Ecology of Lichens on Rock Surfaces

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Abstract

Rock surfaces are one of the more extreme habitats for the development of a lichen ecosystem. By following the life cycle stages of lichens colonizing rock surfaces, this review discusses the progress made over the last 50 years in understanding the ecology of lichens on rock. First, dispersal, attachment, and establishment of lichens are hazardous processes but nevertheless, colonization of many rock surface appears highly efficient. Second, growth to maturity is influenced by many environmental factors including overall climate, local microclimatic conditions, and factors associated with the substratum such as rock type, chemistry, aspect, slope, texture, and degree of weathering. Third, lichens are 'stress-tolerant' rather than 'competitive' organisms, but they compete for space on rock surfaces and such interactions are important in determining which species will become predominant. Hence, despite the hazards of life on rock, lichens successfully develop diverse and dynamic ecosystems. To understand and preserve these ecosystems will require further experimentation as many fundamental ecological processes that occur on rock surfaces are poorly documented.

Key Words: Rock surfaces, Establishment, Growth, Competition, Environmental factors

1. Introduction

Of the three main types of substratum commonly dominated by lichens, viz. tree bark ('corticolous'), the soil surface ('terricolous'), and rock surfaces ('saxicolous'), it is the latter that not only offer the most extreme conditions but also remain the least studied experimentally. Rock surfaces are especially stressful environments because of a combination of high temperature maxima at the surface, a wide temperature range, and xerophytic, often nutrient-poor conditions (Odum 1969, Jung & Büdel 2021) (Fig 1). Hence, in the Atlas Mountains of Morocco, temperatures at the rock surface may vary from -20°C to +60°C (Edwards et al. 2002).

Lichens on rock surfaces are influenced by many environmental factors, few of which have been investigated experimentally. These include overall climate and local microclimate and factors associated with the substratum such as rock type, chemistry, aspect, slope, texture, and degree of weathering (Armstrong 1974a,b; James et al. 1977, Armstrong 2015). The effects of these variables influence the outcome of competition among species for space (Armstrong and Welch 2007). Higher plants in general have been divided into three 'strategy' groups according to whether a 'ruderal', 'competitive', or 'stress-tolerant' life-cycle predominates (Grime 1979). In this scheme, lichens on rock surfaces would be classified as stress-tolerant organisms and therefore, characteristic of ecosystems in which competition is unlikely to be an important factor. Such organisms would be defined by features typical of lichens such as slow growth rates,

considerable longevity, low demands for nutrients, and the presence of specific adaptations to survive the stressful conditions (Grime 1979). Nevertheless, there is experimental evidence indicating that despite the stressful environment, competition plays a significant role in structuring rock surface communities (Armstrong and Welch 2007).

Figure 1. The yellow-green lichen *Rhizocarpon geographicum* on boulders at the summit of Mount Pilchuk at an altitude of 1622 m (Washington State, USA); an environment characterised by high temperature maxima at the surface, a wide temperature range, and xerophytic, often nutrient-poor conditions (Image: taken by Dr K.M. Wade; R.A. Armstrong, lichen archive).

The unique features which characterize the lichen ecosystem on rock surfaces are considered first. Then, by following the various life cycle stages of lichens colonizing rock surfaces, progress made over the last 50 years in understanding the ecology of these communities is discussed. Each stage in the life cycle is considered together with the effects of environmental factors and competition. Emphasis is given to experimental rather than observational studies. Nevertheless, there are many gaps in knowledge, with some topics having little or no experimental data. To fill some of these gaps, data from other types of lichen community or from laboratory experiments are discussed where relevant. Future directions and suggestions for experimental work are also indicated.

2. The rock surface ecosystem

Rock surfaces comprise a series of varied habitats which range from extensive cliffs, rock outcrops, and boulders to small rocks, cobbles, and pebbles. A large number of potential habitats are created on rock surfaces with some lichen species on granite, for example, more or less confined to specific microhabitats such as rock overhangs, quartz veins, cracks, or mafic intrusions within the granite (Rutherford & Reberus 2022). A lichen thallus on any of these surfaces is likely to be influenced by many different factors including its horizontal and vertical location on the rock (Armstrong 1978) and local differences in aspect, slope, porosity, and surface texture (microtopography) (Armstrong 1974a, 2014), as well as variations in access to nutrients (Armstrong 1977). Many of these factors vary among rock surfaces and at different locations over a single rock face. Relatively small differences in aspect, slope, light intensity, rock porosity, and rock texture have been observed over a small near vertical face in north Wales, UK (Armstrong 2014) but more substantial microclimatic gradients may be present on larger rock faces.
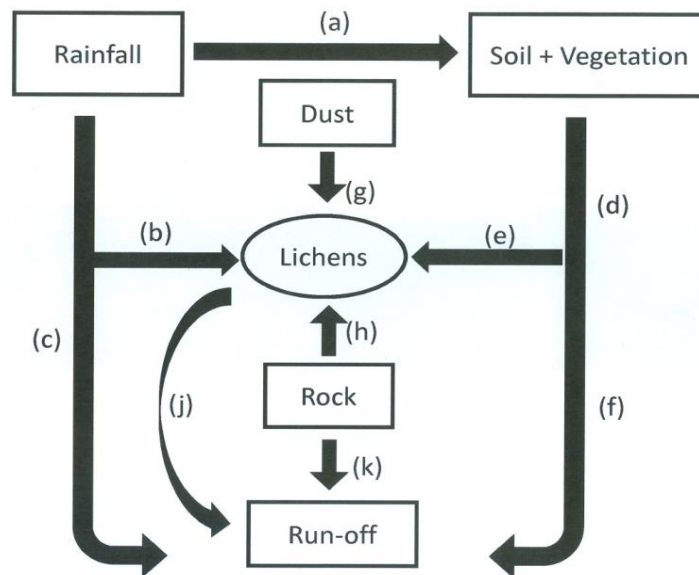
Figure 2. Hypothesised nutrient flow in a lichen ecosystem on a rock surface: (a) Nutrients in rainfall absorbed by soil and vegetation in cracks and crevices, (b) Nutrients in rainfall absorbed by lichens, (c) Nutrients in rainfall appearing as runoff from the rock surface, (d) Nutrients leached from soil and vegetation, (e) Nutrients from soil and vegetation absorbed by lichens, (f) Nutrients leached from soil and vegetation appearing as runoff, (g) Nutrients in dust particles absorbed by lichens, (h) Nutrients in rock absorbed by lichens, (j) Nutrients leached directly from lichens, (k) Nutrients leached from rock (Image: R.A. Armstrong).

The rock surface ecosystem is unusual in that there is little return of nutrients by decomposition, especially on vertical or near vertical surfaces, creating a potentially nutrient-poor environment. The various sources of nutrients available to rock surface lichens together with the hypothesized directions of nutrient flow are shown in Fig 2. Nutrients are present in rain and will flow over the surface of lichens; some of which will be held and trapped by them while some nutrients may be absorbed by soil and vegetation which accumulate on rock ledges or in crevices (Jackson 1971), the remainder appearing in run off (Odum 1969, Armstrong 1997). There are several additional sources of nutrients for lichens on a rock surface including from the rock itself, from dust particles, and nutrient enrichment by birds but the relative importance of these different sources have been little studied (Armstrong 1997). One study measured the concentrations of six trace elements, viz. manganese (Mn), copper (Cu), zinc (Zn), magnesium, (Mg), and calcium (Ca) in samples of rainfall, the rock substratum, and in surface run off collected both at the top and bottom of a near vertical rock surface in northwest Wales (Armstrong 1997). The data (Table 1) suggested that only Ca and Mg were measurable in rainfall but that all cations were present in the substratum and in run-off, with increased concentrations in run-off collected at the bottom compared with the top of the face. Increased concentrations in run-off at the bottom of the face may result from leaching from lichens and the substratum as well as from any soil or vegetation which collects on ledges.

Table 1. Concentrations of trace elements in substratum (mg gm^{-1}), rainfall (ppm), and run-off (ppm) at top (T) and bottom (B) on a near vertical rock surface in north Wales, UK (Data from Armstrong 1997)

Source	Mn	Cu	Zn	Mg	Ca
Rainfall	bdl	bdl	bdl	0.28	1.70
Run-off (T)	bdl	0.67	0.13	2.10	1.73
Run-off (B)	0.33	0.76	0.13	5.80	3.80
Substratum	0.22	0.09	0.34	0.66	0.18

bdl (below detection limit)

Many rock surfaces are dominated by crustose lichens with extremely low growth rates (Armstrong and Bradwell 2010) and together with fragmentation and loss of thallus biomass over time (Armstrong and Smith 1997), the lichens may not provide a significant source of food for herbivores or for the establishment of a complex food web. In addition, the presence of secondary chemical substances in lichens may inhibit predation (Lawrey 1984). Nevertheless, predation of lichens by molluscs, barklice (psocids), collembola, and oribatid mites has been observed but the degree to which potential preditors are supported preferentially either by rock lichens on the face or by vegetation nearby is unknown. Rock surfaces also have a broad diversity of eukaryotic and bacterial taxa with different assemblages on granite and limestone

(Brewer and Fierer 2017) but the role of these organisms in energy flow and nutrient cycling in the rock surface ecosystem is largely unknown. Bacterial communities also colonize the surfaces of lichens as 'biofilms', the growing zone of the lichen having the greatest numbers of potential microbes (Cardinale et al. 2012).
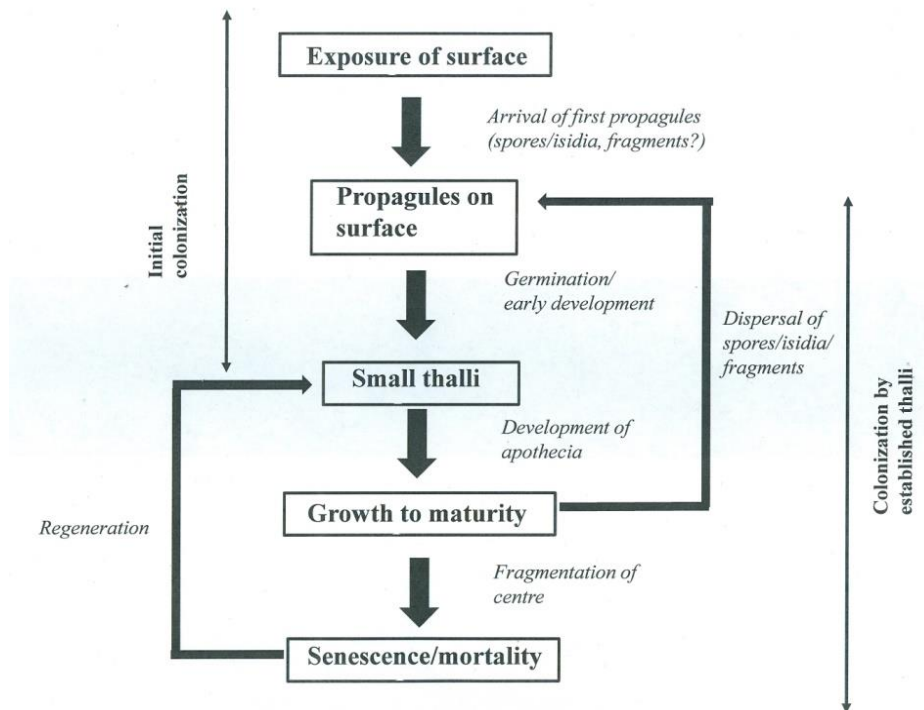
3. The lichen life cycle

Figure 3. Stages in the life cycle of a lichen colonizing a rock surface (Image: R.A. Armstrong)**.**

For a lichen to be able to colonize and succeed on a rock surface, all stages of its life cycle have to be successfully completed (Fig 3). These stages include initial colonization as the result of the dispersal and arrival of the first propagules, followed by attachment, establishment, and survival of these propagules, initiation of growth, and then growth to maturity and reproduction. Subsequent spread over the surface is a consequence of both the reproductive activity of the initial colonizers and the arrival of new propagules. Even the senescence and ultimate mortality of the initial colonizers can result in opportunities for further regeneration and colonization once a population has become established (Armstrong and Smith 1997, Armstrong 2017). All of these stages of the lichen life cycle are influenced by environmental factors and are subject to competition and successful colonization will be prevented if any stage in the life cycle fails. Hence, all of these factors and their various influences on the different life cycle stages will need to be studied to understand lichen communities on rock.

4. Dispersal and initial colonization

Lichens possess a variety of 'propagules'. Some are vegetative 'diaspores' which disperse both the algal and fungal symbionts together whereas others disperse the algal and fungal partners individually. Dispersal of lichen propagules may occur by wind (Brodie and Gregory 1953, Bailey 1966, Rudolph 1970, Armstrong 1991a), water (Bailey 1966, Armstrong 1981, 1991a), or animals (Scharf 1978, Westman 1973). Nevertheless, how lichens disperse their propagules among substrata has rarely been studied experimentally and remains one of the least understood aspects of lichen ecosystems on rock. Many crustose lichens in particular only produce fungal spores and reproduction must therefore involve 'lichenization' which results when a spore arrives and 'germinates' on a substratum where a suitable alga may be present. Because of the potential hazards of this process, however, many lichen species develop from vegetative 'diaspores' (Bailey 1976), most commonly 'isidia' (Armstrong 1981), 'soredia' (Armstrong 1991a), or thallus fragments (Armstrong 1990). Isidia are outgrowths of the thallus which are constricted at their base and hence, easily removed whereas soredia are powdery granules comprising algal cells encased by fungal hyphae borne either in clusters on the thallus surface or in specialised structures termed 'soralia'. In addition, there are crustose lichens which appear infertile, lacking apothecia or any other obvious method of dispersal examples of which include *Chaenotheca ferruginea* (Turner ex Sim.) Mig., *Lecanactis abietina* (Ach). Körb., *Lecanora jamesii* JR Laundon, and species of *Phlyctis* (Wallr.) Flot.

Figure 4. Black fungal 'wefts'of varying size, the earliest identifiable stages of colonization by the yellow-green lichen *Rhizocarpon geographicum* growing on light coloured quartzite adjacent to a mature thallus in the Cascade Mountains, Pacific northwest, USA (Image: taken by Dr K.M. Wade; R.A. Armstrong, lichen archive).

Insights into lichen dispersal among substrata have come from studies of corticolous lichen ecosystems. Hence, *Lobaria oregano* (Tuck.) Müll. Arg., in the Pacific Northwest

produces asexual 'lobules' on the ridges and margins of older thalli (Rhoades 1983). No thalli were observed on the trees smaller than these lobules consistent with the hypothesis that the lobules were being dispersed from tree to tree. Considerable lateral and vertical movement of lobules was also observed among tree canopies which were attributed to the effect of winter storms. In addition, soredia of *Evernia prunastri* (L.) Ach. and *Ramalina farinacea* (L.) Ach., were observed to be dispersed, presumably by wind, up to 30 and 20 m respectively from their source in an avenue of trees (Tapper 1976).

Figure 5. Vertical lichen 'streaks' on a monument in a graveyard which may provide a clue to the method of dispersal of many lichens (Trinity Church, Stratford-upon-Avon, UK) (Image: Taken by Dr. K.M. Wade; R.A. Armstrong, lichen archiv).

Some of the earliest stages in colonization of a rock surface have been observed by studying the 'yellow-green' members of the common crustose genus *Rhizocarpon*, an early pioneer species of rock surfaces (Beschel 1958). Species of *Rhizocarpon* do not produce vegetative diaspores but spore-producing apothecia are abundant on most thalli in association with the areolae. It is likely that initial colonization of a surface is a result of 'lichenization', i.e., germinating fungal spores contacting suitable algal cells, in this case a green alga of the genus *Trebouxia*. On very light-coloured quartz and granodiorite rocks in the north Cascade mountains,

Washington State, USA, for example, the earliest stages of colonization by *Rhizocarpon* can be observed as small wefts of black fungal hyphae, most of which do not appear to be associated with algal cells and to be relatively short lived (Armstrong 2016) (Fig. 4). Many of the wefts appear to aggregate in tiny cracks and some form longer filaments. Fungi with dark coloured cells and mycelia possess melanin in their cell walls which shield black fungi from harmful radiation (Ametrano et al. 2019) and therefore these early wefts of fungi may be protected at least for a short time before lichenization can occur, suitable nutrients being provided in runoff. Free-living *Trebouxia* cells, are often the first organisms to colonize a bare substratum and such cells can be detected on rock surfaces before any lichen thallus has become established (Mukhtar et al. 1994). In addition, scanning electron microscope studies of rock-inhibiting algae and fungi in a region recovering from fire revealed the presence of three types of unicellular green algae, one free-living micro-fungus, and many lichen ascospores (Garty 1992). Hence, random contacts between some of the fungal wefts resulting from spore germination and early colonizing *Trebouxia* cells presumably result in the first thalli of *Rhizocarpon* to appear on a rock surface.
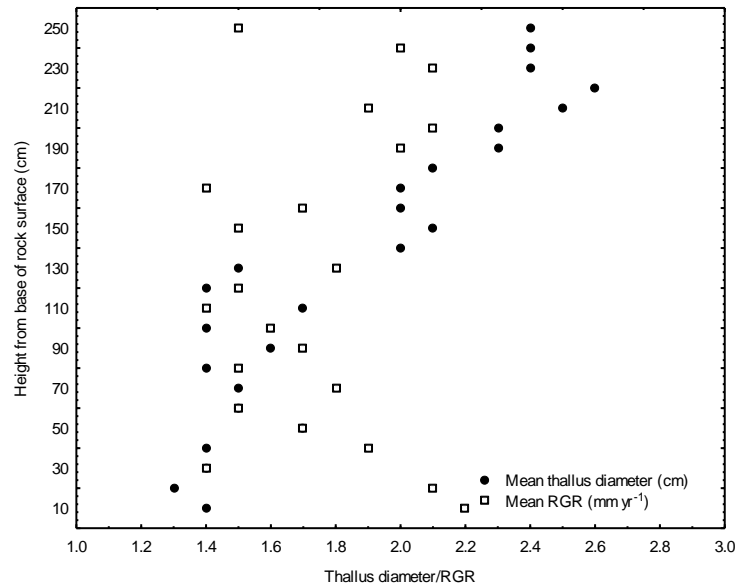

Figure 6. Relationship between the diameter of thalli of the foliose lichen *Melania fuliginosa ssp. fuliginosa,* radial growth rate (RaGR), and vertical height on a steep, slate rock surface in northwest Wales, UK. (Data from Armstrong 1978).

Vertical streaks of lichens are commonly observed on many substrata such as gravestones, statues, and some rock surfaces and may indicate how initial colonization has occurred (Fig 5). Initial delivery of propagules may have been to the top of a substratum, possibly by birds, and is followed by colonization down the surface in rain tracks (Bailey 1976). In support of this hypothesis, in northwest Wales, UK the mean diameter of thalli of the foliose lichen *Melanelia fuliginosa* ssp. *fuliginosa* (Fr. ex Duby) Essl., decreased with distance down the face on a near vertical slate rock surface whereas annual radial growth rates (RaGR) of the thalli did not vary significantly with height suggesting thalli at the top were the oldest and with gradual colonization from top to bottom (Armstrong 1978) (Fig. 6). This process could occur on all

steep-facing rock surfaces and there could be successive waves of colonization down the face during the process of succession.

5. Attachment, establishment and survival

Once propagules have arrived, they must attach themselves to the rock and successfully establish. Establishment and survival of seedlings of higher plants is related to the frequency of 'safe sites' on the soil surface that are suitable for successful germination and establishment (Harper et al. 1961). What constitutes a safe site for lichens, however, is largely unknown but various factors associated with the rock surface are likely to influence establishment and survival such as the micro-texture of the surface (Fig 7). Texture of the surface influences moisture status as highly irregular surfaces trap and retain more rainwater (Jackson 1971). Little is known regarding the relationship of different types of fungal spore to surface texture. Nevertheless, some spore types appear more frequent on certain types of substrata than others, e.g., polarilocular spores (two-celled with a perforated septum) are more frequent on limestone rocks (Pentecost 1981).

Figure 7. Establishment of various lichens including *Xanthoparmelia conspersa* (light colored) and *Candellariella vitellina* (yellow) along a fissure in the slate (North Wales, UK). (Image: Taken by Dr. K.M. Wade; R.A.Armstrong, lichen archiv).

Some experiments have attempted to establish lichen diaspores on rock. Hence, in northwest Wales, a suspension of isidia of the lichen *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale, in rainwater was poured over experimental plots established on pieces of the local slate (Fig 8) (Armstrong 1981). Attachment and survival of isidia were greater on 'pitted' surfaces

compared with smooth, newly exposed slate, an indication of the importance of surface texture on establishment. In addition, establishment of small fragments (2 mm in diameter) cut from the perimeters of *X. conspersa* thalli, and placed on pieces of horizontal slate, survived up to 120 days in cracks, 20 days on thin smears of bird droppings, but only 2-3 days on smooth slate, against small joints in the rock, or in small holes (Armstrong 1981). In the earliest stages of development of *R. geographicum* in the Pacific Northwest, many of the fungal wefts described earlier were located within tiny pits on the surface where presumably some become loosely associated with *Trebouxia* cells (Armstrong 2016) as only later the typical integrated symbiosis actually appears to form (Ott 1987). In addition to bird droppings (Armstrong 1981), attachment of propagules to a surface may also be aided by spider webs and the slime tracks of snails (Bailey 1970) but these processes have been little studied experimentally.
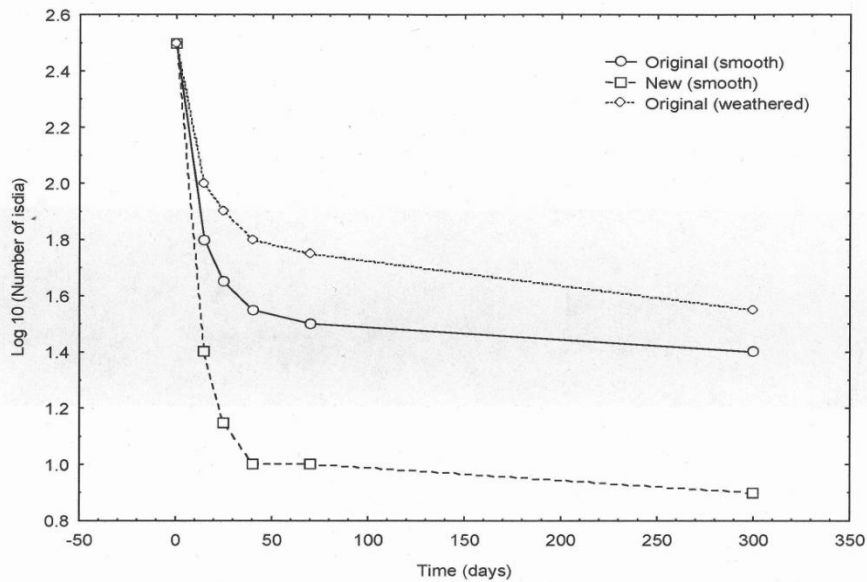

Figure 8. Attachement and survival of isidia of the foliose lichen *Xanthoparmelia conspersa* on a rock surface in northwest Wales, UK. (Data from Armstrong 1981).

The number of lichen propagules formed on a surface is likely to be greatly in excess of the number of safe sites available for successful attachment. Hence, in northwest Wales, abundant fragments of *M. fuliginosa ssp. fuliginosa* and *X. conspersa* of varying size, together with numerous isidia, were found in a sample of runoff collected at the bottom of a near vertical rock surface in a 24-hour period characterised by frequent rain showers (Table 2). Despite this abundance, only a few fragments of the two foliose species were observed to actually establish in permanent plots set up on the same surface over a subsequent six-year period (Armstrong 1981) (Table 3). However, the slow but successful establishment of a small number of thalli is sufficient to enable colonization of the surface over time.

Table 2. Frequency of fragments of different size of *Melania fuliginosa ssp. fuliginosa, Xanthoparmelia conspersa,* and unidentified species in a sample of runoff collected from the base of a slate rock surface in Northwest Wales (data from Armstrong 1981).

Range of size (mm)	X. conspersa	M. fuliginosa	Unidentified
0.2 - 0.5	?	?	243
0.6 – 1.0	9	29	0
1.1 – 1.5	0	17	0
16 – 2.0	5	13	0
2.1 – 3.0	1	8	0
>3.0	0	22	0

Table 3. Frequency of foliose lichen thalli which colonized permanent plots over six years on a vertical slate rock surface in northwest Wales (data from Armstrong 1981)

	Original surface	Original surface removed	
Species	Smooth slate	Smooth slate (no cracks)	Smooth slate (with cracks)
X. conspersa	0	0	17
M. fuliginosa ssp. fuliginosa	4	4	32

6. Early growth

Once established in a safe site, the established propagules must initiate growth, grow to maturity, and reproduce successfully. Apart from a few species, little is known regarding the early growth stages of many lichens in the field. For example, the first stage in the early growth and development of *Rhizocarpon lecanorinum* (Flörke ex Körb) Anders, is a compact granule in which fungal hyphae (the wefts described earlier) associate with a compatible species of *Trebouxia* (Clayden 1998). Thallus differentiation subsequently occurs resulting in the formation of a typical 'areola'. The prothallus is then formed, initiated from the basal margin of the primary areola, and grows out to form a marginal ring. Hence, the earliest clearly identifiable stage of a

Rhizocarpon thallus on a recently exposed rock surface is likely to comprise a single areola surrounded by the fungal prothallus (Fig.9).

Figure 9. Early stage in the growth of the crustose lichen *Rhizocarpon geographicum* showing a single pioneer areola (arrow) in asociation with a black, fungal 'hypothallus'. Other dark patches appear to be develping into other lichen species depending on the alga involved (Image: Taken by Dr K.M. Wade; R.A. Armstrong, lichen archive)

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 then succeeded by a slower phase of growth. Subsequent studies have found varying rates of development from soredia and isidia in different

species. Hence, in the terricolous species *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 form lobe 'primordia' that are then amalgamated to form 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* W.L. Culb and C.F. Culb., 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*, 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).
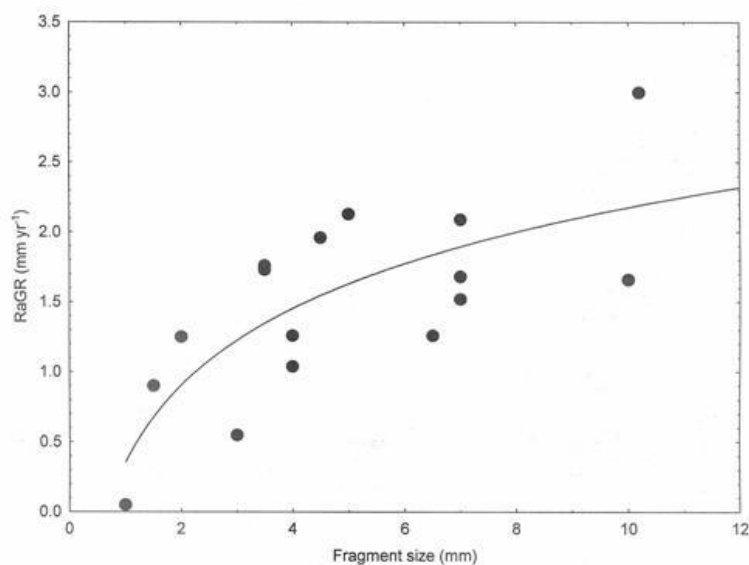

Figure 10. Early stages in growth of the foliose lichen *Xanthoparmelia conspersa* on fragments of slate in which changes in radial growth rate (RaGR) may increase linearly with the logarithm of size. (Data from Armstrong 1974).

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 on pieces of rock in the field. Nevertheless, the growth of small thalli (<1.5cm in diam.) of *X. conspersa* growing on slate was measured, RaGR being described as a logarithmic function of fragment size (Fig. 10) (Armstrong and Bradwell 2011). 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. Hence, the entire thallus area may supply carbohydrate for growth at the margin only for a short time early in the life of the thallus. In a subsequent study, small thallus fragments of *X. conspersa,* with two or three growing points, were cut from mature thalli and glued to pieces of slate rock; their growth and development being studied at intervals over five years (Armstrong 1992). New lobe 'primordia' were established rapidly over the cut surfaces of the fragments and increased in density over time. Moreover, an initial increase in RaGR was followed by a constant phase of growth beginning at a thallus radius of approximately 6 to 8 mm. Subsequently, there was a decline in RGR corresponding to the establishment of a more constant phase of radial growth.

7. Growth to maturity

Lichens can achieve a considerable longevity with estimates of up to thousands of years for the longest-lived species (Beschel 1958, 1961). As a consequence, studies of the changes in growth rate throughout the life of a lichen cannot be directly observed in many species but have employed a cross-sectional design, i.e., where growth is measured from samples of thalli of different size, the result being a 'growth rate-size curve' (Hale 1967; Armstrong & Smith 1996). In foliose genera, e.g, *Xanthoparmelia, Parmelia, and Physcia* (Armstrong and Smith 1996) and in some 'placodioid' species, i.e., those with a crustose centre and marginal lobes, including *Buellia* (*Diploicia) canescens* (Dicks.) DNot. (Proctor 1977, Hill 1981), RaGR increases with size in smaller thalli, the rate of increase diminishing with size and becoming more constant in larger thalli. Subsequently, RaGR does not appear to decline in these species either in the largest thalli measured or after 'senescence' in which fragmentation of the thallus centre occurs (Armstrong and Smith 1997). Some crustose species such as *R. geographicum* (L.) DC. (Armstrong 1983, Bradwell & Armstrong 2007, Armstrong & Bradwell 2010), *R. reductum* Th. Fr. *Buellia aethalea* (Ach.) Th. Fr. (Armstrong 2005), and *Lecidea tumida* Massal. (Armstrong 2005), have a different growth curve in which RaGR increases with size in smaller thalli up to a maximum and then declines in larger thalli (an inverted parabola) (Armstrong 2005). Many lichen species probably follow one of these two growth rate/size curves, but only a small sample of lichens have been actually studied and other types of growth curve are certainly possible.

8. Effect of environmental factors

Growth to maturity on a rock surface is influenced by many environmental factors including overall climate and local microclimate together with factors associated with the substratum such as rock type, chemistry, aspect, slope, texture, and degree of weathering. In addition, the greater the life span the longer a species has to survive potentially catastrophic environmental events so that it can persist and reproduce. In addition, minor environmental fluctuations can result in considerable variations in the lichen community which eventually develops (Orwin 1971). Hence, adjacent, similarly-sized rock surfaces, with no apparent difference in overall environment, often have a different species assemblage and significant differences in distribution over their surfaces (Armstrong 1974a). The effects of many of the environmental factors which are responsible for these distributions await detailed experimental study.

8.1 Climate

Studies of the growth of members of the genus *Rhizocarpon* at different geographical locations have demonstrated the significance of overall climate as a factor (Beschel 1958, 1961) (Table 4). Hence, the slowest growth rates in this genus have been reported from dry, continental Arctic and Alpine environments (Beschel 1958, 1961, Ten Brink 1973). Of these, possibly the slowest RaGR yet recorded is by Benedict (2008) in a study of *Rhizocarpon superficiale* (Schaer.) Vain. carried out over 16 years at the Front Range in Colorado, USA, an overall average RaGR of 0.006 mm yr^{-1} being reported. Other studies of crustose lichens in these environments have confirmed these very slow growth rates. Hence, in a 6-year study in the Cascade Mountains of Washington State, USA, an average RaGR of 0.1 mm yr^{-1} was obtained for thalli of *R. geographicum* growing on a scree slope of granodiorite boulders at Snow Lake (Armstrong 2005b). Similarly, Hooker (1980) studied 63 thalli of *R. geographicum* over three years in south Orkney Island and found no measurable growth, but growth of approximately 0.1 mm yr^{-1} was obtained during the next three-year period. Some higher growth rates have been recorded in more extreme environments in northern Labrador (0.17 mm yr^{-1}) (Rogerson et al. 1986) and in the central Brooks Range of Alaska (0 - 0.18 mm yr^{-1}) (Haworth et al. 1986). Higher growth rates have also been recorded from the maritime Antarctic; on Livingston Island, for example, an RaGR of 0.25 mm yr^{-1} was reported (Sancho and Pintado 2004) similar to growth rates obtained at Tierra del Fuego (Sancho et al. 2011).

At more temperate sites, significantly greater RaGR has been reported. In British Columbia, McCarthy (2003), for example, reported RaGR for *R. geographicum* of 0.26 - 0.42 mm yr^{-1}. Higher rates of growth have also been reported from Mount Monadnock, New Hampshire (Hausman 1948), southern Norway (Trenbirth and Matthews 2010), Iceland (Bradwell and Armstrong 2007), and Switzerland (Proctor 1983).

Table 4. Selected annual radial growth rates (RaGR) of members of the lichen genus *Rhizocarpon* in different climatic regions (Data from Armstrong 2016).

Species	Location	RaGR (mm yr^{-1})	Author
R. superficiale	Colorado	0.006	Benedict (2008)
R. geographicum	West Greenland	0.05–0.1	Beschel (1961)
R. geographicum	S. Orkney	0.1	Hooker (1980)
R. geographicum	WA state	0.1	Armstrong (2005b)
R. geographicum	Alaska	0-0.18	Haworth et al. (1986)
R. geographicum	West Greenland	0.1-0.2	Ten Brink (1973)
R. geographicum	Maritime Antarctic	0.25	Sancho & Pintado (2004, 2011)
R. geographicum	Canada	0.05-0.29	Rogerson et al. (1986)
R. geographicum	South Iceland	0.09-0.37	Bradwell & Armstrong (2007)
R. geographicum	New Hampshire	0.4	Hausman (1948)
R. geographicum	BC, Canada	0.26–0.41	McCarthy (2003)
Rhizocarpon sp.	South Norway	0.18-0.44	Matthews (1994)
R. geographicum	Switzerland	0.5 (max)	Proctor (1983)
R. geographicum	Scotland	0.29 -0.67	Bradwell (2010)
R. geographicum	North Wales	0.03-0.94	Armstrong (1983, 2005b)
R. geographicum ssp. *prospectans*	North Wales	0.67-0.81*	Winchester & Chaujar (2002)
R. reductum	North Wales	0.31-2.00	Armstrong (2005b)

The highest growth rates for *R. geographicum* have been measured at European sites. In a maritime, subpolar environment in Scotland (Bradwell 2010), growth rates were 0.67 mm yr^{-1} in thalli greater than 10 mm in diameter while thalli less than 10 mm had growth rates of 0.29 mm yr^{-1}. In north Wales, the growth of *R. geographicum* spp. *prospectans* was studied on gravestones RaGR being estimated to be 0.74 mm yr^{-1} (Winchester and Chaujar 2002). Comparable results have been reported in the studies of Armstrong (1983) in northwest Wales. A combination of climatic variables may be responsible for these growth variations with temperature having the predominant influence.

Studies of annual or seasonal variations in growth have revealed evidence of the effects of more specific climatic factors (Rydzak 1961, Hale 1970, Armstrong 1973, Showman 1976, Lawrey and Hale 1977, Fisher and Proctor 1978, Moxham 1981, Benedict 1990a). Hence, in northwest Wales, monthly RGR of *M. fuliginosa* ssp. *fuliginosa* growing on slate was measured over a year (Armstrong 1973), a large peak of growth occurring in June with smaller growth peaks in March and November corresponding with periods of maximum rainfall. A number of

studies have reported that monthly fluctuations in growth correlate best with average or total rainfall per month (Karenlampi 1971, Armstrong 1973, Golm et al. 1993), although this variable often accounts for relatively small amounts of the total variance in growth (usually <40%) (Armstrong 1988). Hence, growth of *X. conspersa* on slate was measured in each of 22 successive months in northwest Wales, a significant positive correlation between growth and rainfall being evident over this period, but only 37% of the variance in growth was accounted for by rainfall variations alone (Armstrong 1988). There have been fewer studies of seasonal growth in crustose species because of their significantly lower growth rates, but growth over three-month growth periods was studied in *Rhizocarpon reductum* and *Lecidea tumida* (Armstrong 1973); both showing maximum growth between May and July and relatively little growth in November to January suggesting that periods of high rainfall in combination with lower temperatures was not supportive of growth.

Additional climatic factors affecting growth to maturity have also been identified. In south Norway, for example, diameter growth of *R. geographicum* was studied at 47 different sites. Annual growth rates were related to winter mean but not to summer temperatures and less correlation with rainfall was evident (Trenbirth and Mathews 2010). In a study of the seasonal growth of *R. geographicum* in northwest Wales (Armstrong 2006), RaGR of 20 thalli was measured *in situ* on a southeast-facing rock surface at 17 three-month intervals over 51 months. Five periods of significant growth were identified, four of them corresponding with a maximum temperature exceeding 15°C and three also coincided with >450 sunshine hours. Moreover, two of the growth maxima coincided with three-month periods of total rainfall exceeding 300 mm and one with greater than 50 rain days. There were no significant linear relationships between growth and individual climatic variables but more complex curvilinear 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 reliable predictor (Armstrong 2006). Coxon and Kershaw (1983) studied changes in photosynthetic capacity of thalli of *R. superficiale*, throughout 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.

Growth changes attributable to climate are also evident at different altitudes on mountains. At higher altitudes, the degree of winter frost injury and snowfall are important factors and some species have a preference for these habitats. Hence, members of the genus *Rhizocarpon*, although tolerating a broad range of temperatures, have a clear preference for polar, alpine, and cooler temperatures (Armstrong 2016). In the north Cascades, Washington State, for example, thalli of *R. geographicum*, are abundant on the summit rocks of Mount Pilchuk (Fig. 1) (altitude 1622 m) (Armstrong 2016), where they are exposed to high insulation, low moisture, and abrasion by wind-borne particles (Benedict 2009). Fahselt (1998) studied thalli of *R. superficiale* and *Lecidea tesselata* Flörke, at different elevations in Canada and observed that the production of apothecia was lower at high altitudes where conditions were growth limiting. In addition, thalli of *Rhizocarpon* are often smaller on rocks close to snow

patches due to reduced growing season and ground instability (Innes 1985). At some sites, however, the effects of increasing moisture balance 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 *Rhizocarpon riparium* Räsänen, were less affected but some spalling of the surface of the areolae was present. In addition, photosynthesis under snow was limited due to impaired light penetration but thalli did continue to respire (Benedict 1991). This effect was demonstrated by placing lines of lichen-covered rocks in two semi-permanent snow patches. Thalli of *R. geographicum* survived 5 - 8 years 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 transects 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, the characteristic zonation of lichen communities adjacent to snow patches, is more likely to be attributable to episodic snow kill than slow growth under seasonal cover.
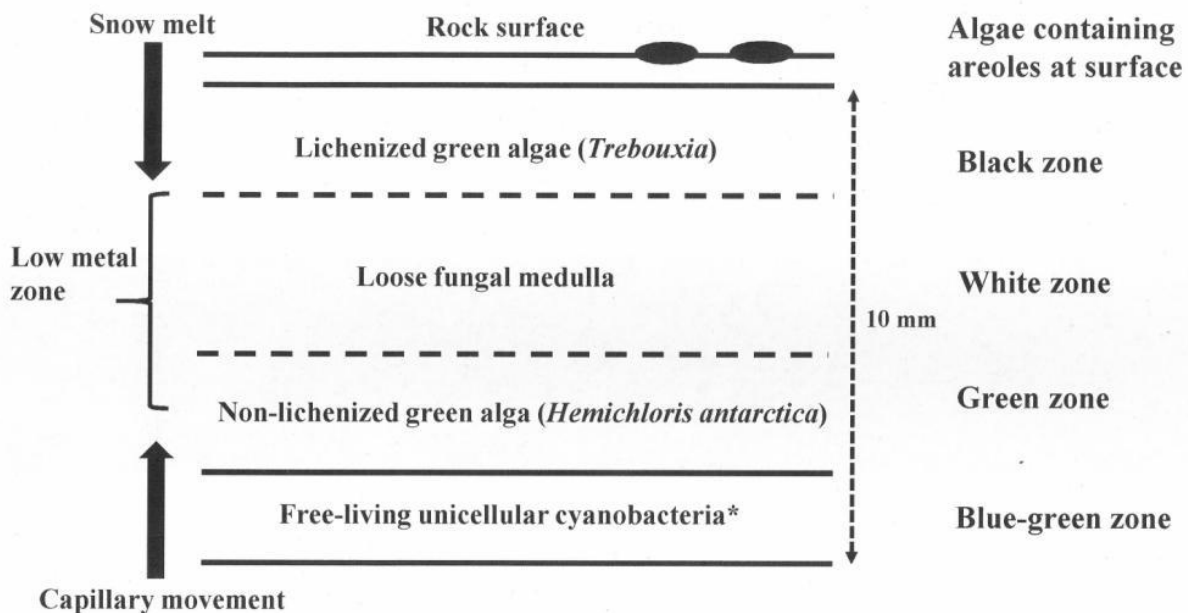

Figure 11. Vertical structure of a cryptoendolithic lichen and associated microorganisms living in the rocks of the Beacon sandstone, Antarctica (Image: R.A. Armstrong based on a description by Friedmann 1977); *Cyanobacteria present only in some samples.

The continent of Antarctica offers some of the most challenging climatic conditions for rock lichens, with overall, a two-time order of magnitude decline in lichen growth from the warmer wetter peninsula to the 'cold dry valleys' of the interior (Sancho et al. 2007). At Wilkes

Island, there is a sharp discontinuity in the distribution of lichens at the top of rocks determined by wind stress, ice blast, erosion, and low temperature effects (Bolton et al. 1989). In the most extreme rock environments, the endolithic growth form, also found in deserts, predominates (Friedmann 1977). Three types of endolithic organisms have been described (Jung & Büdel 2021): (1) 'chasmoendoliths' which occupy fissures and cracks in rocks, the organism being partially exposed on the surface, (2) 'cryptoendoliths' which occupy pores and pre-existing structural cavities, and (3) 'euendoliths' that bore into relatively soluble rock substrates such as those rich in carbonate (Lawrey 1984). Numerous microorganisms have also been recorded in the Beacon sandstone rocks of the dry valleys. Hence, cyanobacteria are often present but the dominant flora is chasmoendolithic and cryptoendolithic lichens which occupy a narrow zone of the rock subsurface 10 mm thick and form colonies from a few centimeters to a meter in diameter (Friedmann 1982). The lichens exhibit a similar structure to those living on the rock surface but a true fungal zone is often absent, the fungal hyphae filling the available pore space. In cross section (Fig 11), a typical rock consists of a black zone just below the surface containing a green alga, most frequently of the genus *Trebouxia*, and below that a white zone of fungal tissue, then a eukaryotic green layer of non-lichenized green algae (*Hemichloris antarctica* gen. et sp. nov.) (Tschermak-Woess & Friedmann 1984), and finally, in some samples, a layer of cyanobacteria. Cryptoendoliths only occasionally develop sexual reproductive structures and these usually appear on the surface of the rock as algal containing areoles (Friedmann 1982). Various metals are mobilized in the rock and are carried upwards by capillary movement and downwards by snow melt resulting in the lichen layers having low concentrations of metals. The subsurface layers are often colonized by fungal hyphae resulting in the upper surface peeling away to expose the lichen tissue. Further penetration of the rock then occurs, more rock layers being lost and the consequence of this 'biogenic weathering' is a characteristic pockmarked surface of many of the rocks.

8.2 Microclimate factors

Experiments in lichen physiology indicate that interactions between microclimatic factors such as light intensity, temperature, and moisture are important in determining lichen growth at more local levels (Farrar 1973). An experimental demonstration of the influence of moisture regime was reported by Armstrong (1976) who wetted thalli of three foliose species at intervals over a year in the field. The RaGR 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 to a maximum before decreasing on further wetting. These data show that the frequency of wetting events and the ability of thalli to dry out and recover after each wetting has a significant influence on growth. These conditions are likely to vary considerably on different surfaces.
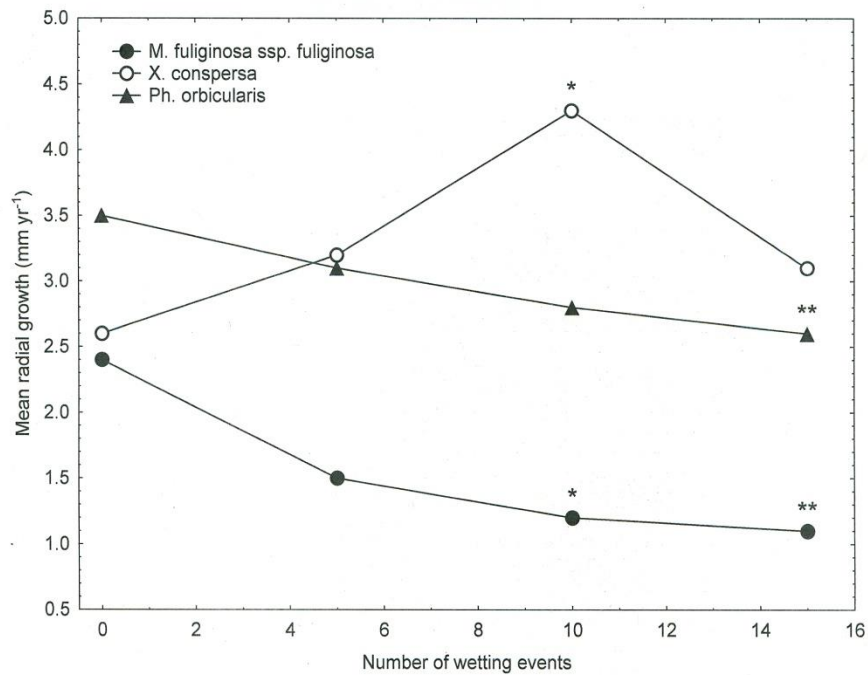
Figure 12. Influence of the frequency of wetting and drying on the radial growth of three lichens growing on slate; asterisks indicate significant differences from controls (Data from Armstrong 1976)

Many lichens exhibit distinctive distributions with rock aspect (Armstrong 1974a). Hence, at the base of grey limestone clasts, McCarthy (1997) found that the largest thalli of *Xanthoria elegans* (Link) Th.Fr. occurred on steep or overhanging facets facing south-south-east to south reflecting their higher solar input. In northwest Wales, lichens growing on slate exhibit striking aspect distributions. As an example, Fig 13 shows the distribution of two foliose species plotted as a 'polar graph' in which location on the circumference indicates compass direction and distance along radii decreasing slope towards the centre. With the exception of one site, *X. conspersa* is largely confined to south/southeast faces of variable slope whereas *Parmelia saxatilis* (L.) Ach is more widely distributed in respect to both aspect and slope. Light, temperature, and drying regimes all vary with aspect (Armstrong 1975) and slope (Sletvold and Hestmark 1998) and will influence growth. The influence of aspect on the seasonal 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 involving interactions between the levels of light, wetting frequency, and drying regime was necessary to explain growth on these two surfaces (Armstrong 1975).
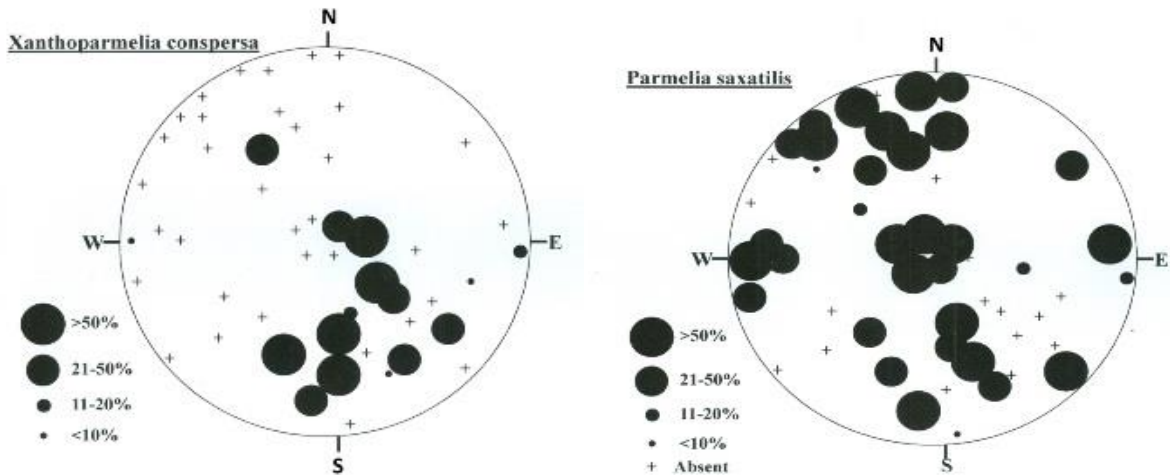
Figure 13. Polar graphs showing the contrasting distributions of two lichen species: *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale, and *Parmelia saxatilis* (L.) Ach. in relation to aspect (position on circumference) and decreasing slope (radial distance towards the centre) in northwest Wales, UK. (Data from Armstrong 1974a).

Studies have also reported the effects of aspect on the growth of crustose species. Hence, in New Zealand, Orwin (1971) found that sheltered rock facets supported most species with densest lichen cover on southerly faces. In the Brooks Range, Alaska, RaGR of *R. geographicum* at sites with high to moderate light intensities was twice that at shaded locations (Haworth et al. 1986). Similarly, in Iceland, Bradwell (2001b) reported that the largest thalli of *R. geographicum* were found on south-facing surfaces of boulders. 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. These results suggest that it is well-lit, southern-facing surfaces which are optimal for the growth of *R geographicum* (Armstrong 2005b); a likely consequence of their longer thermal operating period and higher temperatures. There is less evidence for the significant effects of slope on lichen growth. Nevertheless, in the Arctic, Link and Nash (1984) found that slope played a major role in determining the composition of lichen communities.

Lichens exhibit significant changes in abundance with height on rock surfaces (Armstrong 1974b). Hence, in Ontario, Canada, Yarranton and Green (1966) studied the spatial pattern of lichens on limestone cliffs and observed changes in abundance with height on the face which they attributed to microclimatic gradients and variations in slope. In addition, the distribution of lichens was studied on cliffs of the Big South Fork National River and Recreation area in Tennessee, USA, large differences in distribution being observed both across and within transects (Boggess et al. 2017). Changes in percent cover of two foliose species on a rock surface in northwest Wales are shown in Fig 14. The distribution of *Xanthoparmelia conspersa* (Ehrh ex Ach) Hale, was fitted by fourth-order polynomial curve indicating a bimodal distribution, maximum peaks of cover being located in the upper and lower regions of the rock surface, both

peaks being of similar magnitude The distribution of *Melanelia fuliginosa ssp fuliginosa* was also fitted by a fourth-order polynomial (r = 0.57, P < 0.05) with peaks of cover in the middle and lower regions of the face, the upper peak being significantly larger than the lower peak. The larger peak corresponds to a region of the surface where *X. conspersa* is least abundant suggesting possible competitive effects.
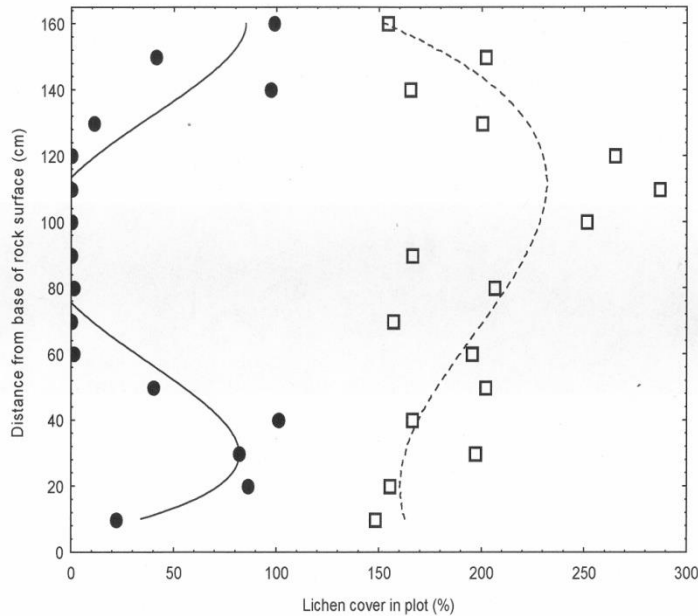

Figure 14. Vertical distribution (% Cover) of two foliose lichen species, viz. *Xanthoparmelia conspersa* (dark circles) and *Melanelia fuliginosa ssp. fuliginosa* (open squares) on a slate rock surface in northwest Wales. (Data from Armstrong 1974b)

Vertical distribution of lichens on trees has been largely explained by the influence of microclimatic gradients, especially of light intensity and water availability, both of which change with height and are known to effect lichen physiology (Harris 1971b, Armstrong 1975) but there are few comparable data for rock surfaces. Vertical distribution on rocks could also reflect variation in the degree of exposure to wind, which is related to height above the ground (Hess 1959), and which may affect drying rates (Armstrong 1976). Vertical distribution could also vary with aspect of the surface, as accelerated weathering may occur on more northerly faces due to more prolonged wetting and drying cycles (Armstrong 1976) while on southerly sunlit surfaces increasing solar flux may cause more rapid heating and cooling cycles (Paradise 2013).

Microclimate can also act on very small scales to influence lichen distributions. Hence, in the Negev desert, lichens on cobbles are exposed to twice the average daily dew at the top compared with the margins resulting in a zonation (Kidron 2002). In addition, there was greater moisture at the margins of partially embedded cobbles after rain which was attributable to water capillary rise. This study emphasises that distinct environmental gradients may be influence lichens at very small scales.

8.3 Substratum factors

The physical and chemical nature of the substratum has a profound influence on lichens (Brodo 1973, Easton 1994). Some aspects of the influence of the substratum have been investigated experimentally by transplant experiments in which thalli are removed from one surface and 'glued' to another (Armstrong 1993). Usually this type of experiment has been carried out with foliose species, it not being possible to separate most crustose species intact from their substratum.

Data suggest rough-textured rock surfaces have a richer lichen flora than smooth, the latter constituting a more extreme environment especially for the attachment of propagules (Brodo 1973). Crustose species such as *R. geographicum* appear to be able to grow on a wide variety of siliceous rocks of different textures (Innes 1985). Nevertheless, *R. geographicum* thalli do not appear to grow well on substrata that weather rapidly or which are susceptible to frost shattering (Caseldine 1995, Cerrara and Andrews 1973). In addition, observations suggest *R. geographicum* may exhibit faster growth rates on sandstone than gneiss (Belloni 1973) and on andesite compared with granodiorite (Porter 1981). By contrast, there was little variation in growth of *R. geographicum* on two slate rock surfaces in northwest Wales which differed in both porosity and texture of the surface (Armstrong 2014). Benedict and Nash (1990) studying the genus *Xanthoparmelia*, found that *X. subdecipiens* (Vain.) Hale, was predominant on dark coloured biotite gneiss while *X. lineola* (E.C. Berry) Hale, was found on light-coloured granodiorite and quartz. In an area of south India, significant trace element differences were observed among charnokite, granite, quartzite, and gneiss rocks with some species, e.g., *Flavoparmelia caperata* restricted to gneiss while *Heterodermia leucomeles* was able to colonize charnokite, granite, and quartzite (Rajendran et al. 2020).

The lichen flora of lime-rich rocks differs significantly from that of lime-poor, siliceous rocks and there are few species able to grow successfully on both (James et al. 1977, Hill 1994). To test the hypothesis that rock chemistry influences growth, fragments were cut from the perimeters of several foliose lichens and glued onto different substrata which included slate, granite, cement, and asbestos (Armstrong 1993). The data for two foliose species (Fig 15) suggest growth of *X. conspersa* was inhibited on the calcium-rich compared with the siliceous substrates while *Xanthoria parietina* (l.) Th. Fr., would only grow on the calcium-rich substrata, the fragments initially becoming discoloured and then fragmented on lime-poor substrates.
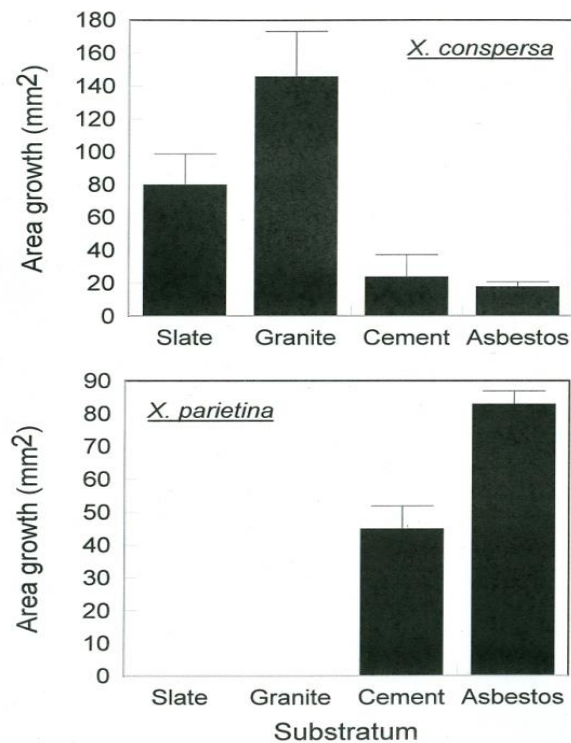
Figure 15. Growth of *Xanthoparmelia conspersa* and *Xanthoria parietina* on different substrata in northwest Wales. (Data from Armstrong 1993).

Xanthoria parietina in the UK is often considered to be a nitrophilous species as it is found most commonly in nitrogen-rich habitats (Armstrong 1990). Nevertheless, a requirement for calcium could also explain many aspects of its distribution as it occurs on limestone rocks and walls, wall mortar, asbestos roofs, tree bark where stemflow is enriched with calcium, and siliceous rocks close to the sea, calcium being common to all of these environments (Armstrong 1990). By contrast, *P. saxatilis* is virtually restricted to acid substrata, thalli of this species adopting a 'crescent-shaped' form after treatment with calcium carbonate, after which the thalli often fragment and disappear from the surface (Armstrong 1990). Treatment with a 0.250 mM solution of calcium as calcium chloride has little effect on growth of *P. saxatilis* (Fig 16), however, suggesting that this species may tolerate mildly alkaline conditions. Gilbert (1971) found that *P. saxatilis* could occur at more alkaline sites in polluted environments. Zinc, copper, and mercury in rocks may also influence lichen growth and can affect the chlorophyll content of lichen algae (Backor and Djubai 2004).
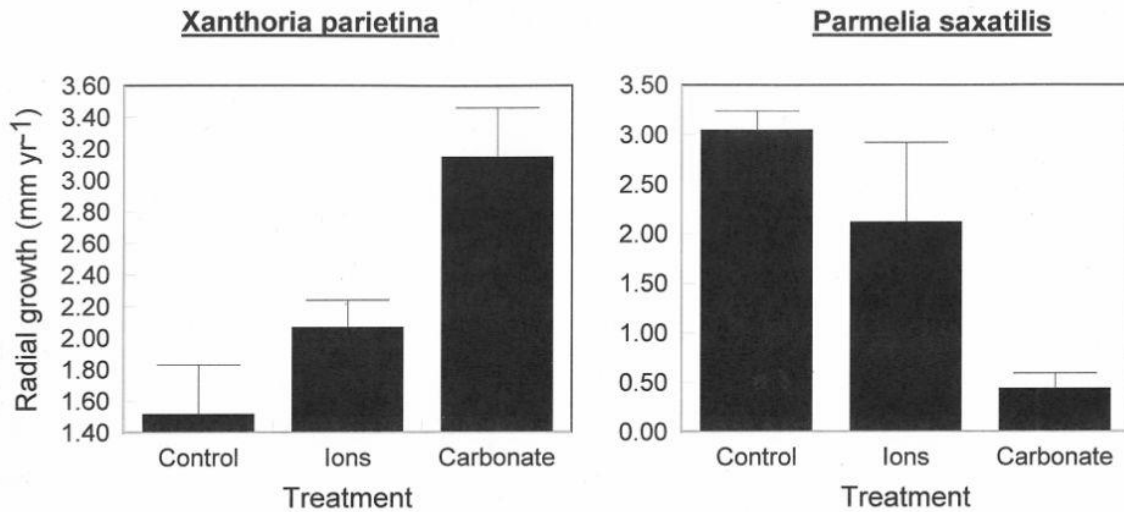
Figure 16. Effect on growth of treating *Xanthoparmelia conspersa* and *Xanthoria parietina* thalli with calcium carbonate paste (carbonate) and a solution of calcium chloride (ions). (Data from Armstrong 1990).

The degree of nutrient enrichment of a substratum, especially by bird droppings, has a particularly significantly affect on lichen growth (Hale 1967). Bird droppings may influence growth by a variety of means including covering the thalli and reducing light levels, altering the pH, and by adding compounds that directly stimulate or inhibit growth (Armstrong 1984). In a growth experiment, droppings were collected from a variety of bird-perching sites in northwest Wales and applied either as a thick paste or a suspension in deionized water to several foliose lichens (Armstrong 1984). Treatment with bird droppings increased the growth of *X. conspersa*, a species often present on well-lit, nutrient enriched rocks while the suspension inhibited growth of *P. saxatilis* a species which is less common on bird perching stones. Treatment with uric acid, the most abundant nitrogenous component of bird droppings, did not influence growth of either species (Armstrong 1984) indicating the effect of bird droppings was likely to be attributable to either an increase in pH or to the addition of active chemicals.

There have been few experiments on the influence of nutrient enrichment on the growth of crustose species. At Signy Island in the Maritime Antarctic, however, lichen growth at sites enriched by nitrogenous compounds derived from sea birds was rapid, and especially that of *Acarospora macrocyclos* Vain. and species of *Buellia* De Not. and *Caloplaca* Th.Fr. (Smith 1995). In addition, different maritime lichen communities with and without overhead seabird colonies were compared by Wootton (1991). In the presence of bird droppings, the vertical distribution of the orange lichen zone dominated by *Xanthoria elegans* (Link) Th.Fr. and *Caloplaca marina* Wedd. was elevated on the shore while that of the grey lichen zone dominated by *Physcia* species, was eliminated. In the splash zone, *Verrucaria mucosa* Wahlenb. Ex Ach. declined as a result of enhanced competition with the green alga *Prasiola*. Furthermore,

there was evidence to suggest that *X. parietina* (which only reproduces sexually) parasitizes the algal component of *Physcia* species in an effort to promote its dispersal (Ott 1987). Such competition effectively removes some *Physcia* species from rocks colonised by *X. parietina*.

Figure 17. Vertical zonation on a boulder on the seashore with from bottom to top: barnacles and brown seaweed, a black lichen zone (*Lichina* sp.), an orange zone (*Caloplaca marina*), and a grey zone. (Image: Taken by Dr. K.M. Wade; R.A.Armstrong lichen archiv)

Maritime rock surfaces, where a characteristic zonation of lichens occurs (Fig 17), may be influenced by several complex chemical interactions (Hakulinen 1966, Fletcher 1976). Hence, although calcium was shown experimentally to be an important ion in these environments, salinity exerted less effect, the species responding more to length of immersion by the tides (Fletcher 1976). By contrast, Ramkaer (1978) found that the response of four different lichen fungi to salinity correlated well with the zonation of the lichens, in which they were the fungal partner, 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 suppralittoral (Fletcher 1976) and many nutrient enriched sites inland (Brodo 1973), however, was inhibited when transplanted from the seashore to an inland site (Armstrong 1990). The transplanted thalli grew successfully at inland sites only when calcium carbonate was added as a paste to the thalli over one year, a 0.250 mM solution of calcium chloride having little benefit. A constant supply of calcium may be necessary for successful growth of this species. Experiments have demonstrated that *X. parietina* thalli lose potassium ions after treatment with distilled water whereas an application of a 0.250 mM calcium

solution prevents this loss in the light and support this contention (Fletcher 1976). By contrast, addition of calcium carbonate to the calcifuge species *P. saxatilis* significantly inhibited growth which may explain its absence from lime-rich rocks (Armstrong 1990).

A zonation of lichens also occurs on rocks bordering freshwater streams, ponds, and lakes (Reid 1960). Four main zones of lichen vegetation were described from several sites in Europe, each composed of a characteristic group of species. The limits of each zone show a marked relationship with the length of time each year the species were moistened or submerged by the water (Reid 1960).

9. Competition

Within a single climatic region, each type of rock surface tends to assume eventually a characteristic assemblage of species but variations within such a region occur and are often interpreted as attributable to competitive effects (James et al. 1977). Competition among lichens, however, has not been frequently studied experimentally, in part because of the perception that lichens are 'stress-tolerant' rather than 'competitive' organisms (Grime 1979; Lawrey 1984) and the difficulties in setting up such experiments.

Evidence both for and against competition on rocks has emerged from studies of lichen succession. On rocks in New Zealand (Orwin 1970), for example, crustose species are often the first colonizers of freshly deposited surfaces usually within five years of exposure, foliose species appearing only after an initial 'crustose' phase. Once present, however, individual species tend to persist throughout the succession and their frequency increases with increasing surface age rather than being lost by competition. A similar pattern was observed on rocks in Ontario, Canada (Woolhouse et al. 1985) resulting in an increase in diversity over time. These types of succession are often attributed to 'allogenic' processes, such as the gradual physical and chemical weathering of the rock (Syers and Iskander 1973, Tansey 1977). Nevertheless, the contribution of these processes to actual rock weathering is controversial (Lawrey 1984), with dissolved respiratory carbon dioxide being regarded by some authors as more important (Tansey 1977).

In many rock communities, there is a significant amount of bare surface which remains unoccupied by lichens even at sites which have been exposed for many years (Woolhouse et al. 1985) (Fig 18). A proportion of this bare space may be attributable to lichen mortality. The apparent 'death' of a lichen thallus is often preceded by a period of senescence characterised by fragmentation. This process results in new areas becoming available for colonization but is also an indication that the intensity of competition for space may be reduced in more advanced communities. By contrast, studies of the Jonas Rockslide in the Canadian Rocky Mountains showed that competition played a significant role in the patterning of the species (John 1990). Similar conclusions have been reported by Reid (1960) and Yarranton & Green (1966) from studies of the zonation of lichen vegetation on rocks bordering streams and the pattern of vertical distribution on cliffs at Rattlesnake Point, Ontario respectively.

Figure 18. Fragmentation of the centre of thalli of *Melania fuliginosa ssp. fuliginosa* (Fr. ex Duby) Essl. with evidence of re-colonisation of the centre (North Wales, UK). (Image: taken by Dr. K.M. Wade; R.A.Armstrong lichen archiv)

Consideration of aspect distributions has also provided evidence for competitive effects. Hence, in northwest Wales, the growth of foliose lichen species transplanted to north and south-facing rock surfaces was studied (Armstrong 1977). Growth of *X. conspersa* and *Ph. orbicularis* was significantly reduced when transplanted to north-facing compared with south-facing surfaces consistent with their distributions on well-lit rocks. By contrast, thalli of *P. saxatilis* .grew equally well when transplanted to north and south-facing rock surfaces whereas this species is found predominantly on north-facing slopes at the site. The implication is that *P. saxatilis* is eliminated from south-facing rocks as a result of competition from faster-growing foliose species (Armstrong 1977). The crustose lichen *Rhizocarpon geographicum* (L.) DC. is abundant on south-facing rock surfaces at the same site but can also be observed on some north-facing rocks (Armstrong 1974a) where significantly more competitors are present (Armstrong 2002). The mean frequency of the competitors, however, is significantly lower on the surfaces where *R. geographicum* is present. This suggests that the intensity of competition within a 'multi-species' community is greater on some north-facing surfaces, reducing the effectiveness of the strongest competitors, and favouring the survival of *R. geographicum* (Armstrong 2002).
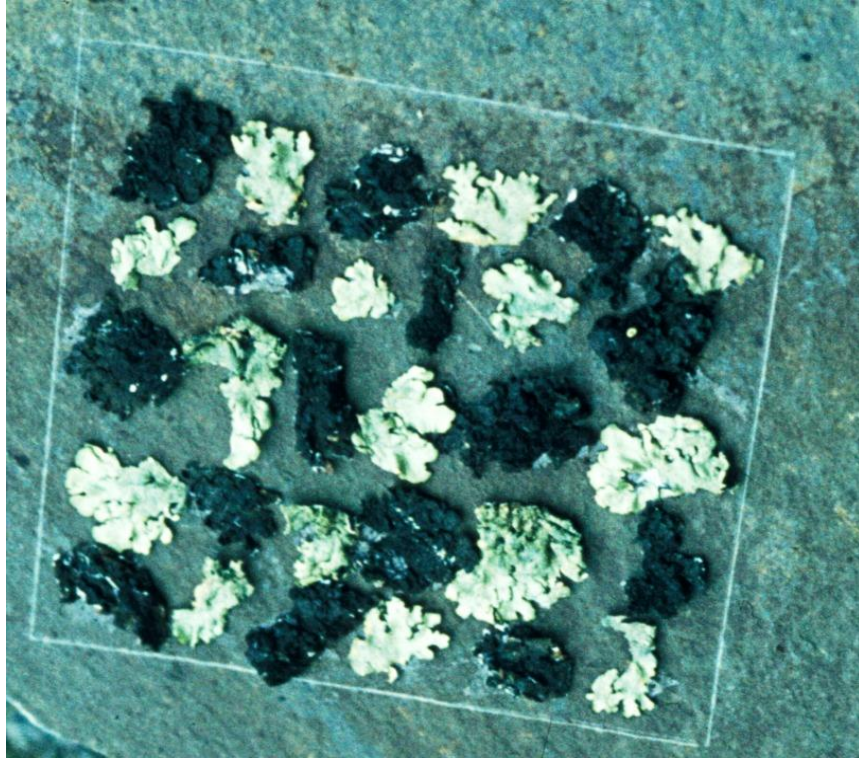
Figure 19. Lichen competition experiment: fragments of thalli of *Xanthoparmelia conspersa* (light) and *Melania fuliginosa ssp. fuliginosa* (dark) glued in an alternating pattern in an experimental plot marked out on a piece of slate. (Image: taken by Dr. K.M. Wade; R.A.Armstrong lichen archiv)

Useful insights into the importance of competition among lichens on rock surfaces has come from experiments in which fragments of various foliose thalli are glued in various combinations in experimental plots in the field (Fig 19) (Armstrong and Welch, 2007). Armstrong (1991c) studied competition between four foliose lichen species in experimental plots facing north and south (Fig 20). In south-facing plots, the growth of *X. conspersa* was not affected by any of its competitors but the growth of this species was reduced by *P. saxatilis* in north-facing plots. *P. conspersa* is a characteristic species of well-lit, south facing rock surfaces at the site (Armstrong 1974a) and therefore, competition with *P. saxatilis* may be important in determining the low frequency of this species in north-facing plots. In a further experiment (Armstrong 2000), the same four species were grown in well-lit plots with and without nutrient enrichment by bird droppings. In monoculture, addition of bird droppings increased the growth of *P. conspersa*, decreased that of *P. saxatilis* and *P. glabratula ssp. fuliginosa* while the growth of *P. orbicularis* was unaffected. In the mixtures, *P. conspersa* and *P. orbicularis* were equally effective competitors in plots with and without nutrient enrichment but addition of bird droppings reduced the ability of *P. glabratula ssp. fuliginosa* and *P. saxatilis* to compete with the other two species. Hence, nutrient enrichment altered the competitive balance between the four species suggesting that a different combination of species would occur on nutrient rich and poor

rocks. Therefore, nutrient application, by increasing the growth of some species and reducing the growth of others, may increase the chance of competitive exclusion and reduce the species diversity of a site (Lawrey 1981, Vagts & Kinder 1999).
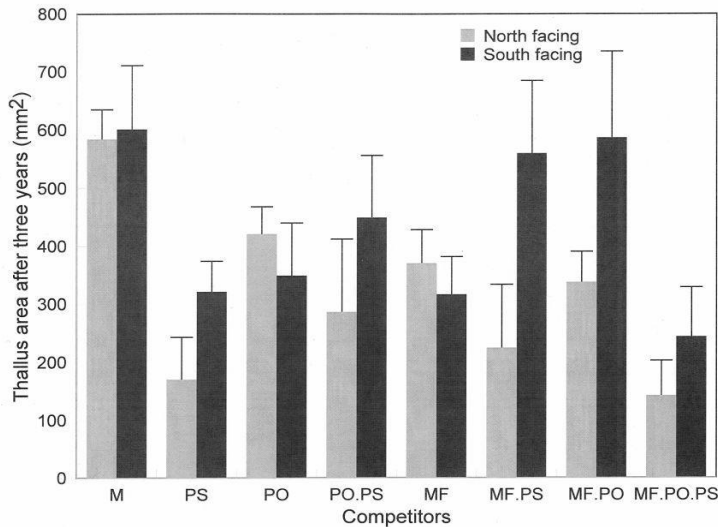

Figure 20. Competition beween *Xanthoparmelia conspersa* and three other foliose species: *Parmelia saxatilis* (PS), *Phaeophyscia orbicularis* (PO), and *Melania fuliginosa ssp. fuliginosa* glued to pieces of slate and oriented in a northerly and southerly direction (data from Armstrong 1991c).

Species such as *Rhizocarpon* are slow-growing and therefore, potentially can be out-competed by faster-growing foliose species. Alternatively, different species growing together may achieve a state of 'equilibrium' (Pentecost 1980, Armstrong and Welch 2007). Hence, Hawksworth and Chater (1974) observed that *Ochrolechia parella* (L.) A. Massal., thalli overgrew those of *R. reductum* but reached an equilibrium with *Lecanora gangaleoides* Nyl. Malinowski (1911) observed thallus overgrowth in six crustose species on rock and comments on the importance of this phenomenon in lichen community dynamics. Crustose species, however, are often dominant, not only on recently exposed surfaces, but also on more mature faces. In New Zealand, species of *Rhizocarpon* achieve dominance on many rock surfaces and occur on a greater number of rocks than any other species (Orwin 1970). The abundance and widespread distribution of *Rhizocarpon* could be attributable to its high tolerance of harsh conditions but it is also possible that it may have a competitive advantage due to the production of toxic chemicals ('allelopathy') (Fig 21). Some species of *Rhizocarpon* are surrounded by bare 'zones of inhibition' 1 – 5 cm wide (Beschel and Weideck 1973, Benedict 2009). Faster-growing foliose species that invade this space often disintegrate on its outer rim suggesting an allelopathic effect (Beschel and Weideck 1973). The potential role of allelopathy as a factor determining the

outcome of competition on rocks has been little studied experimentally and therefore, its potential ecological significance remains unknown (Armstrong and Welch, 2007).

Figure 21. Fragmentation and discolouration of thalli of the foliose species *Parmelia saxatilis* as it grows in the vacinity of the crustose lichen *Rhizocarpon geographicum* suggestive of an allellopathic effect. (Image: Taken by Dr. K.M. Wade; R.A.Armstrong lichen archiv)

10. Senescence and mortality

As an established lichen thallus grows to maturity, there is an increasing risk of mortality attributable to age-related processes or catastrophic environmental effects. Understanding the processes of mortality is a significant part of the study of 'population dynamics' of a species, but this type of study has rarely been carried out in lichens. An important sign of mortality, as a consequence of senescence, is fragmentation which usually begins in the thallus centre and gradually spreads to affect the perimeter (Armstrong and Smith 1997). Hence, McCarthy (1989) observed in the crustose species *O. parella*, that all thalli with evidence of fragmentation completely disappeared from the rock after 26 months. In northwest Wales, the percentage of foliose thalli with fragmenting centres increased with size, the size class at which 50% and 100% of thalli were fragmenting differing significantly among populations (Armstrong and Smith 1997). Hence, the size-frequency distribution of thalli with fragmenting centres could be used to study the pattern of mortality in a lichen population. Examples of 'survival curves' for two contrasting populations of *R. geographicum* growing in northwest Wales, based on the size-frequency distribution of fragmenting thalli, are shown in Fig 22 (Armstrong 2017). In population A, 75% of thalli ≤ 3.0 cm had fragmenting centres and the estimated maximum

thallus diameter (TDmax) in the population was 4.5 cm while in population B, 75% of thalli ≤4.25 cm were fragmenting and TDmax was 7.5 cm. These data suggest that at sites in northwest Wales, there is significant mortality of *R. geographicum* and the probability that an individual thallus will survive to achieve a larger size quite low.
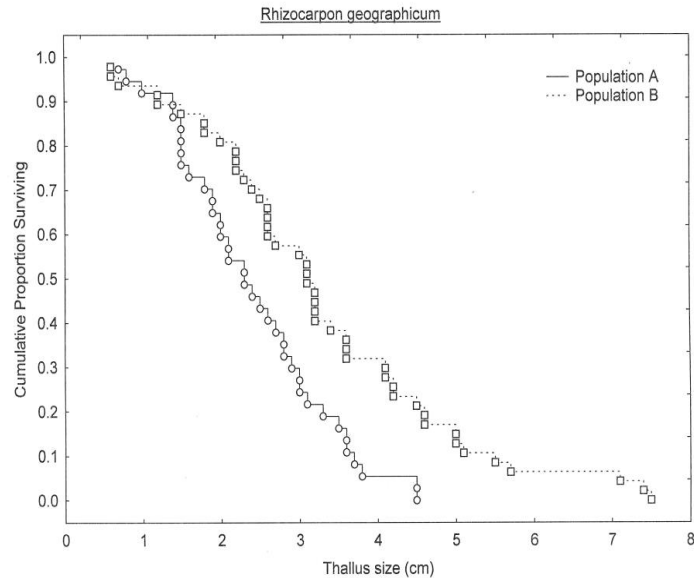

Figure 22. Survival curves of two *Rhizocarpon geographicum* populations (A,B) growing on slate rock surfaces in northwest Wales based on the Kaplan-Meier estimator (Data from Armstrong 2017).

In a larger-scale study in northwest Wales, fragmentation rates were studied in 21 populations of three foliose lichens, viz. *X. conspersa*, *M. fuliginosa ssp. fuliginosa*, and *P. saxatilis,* and the crustose species *R. geographicum* (Armstrong 2017). Significant differences in fragmentation rates among populations were again present in three of the four species. In addition, in *M. fuliginosa ssp. fuliginosa,* regression analysis suggested higher rates of fragmentation on rocks with a greater percent lichen cover and increased diversity. Slope angle, aspect, texture, and location of a population relative to the sea also influenced fragmentation rates. The data suggest considerable variation in mortality among populations within the same area which could be determined primarily by the intensity of competition.

On coastal cliffs in Scandinavia, Hestmark (1997) demonstrated how thalli of *Lasallia pustulata* (L.) Mérat, were subject to disturbance and were removed thus creating gaps which were major sites of recruitment; the age-size structure of the population being spatially structured by the pattern of gap formation. Fragmentation of members of existing populations therefore may be an essential feature of how lichen communities are maintained on rocks, first, by supplying new safe sites on the surface for the establishment of propagules and second, by producing a ready supply of thallus fragments for colonization.

A further indication of the degree of mortality in lichen populations is the rapidly diminishing frequency of thalli in successive size classes (Armstrong 1974b). Absence or low frequency of thalli within a particular size class may be an indication of a catastrophic event in the past. Hence, at seven sites in north Iceland, Caseldene and Baker (1998) studied the size-frequency distribution of *R. geographicum*. All frequency distributions were similar but with a consistent pattern of disruption at specific size classes corresponding to four periods over the last 120 years in which 80-100% of the thalli were lost. Such mortality was attributable to snow kill or competition.

11. Succession

If all stages of the lichen life cycle are successful, then a species will colonize a significant part of a rock surface. Change in species composition of lichens on a surface over time is known as 'succession'. The potentially long time periods over which this process takes place on rocks, however, makes it almost impossible to study directly either by observing newly-exposed surfaces or by clearing lichens on established surfaces in permanent plots and studying their redevelopment (Armstrong 1974b). Lichen succession has been studied by investigating surfaces of different age of exposure (cross-sectional study) (Degelius 1964, Beschel 1965, Orwin 1970) or by studying a 'zonation' where environmental gradients have rendered a temporal succession spatially (Karenlampi 1966). As a result, there is a degree of uncertainty regarding the duration of any 'lag phase' before colonization begins, the likely sequence of species during succession, and more specifically, the relative role of crustose and foliose species (Armstrong 2011). In the eastern Nearctic, for example, Beschel (1965) observed that crustose species, such as *R. geographicum,* were not the first colonizers but often replaced earlier faster-growing species. Similarly, in north Wales, Winchester and Chaujer (2002) suggested there may be a delay of at least 18 years before the colonization of gravestones by *R. geographicum.*

Different species within a genus may colonize a rock surface at different rates. Hence, species of the genus *Rhizocarpon* in the section *Rhizocarpon* may establish earlier than those in section *Alpicola*. Nevertheless, *R. alpicola* (Anzi) Rabenh., exhibits faster growth than those in the *Rhizocarpon* section and often becomes the predominant species (Innes, 1985). Colonization may also occur continuously or intermittently. In southeast Norway, Innes (1986) studied the size-frequency distribution of thalli of *R. alpicola* and showed that colonization only occurred during limited periods. In addition, colonization was apparently restricted at the time of observation, even on relatively young surfaces. Further studies on gravestones in highland Scotland also revealed that establishment was erratic and that a minimum period of exposure was necessary before colonization (Innes 1983). Erratic establishment and colonization by the foliose lichen *Xanthoparmelia cumberlandisma* (Gyeln.) Hale, has also been observed in a Tulsa cemetery, recruitment being particularly sporadic (Golm et al. 1993).
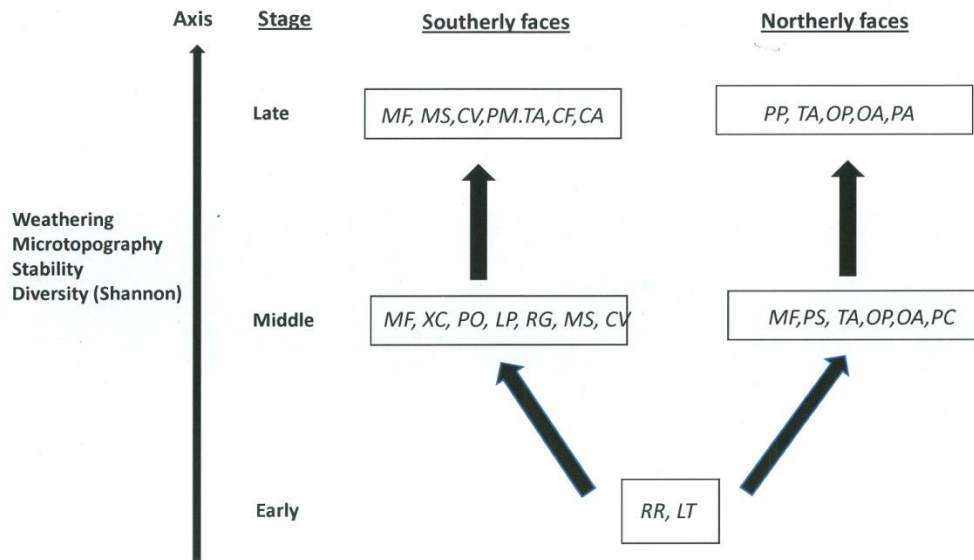
Fig 23. Possible pathways of successsion on northerly and southerly slate rocks in north Wales based on a cross-sectional study of 79 rock surfaces. Abbreviations: *RR = Rhizocarpon reductum, LT = Lecidea tumida, MF = Melanelia fuliginosa ssp. fuliginosa, XC = Xanthoparmelia conspersa, PO = Phaeophyscia orbicularis, PM = Porpidia macrocarpa, TA = Tephometra atra, MS = Myrospora smaragdula, CF = caloplaca ferruginea, CA = Cornicularia aculeata, CV = Candellariella vittelina, PS = Parmelia saxatilis, OP = Ochrolechia parella, OA = Ochrolechia androgyna, PC = Pertusaria corallina, PP = Parmelia pastillifera* (Based on Armstrong 1974b, Chapter 7).

On rocks in New Zealand, the number of lichen species and degree of lichen cover are both positively correlated with surface age, some of the variation in species among resulting communities being attributable to the surface area of the rock available for colonization (Orwin 1970). Hence, the smaller the surface area, the more profound the effect of a strong competitor thus potentially reducing species diversity. On rocks in Ontario, Canada, Woolhouse et al. (1985) demonstrated an increase in diversity over time but with a persistent percentage of bare rock present at the oldest sites. The succession appeared to be determined by a combination of allogenic processes and competitive effects, a considerable mortality at older sites creating bare rock. There is also further evidence that crustose species are not always the first colonizers. Hence, in the study of Woolhouse et al. (1985), *R. geographicum* was not present on the youngest (5 years) or oldest (40 years) surfaces, but on surfaces of intermediate age, maximum thallus area and number of individuals being observed on approximately 30 year-old surfaces.

On slate rock surfaces in north Wales, UK, a cross-sectional study ordered 79 different rock surfaces along an axis reflecting increasing degrees of rock weathering, microtopography, stability, and diversity, the latter measured as the Shannon index, all of which were assumed to increase with age of exposure of the surfaces (Armstrong 1974b). Changes in the abundance of various species along this axis may be indication of the general pathways of succession on slate

rock in northwest Wales. A possible scheme is outlined in Fig 23 which shows the possible pathways of succession on rocks facing in southerly (SE, S, SW) and northerly (NE, N, NW) directions often associated with large differences in the lichen flora (Armstrong 1974a). An early crustose phase comprising *Rhizocarpon reductum* and *Lecidea tumid*a occurs on both north- and south-facing surfaces but the lichen flora the apparently diverges as they age. On southerly faces, the early crustose phase is invaded by foliose species, e.g., *M. fuliginosa ssp. fuliginosa*, *X. conspersa*, and *Ph. orbicularis* and a variety of further crustose species. In the later stages, some of the foliose and crustose species are lost which some new species appear for the first time, e.g., *Caloplacan ferruginea* Th. Fr. and *Cornicularia aculeata*. (Schreb.) Ach. The sequence on northerly rocks is similar but with some differences in detail of the crustose species represented. Hence, an early crustose phase leads to the development of communities of mixed foliose and crustose species but crustose species may predominate in the later stages as many of the foliose species decline. In addition, on some particularly unstable surfaces, the earliest stages often persist without further development ('arrested succession') while on surfaces of more moderate slope, bryophytes and flowering plants eventually invade and may terminate the lichen succession.

The development of lichen communities on rock may be influenced by three further processes. First, there are changes in abundance with height on vertical or near vertical surfaces (Yarranton and Green 1966, Armstrong 1974b, 2014) suggesting a microclimatic gradient down the surface (Hess 1959, Harris 1971, Armstrong 2014). On near vertical slate rock surfaces in northwest Wales, however, *R. geographicum* can exhibit quite different vertical distributions at sites a short distance apart (Armstrong 1974b), i.e., exclusively present at the top of one face whereas on an adjacent face, there is a peak of abundance close to the top but then a declining trend of abundance down the face. Furthermore, there may be a consistent change in thallus size from top to bottom on some faces, largest thalli occurring at the top associated with little significant difference in growth with height on the face (Armstrong 1978, 2014). These results support a process of colonization by species which takes place from top to bottom. There may be successive waves of this colonization as succession proceeds, each species establishing on the upper part of the face at first and then spreading gradually downwards. The subsequent influence of environmental gradients and increasing competition on the face may then modify these vertical distributions resulting in the observed and often unpredictable outcomes on adjacent rock surfaces.

Second, on more unstable substrata, such as shale and slate, more unstable portions of the rock surface may weather and flake off (Armstrong 1974b, Innes 1985). The results of the weathering process can be observed beneath lichens and is characterised by mineral dissolution and crumbling (Bjellend et al. 2002). The lichen thallus and endolithic fungal hyphae can bind partly fragmented rock to protect it from abrasion and erosion. When a lichen thallis dies, however, loose mineral grains and fragments of the lichen-mineral interface are removed creating a new surface for colonization. As a result, a surface over time may become a mosaic of different ages adding further complexity to the interpretation of the lichen succession (Fig 24) as

different stages could coexist on the same surface. Significant variations in lichen size over a rock surface could be partly explained by this process (Armstrong 2014).

Figure 24. Cross-bedding and flaking (Arrows) of Ordovician-age slate rock in North Wales, UK, resulting in a surface made up of a mosaic of different ages. (Image: Taken by Dr. K.M. Wade, R.A. Armstrong lichen archiv).

Third, there may be natural cyclic changes in abundance of lichens on rock surfaces over time. Hence, Hale (1967) observed cycles in percent surface cover of the foliose species *X. conspersa* with a wavelength of at least 20 years suggesting the population exhibited both building and declining phases. How frequent these changes are on rock surfaces and whether they are properties of the dynamics of the lichen population, e.g. cyclic changes in mortality and re-colonization, are unknown.

12. Future research

Although progress has been made in understanding the ecology of lichens on rock surfaces over the last fifty years, there are many gaps in knowledge. First, the duration of the time interval between surface exposure, actual colonization, and the appearance of the first 'identifiable' lichen thalli are uncertain for many types of substrata. There have also been few experimental studies on the early developmental stages of colonizing species, including the

majority of crustose species, and therefore, little information on how to recognise and identify the first colonizers of recently exposed surfaces. There is also little consensus on whether crustose or foliose species or both are the first colonizers of a face.

Second, how lichens disperse their propagules from one rock surface to another, the propagules involved, and the agents of dispersal is unknown for many species. Although some of the processes which take place during early colonization of a rock surface have been studied, e.g., the possible spread down the rock, there are likely to be many others so far not investigated.

Third, the factors that determine the critical stages of attachment, establishment, and survival of propagules remain to be established. Micro-texture of the surface appears to be an important factor during attachment but the relative role of other factors such as the presence of bird droppings or mollusc slime trails is unknown.

Fourth, there is uncertainty regarding how lichens grow to maturity, i.e., the shape of the growth curve over time from initial establishment to the development of mature reproductive thalli. There are data for some crustose species such as *Rhizocarpon*, (Armstrong 2005b), foliose species such as *X. conspersa* (Armstrong and Bradwell 2011), and placodiod species such as *Buellia canescens* (Proctor 1977, Hill 1981). These growth curves are usually based on measurements made over short intervals of time on samples of thalli of different size (Trenbirth and Mathews 2010, Armstrong 2014) and suffer the limitation that between-thallus variability in growth is often larger among similarly-sized thalli than the growth-size fluctuations themselves (Armstrong 2014). Hence, in species of *Rhizocarpon,* a number of different models have been proposed for the shape of the lichen growth-rate size curve (Bradwell and Armstrong 2007, Trenbirth and Matthews 2010) including parabolic, linear, or increasing RaGR over time. It is also possible that a species exhibits different types of growth curve at different sites or even at the same site in successive years (Trenbirth and Matthews 2010).

Fifth, the quantitative analysis of plant growth ('plant growth analysis') has long been valuable in understanding how higher plants grow and in studying the influence of the environment (Hunt 1978, Evans 1983). In the 'classical' approach, growth events are followed over time often using infrequent large harvests and considerable replication. By contrast, in the 'functional' approach, harvests are often smaller with less replication but are more frequent. Although studies have been carried out on lichen growth in the field under a range of environmental conditions (Armstrong and Bradwell, 2010, 2011, Armstrong 2015), there has been little attempt to adapt and apply formally the methods of growth analysis specifically to lichens ('lichen growth analysis') which would be of considerable benefit in the study of environmental effects. A recent attempt to apply such methods specifically to lichens has been published by the author (Armstrong 2022).

Sixth, both foliose and crustose species exhibit seasonal fluctuations in growth and significant annual variations in growth (Armstrong 1973, 2006). These variations may correlate with specific climatic and microclimatic factors (Armstrong 2006, Trenbirth and Matthews 2010) and further studies of such relationships and their interactions are needed to enable the effects of climatic and microclimatic variations between rock surfaces to be taken into account.

Seventh, there can be substantial mortality of young thalli on a rock (Loso and Doak 2006) resulting in relatively few survivors of the first colonists. Whether or not any of the initial colonizers actually survive to maturity will depend on the shape of the mortality curve of the population, a factor little studied in lichens. Hence, further studies of thallus senescence, mortality, and survival on a variety of surfaces are needed to establish demographic models, and possibly 'life tables', for lichens (Loso et al. 2014).

Eighth, there has been debate regarding the impact of competition on the processes of colonization, growth, and mortality in lichen ecosystems (Armstrong and Welch 2007). On older surfaces, increased competition can lead to overgrowth, mortality, cessation of growth, or the formation of lichen 'mosaics' (Pentecost 1980, Armstrong and Welch 2007). Hence, Bradwell (2010) measured the growth of *R. geographicum* at two contrasting sites in Scotland, and found that more intensive competition at one site ruled out a meaningful comparison between the two. In addition, the rate of lichen growth may decline on older surfaces as a consequence of increased competition (Gellatly 1982). Increased competition may also be a factor determining variability of lichen sizes and lower growth rates on older surfaces. Although experimental studies of lichen competition on rock involving foliose species have been reported (Armstrong and Welch 2007), there are have been no comparable studies involving crustose species or of the competitive interactions among foliose and crustose species.

Ninth, there are few data regarding how lichens colonize a surface, at which stage of a succession, and whether there are natural cyclic changes in abundance over time (Hale 1967). Existing data suggest that crustose species may not necessarily be the first colonizers (Orwin 1970) and that lichens may establish on the upper part of a face initially and subsequently spread from top to bottom over the surface (Armstrong 1978). Hence, detailed studies of the vertical distribution of lichens on surfaces of different age are needed to take this factor into account.

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