.

Addition of nutrients, by increasing the growth of some species and reducing the growth of others, could increase the chance of competitive exclusion of a species and therefore could reduce species diversity (Lawrey 1981; Vagts and Kinder 1999). By contrast, Welch et al. (2006) grew lichen fragments attached to roofing slate in various combinations and sprayed them at different frequencies with a nutrient solution. At medium application rates, there was increasing thallus growth and an increase in the number of 'overlaps' between adjacent thalli compared with controls. In addition, where nutrients were added, *Flavoparmelia caperata* (L.) Hale and *X. parietina* were equally strong competitors as also were *Parmelia reddenda* Stirt. and *F. caperata*. Where no nutrients were added, this balance between the pairs of species was lost with *F. caperata* outcompeting *X. parietina* and

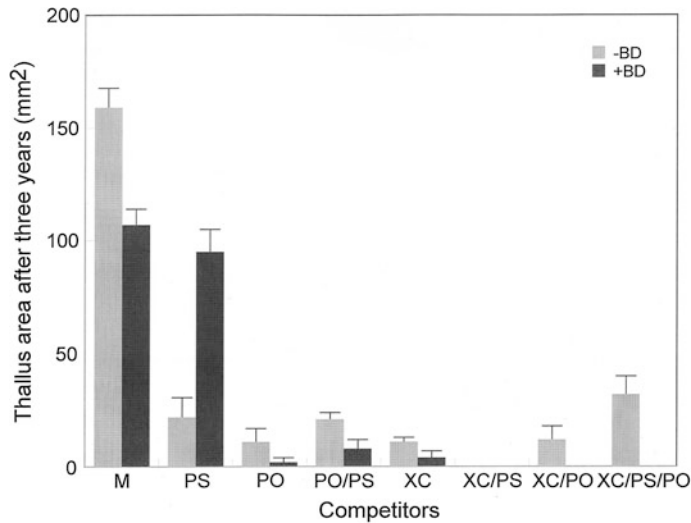


Fig. 1.6 The influence of nutrient enrichment by bird droppings (+BD) on the pattern of competition between *Melanelia fuliginosa* ssp. *fuliginosa* and three foliose saxicolous lichens (*M* growth of *M. fuliginosa* ssp. *fuliginosa* in monoculture, *PS* *Parmelia saxatilis*, *PO* *Phaeophyscia orbicularis*, *XC* *Xanthoparmelia conspersa*). Without addition of bird droppings, area growth of *M. fuliginosa* ssp. *fuliginosa* was reduced by each of the other three species, most notably by *X. conspersa*. In addition, performance in the 3-species mixtures was not predictable from the 2-species mixture. Hence, *M. fuliginosa* ssp. *fuliginosa* survived better in the *Ph orbicularis*/

P. saxatilis and *X. conspersa*/*Ph. orbicularis* mixtures than predicted but was completely eliminated in the *X. conspersa*/*P. saxatilis* mixture. In addition, the performance of *M. fuliginosa* ssp. *fuliginosa* in the 4-species mixture was not predictable from the 3-species mixture, this species surviving better than expected. In plots with bird droppings added, however, *M. fuliginosa* ssp. *fuliginosa* was not significantly reduced by *P. saxatilis* but was substantially reduced by *Ph. orbicularis* and *X. conspersa* and eliminated completely in the *X. conspersa*/*P. saxatilis*, *X. conspersa*/*Ph. orbicularis*, and *X. conspersa*/*P. saxatilis*/*Ph orbicularis* mixtures (Data from Armstrong 2000)

P. reddenda outcompeting *F. caperata*. Hence, nutrient additions may not always reduce species diversity of a lichen community and further experiments of this type would be useful to understand the role that nutrient enrichment may play in determining the structure of lichen communities.

1.8 Conclusions

Despite the difficulties of growing lichens under controlled conditions and the challenges of field experimentation, there is a substantial literature on the effects of environmental factors on lichen growth. The major conclusions that can be drawn from these studies are as follows:

1. Seasonal fluctuations in radial growth often correlate best with average or total rainfall,

the number of rain days, or rainfall in a specific season. Temperature may also an important climatic factor in some regions.

2. Interactions between microclimatic factors and especially light intensity, temperature, and moisture are important in determining local annual growth rates and differences in growth with aspect and slope of the substratum or with height on trees.
3. The physical and chemical nature of the substratum can affect growth especially the effects of texture, porosity, and rate of drying.
4. Whether the substratum is lime-rich or lime-poor and the degree of nutrient enrichment or maritime influence can have profound effects on growth both directly and by altering the competitive balance between species.
5. Effects of environmental factors on growth can alter the competitive balance on a substratum

ultimately influencing the composition of lichen communities.

6. Factorial experiments are needed to investigate the synergistic influence of different environmental factors and between the environment and competition and would lead to a more realistic understanding of the interactive processes influencing lichen growth in the field.

References

- Armstrong RA (1973) Seasonal growth and growth rate-colony size relationships in six species of saxicolous lichens. *New Phytol* 72:1023–1030. doi:[10.1111/j.1469-8137.1973.tb02078.x](https://doi.org/10.1111/j.1469-8137.1973.tb02078.x)
- Armstrong RA (1974) The descriptive ecology of saxicolous lichens in area of South Merionethshire, Wales. *J Ecol* 62:33–45. doi:[10.2307/2258878](https://doi.org/10.2307/2258878)
- 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. doi:[10.1111/j.1469-8137.1975.tb-01393.x](https://doi.org/10.1111/j.1469-8137.1975.tb-01393.x)
- Armstrong RA (1976a) Studies on the growth rate of lichens. In: Brown DH, Bailey RH, Hawksworth DL (eds) *Progress and problems in lichenology*. Academic Press, London, pp 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. doi:[10.1111/j.1469-8137.1976.tb-04666.x](https://doi.org/10.1111/j.1469-8137.1976.tb-04666.x)
- Armstrong RA (1978) The colonization of a slate rock surface by a lichen. *New Phytol* 81:85–88. doi:[10.1111/j.1469-8137.1978.tb01606.x](https://doi.org/10.1111/j.1469-8137.1978.tb01606.x)
- Armstrong RA (1984) The influence of bird droppings and uric acid on the growth of five species of saxicolous lichens. *Environ Exp Bot* 4:95–99. doi:[10.1016/0098-8472\(84\)90065-0](https://doi.org/10.1016/0098-8472(84)90065-0)
- Armstrong RA (1988) Substrate colonization, growth and competition. In: Galun M (ed) *Handbook of lichenology*. CRC Press, Cleveland, pp 3–16
- Armstrong RA (1990) The influence of calcium and magnesium on the growth of the lichens *Xanthoria parietina* and *Parmelia saxatilis*. *Environ Exp Bot* 30:51–57. doi:[10.1016/0098-8472\(90\)90008-R](https://doi.org/10.1016/0098-8472(90)90008-R)
- Armstrong RA (1991) Competitive interactions between four foliose lichens on north and south facing rock surfaces. *Environ Exp Bot* 31:51–58. doi:[10.1016/0098-8472\(91\)90007-B](https://doi.org/10.1016/0098-8472(91)90007-B)
- Armstrong RA (1993a) Seasonal growth of foliose lichens in successive years in South Gwynedd, Wales. *Environ Exp Bot* 33:225–232. doi:[10.1016/0098-8472\(93\)90068-Q](https://doi.org/10.1016/0098-8472(93)90068-Q)
- Armstrong RA (1993b) 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 (2000) Competitive interactions between four foliose lichen species with and without nutrient enrichment. *Symbiosis* 28:323–335
- Armstrong RA (2002) The effect of rock surface aspect on growth, size structure and competition in the lichen *Rhizocarpon geographicum*. *Environ Exp Bot* 48:187–194. doi:[10.1016/S0098-8472\(02\)00040-0](https://doi.org/10.1016/S0098-8472(02)00040-0)
- Armstrong RA (2005) Radial growth of *Rhizocarpon* section *Rhizocarpon* lichen thalli over six years at Snoqualmie Pass in the Cascade Range, Washington State. *Arct Antarct Alp Res* 37:411–415. doi:[10.1657/1523-0430\(2005\)037\[0411:RGORSR\]:RGORSRJ2.0.CO;2](https://doi.org/10.1657/1523-0430(2005)037[0411:RGORSR]:RGORSRJ2.0.CO;2)
- Armstrong RA (2006) Seasonal growth of the crustose lichen *Rhizocarpon geographicum* (L.) DC. in south Gwynedd Wales. *Symbiosis* 41:97–102
- 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 (2013) Development of areolae and growth of the peripheral prothallus in the crustose lichen *Rhizocarpon geographicum*: an image analysis study. *Symbiosis* 60:7–15. doi:[10.1007/s13199-013-0234-2](https://doi.org/10.1007/s13199-013-0234-2)
- Armstrong RA, Welch AR (2007) Competition in lichen communities. *Symbiosis* 43:1–12
- Armstrong RA, Bradwell T (2010) Growth of crustose lichens: a review. *Geogr Ann A Phys Geogr* 92A:3–17
- Armstrong RA, Bradwell T (2011) Growth of foliose lichens: a review. *Symbiosis* 53:1–16. doi:[10.1007/s13199-011-0108-4](https://doi.org/10.1007/s13199-011-0108-4)
- Armstrong RA, Smith SN (1997) Factors associated with degeneration of the thallus center in foliose lichens. *Symbiosis* 22:293–302
- 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 Hattori Bot Lab* 95:271–284
- Belloni S (1973) Eicerche lichenometriche in Valfurva e nella Valle di Solda. *Bull Com Glaciol Ital* 21:19–33
- Benedict JB (1990a) Experiments on lichen growth. I. Seasonal patterns and environmental controls. *Arct Alp Res* 22:244–254. doi:[10.2307/1551587](https://doi.org/10.2307/1551587)
- Benedict JB (1990b) Winter frost injury to lichens: Colorado Front Range. *Bryologist* 93:423–426. doi:[10.2307/3243606](https://doi.org/10.2307/3243606)
- Benedict JB (1991) Experiments on lichen growth II. Effects of a seasonal snow cover. *Arct Alp Res* 23:189–199. doi:[10.2307/1551382](https://doi.org/10.2307/1551382)
- Benedict JB (2009) A review of lichenometric dating and its applications to archeology. *Am Antiq* 74:143–172
- Beschel RE (1958) Lichenometrical studies in West Greenland. *Arctic* 11:254
- Beschel RE (1961) Dating rock surfaces by lichen growth and its application to the glaciology and physiography (lichenometry). In: Raasch GO (ed) *Geology of the*

- Arctic. University of Toronto Press, Toronto, pp 1044–1062
- Bohuslavova O, Smilauer P, Elster J (2012) *Usnea* lichen community biomass estimation on volcanic mesas, James Ross Island, Antarctica. *Polar Biol* 35:1563–1572. doi:10.1007/S00300-012-1197-0
- Boucher VL, Nash TH (1990) Growth patterns in *Ramalina menziesii* in California; Coastal vs. inland populations. *Bryologist* 93:295–302. doi:10.2307/3243516
- Bradwell T (2001a) A new lichenometric dating curve for southeast Iceland. *Geogr Ann* 83A:91–101. doi:10.1111/j.0435-3676.2001.00146.x
- Bradwell T (2001b) Glacier fluctuations, lichenometry and climatic change in Iceland. PhD thesis, University of Edinburgh, 365 pp
- Bradwell T (2010) Studies on the growth of *Rhizocarpon geographicum* in northwest Scotland and some implications for lichenometry. *Geogr Ann A Phys Geogr* 92:41–52. doi:10.1111/j.1468-0459.2010.00376.x
- Brightman FH (1959) Some factors influencing lichen growth in towns. *Lichenologist* 1:104–108
- Brodo IM (1965) Studies on growth rates of corticolous lichens on Long Island, New York. *Bryologist* 68:451–456
- Brodo IM (1973) Substrate ecology. In: Ahmadjian V, Hale ME (eds) *The lichens*. Academic Press, London
- Colesie C, Scheu S, Green TGA, Weber B, Wirth R, Budel B (2012) The advantage of growing on moss: facilitative effects on photosynthetic performance and growth in the cyanobacterial lichen *Peltigera rufescens*. *Oecologia* 169:599–607. doi:10.1007/S00442-011-2224-5
- 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, Kershaw KA (1983) The ecology of *Rhizocarpon superficiale* II. The seasonal response of net photosynthesis and respiration to temperature, moisture and light. *Can J Bot* 61:3019–3030
- 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. *Forest Ecol Manage* 242:5–16. doi:10.1016/j.foreco.2007.01.031
- Farrar JF (1973) Lichen physiology. In: Ferry BW, Baddeley MS, Hawksworth DL (eds) *Progress and problems in lichenology*. Athlone Press, University of London, London, pp 238–282
- Farrar JF (1976) The lichen as an ecosystem: observation and experiment. In: Brown DH, Bailey RH, Hawksworth DL (eds) *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. doi:10.1017/S0024282978000092
- Fletcher A (1976) Nutritional aspects of marine and maritime lichen ecology. In: Brown DH, Bailey RH, Hawksworth DL (eds) *Progress and problems in lichenology*. Academic Press, London, pp 359–384
- Fremstad E, Paal J, Mois T (2005) Impacts of increased nitrogen supply on Norwegian lichen-rich alpine communities: 1 10-year experiment. *J Ecol* 93:471–481. doi:10.1111/j.1365-2745.2005.00995.x
- Gaio-Oliveira G, Dahlman L, Maguas C, Palmqvist K (2004) Growth in relation to microclimatic conditions and physiological of four *Lobaria pulmonaria* populations in two contrasting habitats. *Ecography* 27:13–28. doi:10.1111/j.0906-7590.2004.03577.x
- Gaio-Oliveira G, Dahlman L, Palmqvist K, Maguas C (2005) Responses of the lichen *Xanthoria parietina* (L.) Th Fr. to varying nitrogen concentrations. *Lichenologist* 37:171–179. doi:10.1017/S0024282904014598
- 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. doi:10.1139/X07-048
- 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. doi:10.1111/j.1469-8137.2008.02690.x
- 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. doi:10.2307/2426518
- 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, Hale ME (eds) *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. doi:10.2307/2258038
- Haworth LA, Calkin PE, Ellis JM (1986) Direct measurement of lichen growth in the central Brooks Range, Alaska USA, and its application to lichenometric dating. *Arct Alp Res* 18:289–296. doi:10.2307/2258323
- Hooker TN (1980) Lobe growth and marginal zonation in crustose lichens. *Lichenologist* 12:313–323. doi:10.2307/2258324

- Hyvarinen M, Crittenden PD (1998) Growth of the cushion-forming lichen *Cladonia portentosa* at nitrogen-polluted and unpolluted heathland sites. *Environ Exp Bot* 40:67–76. doi:[10.1016/S0098-8472\(98\)00022-7](https://doi.org/10.1016/S0098-8472(98)00022-7)
- Hyvarinen M, Walters B, Koopmann R (2003) Impact of fertilization on phenol content and growth rate of *Cladonia stellaris*: a test of the carbon-nutrient balance hypothesis. *Oecologia* 134:176–181. doi:[10.1007/S00442-002-1105-3](https://doi.org/10.1007/S00442-002-1105-3)
- Innes JL (1983) Development of lichenometric dating curves for highland Scotland. *Trans R Soc Edinb* 74:23–32
- Innes JL (1985) Lichenometry. *Prog Phys Geog* 9:187–254. doi:[10.1177/030913338500900202](https://doi.org/10.1177/030913338500900202)
- James PW, Hawksworth DL, Rose F (1977) In: Seaward MRD (ed) *Lichen communities in the British Isles: a preliminary conspectus*. Academic Press, London, pp 295–419
- Jones JM, Platt RB (1969) Effects of ionizing radiation, climate and nutrition on growth and structure of a lichen *Parmelia conspersa* (Ach.) Ach. *Radioecology Symp* 2:111–119
- Karenlampi L (1970) Morphological analysis of the growth and productivity of the lichen *Cladonia alpestris*. *Rep Kevo Subarct Res* 7:9–15
- Karenlampi L (1971) Studies on the relative growth rate of some fruticose lichens. *Rep Kevo Subarct Res* 7:33–39
- Keon DB, Muir PS (2002) Growth of *Usnea longissima* across a variety of habitats in the Oregon Coast range. *Bryologist* 105:233–242. doi:[10.1639/0007-2745\(2002\)105\[0233:GOULAA\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2002)105[0233:GOULAA]2.0.CO;2)
- 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, Rouse WR (1971) Studies on lichen-dominated systems II. The growth pattern of *Cladonia alpestris* and *Cladonia rangeriferina*. *Can J Bot* 49:1401–1410
- Lawrey JD (1981) Evidence for competitive release in simplified saxicolous lichen communities. *Am J Bot* 68:1066–1073. doi:[10.2307/2442716](https://doi.org/10.2307/2442716)
- Lawrey JD, Hale ME (1977) Studies on lichen growth rates at Plummers Island, Maryland. *Proc Biol Soc Wash* 90:698–725
- Locke WW, Andrews JT, Webber PJ (1979) A manual for lichenometry. *British Geomorphological Research Group, Technical Bulletin* 26, pp 1–47
- Makkonen S, Hurri RSK, Hyvarinen M (2007) Differential responses of lichen symbionts to enhanced nitrogen and phosphorus availability: an experiment with *Cladonia stellaris*. *Ann Bot* 99:877–884. doi:[10.1093/aob/mcm042](https://doi.org/10.1093/aob/mcm042)
- Mathews JA (1994) Lichenometric dating: a review with particular reference to ‘Little Ice Age’ moraines in southern Norway. In: Beck C (ed) *Dating in surface context*. New Mexico Press, Albuquerque, pp 185–212
- Mathews JA (2005) Little Ice Age glacier variations in Jotunheimen, southern Norway: a study in regionally controlled dating of recessional moraines with implications for climate and lichen growth rates. *Holocene* 15:1–19
- McCune B, Caldwell BA (2009) A single phosphorus treatment doubles growth of cyanobacterial lichen transplants. *Ecology* 90:567–570. doi:[10.1890/08-0344.1](https://doi.org/10.1890/08-0344.1)
- Moxham TH (1981) Growth rates of *Xanthoria parietina* and their relationship to substrate texture. *Cryp Bryol Lichenol* 2:171–180
- 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 Env* 23:1–14. doi:[10.1046/j.1365-3040.2000.00529.x](https://doi.org/10.1046/j.1365-3040.2000.00529.x)
- Palmqvist K, Dahlman L (2006) Responses of the green algal foliose lichen *Platismatia glauca* to increased nitrogen supply. *New Phytol* 171:343–356. doi:[10.1111/j.1469-8137.2006.01754.x](https://doi.org/10.1111/j.1469-8137.2006.01754.x)
- 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. doi:[10.1111/j.1469-8137.1983.tb04869.x](https://doi.org/10.1111/j.1469-8137.1983.tb04869.x)
- Porter SC (1981) Lichenometric studies in the Cascade range of Washington: establishment of *Rhizocarpon geographicum* growth curves at Mount Rainier. *Arc Alp Res* 13:11–23. doi:[10.2307/1550622](https://doi.org/10.2307/1550622)
- Ramkaer K (1978) The influence of salinity on the establishment phase of rocky shore lichens. *Bot Tidsskr* 72:119–123
- Rydzak J (1961) Investigations on the growth rate of lichens. *Ann UMCS (Lublin, Poland) Sec C* 16:1–15
- Seaward MRD (1976) Performance of *Lecanora muralis* in an urban environment. In: Brown DH, Bailey RH, Hawksworth DL (eds) *Progress and problems in lichenology*. Academic Press, London, pp 323–358
- 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
- Smith DC, Molesworth S (1973) Lichen physiology XIII. Effects of rewetting dry lichens. *New Phytol* 72:525–533. doi:[10.1111/j.1469-8137.1973.tb04403.x](https://doi.org/10.1111/j.1469-8137.1973.tb04403.x)
- Smith RIL (1995) Colonization by lichens and the development of lichen-dominated communities in the maritime Antarctic. *Lichenologist* 27:473–483. doi:[10.1016/S0024-2829\(95\)80007-7](https://doi.org/10.1016/S0024-2829(95)80007-7)
- Sonesson M, Grimberg A, Sveinbjornsson B, Carlsson BA (2011) Seasonal variation in concentrations of carbohydrates and lipids in two epiphytic lichens with contrasting, snow-depth related distribution on sub-arctic birch trees. *Bryologist* 114:443–452. doi:[10.1639/0007-2745-114.3.443](https://doi.org/10.1639/0007-2745-114.3.443)
- Stevenson SK, Coxon DS (2008) Growth responses of *Lobaria retigera* to forest edge and canopy structure in the inland temperate rainforest, British Columbia.

- Forest Ecol Manage 256:618–623. doi:[10.1016/j.foreco.2008.05.025](https://doi.org/10.1016/j.foreco.2008.05.025)
- Sundberg B, Nasholm T, Palmqvist K (2001) The effect of nitrogen and key thallus components in the two tripartite lichens *Nephroma arcticum* and *Peltigera aphthosa*. Plant Cell Environ 24:517–527. doi:[10.1046/j.1365-3040.2001.00701.x](https://doi.org/10.1046/j.1365-3040.2001.00701.x)
- Tenbrink NW (1973) Lichen growth rates in West Greenland. Arct Alp Res 5:323–331
- Trenbith HE, Matthews JA (2010) Lichen growth rates on glacier forelands in southern Norway: preliminary results from a 25-year monitoring programme. Geogr Ann A Phys Geogr 92A:19–40
- Uchida M, Nakatsubo T, Kanda H, Koizumi H (2006) Estimation of annual primary production of the lichen *Cetrariella delisei* in a glacier foreland in the high Arctic, Nylalesund, Svalbard. Polar Res 25:39–49. doi:[10.1111/j.1751-8369.2006.tb00149.x](https://doi.org/10.1111/j.1751-8369.2006.tb00149.x)
- Vagts I, Kinder M (1999) The response of different *Cladonia* species after treatment with fertiliser or lime in heathland. Lichenologist 31:75–83
- Webster M, Brown DH (1997) Preliminary observations on the growth of transplanted *Peltigera canina* under semi-natural conditions. Lichenologist 29:91–96
- Welch AR, Gillman MP, John EA (2006) Effect of nutrient application on growth rate and competitive ability of three foliose lichen species. Lichenologist 38:177–186. doi:[10.1017/S0024282906004555](https://doi.org/10.1017/S0024282906004555)
- Wootton JT (1991) Direct and indirect effects of nutrients on intertidal community structure: variable consequences of seabird guano. J Exp Mar Biol 151:139–153. doi:[10.1016/0022-0981\(91\)90121-C](https://doi.org/10.1016/0022-0981(91)90121-C)