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## Review article

# Competition in lichen communities

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### Abstract

Lichens are symbiotic organisms that often dominate stressful environments such as the surfaces of rock and tree bark. Whether or not competition occurs between lichens in these environments, however, is controversial. This review considers various aspects of the competitive interactions between lichens including the observational studies that suggest competitive effects may be important, the methods that have been used to study lichen competition in the field, the result of marginal contacts between lichen thalli, the attributes that may give a species a competitive advantage, and the role of competition in structuring lichen communities. These studies suggest that competition for space and light does occur in lichen communities and that individual lichen species can be excluded from a substratum as a result of competition. Moreover, competitive interactions in multi-species communities can also lead to stable assemblages of species. Future research should consider those aspects of the lichen symbiosis that may confer a competitive advantage and the factors that may promote stability in multi-species communities. Studies of competition in lichen communities may have implications for other stressful environments in which symbiotic organisms play a significant role.

**Keywords:** Lichen, competition, additive design, substitutive design, overgrowth, allelopathy

### 1. Introduction

Competition between organisms is one of the most important factors that determine community structure and diversity. Competition, however, has been defined in a variety of different ways. First, as the tendency of neighbours to utilise the same quantum of light, molecule of water, ion of mineral nutrient, or volume of space (Grime, 1973). Second, as the interaction that takes place between organisms when two or more individuals seek a common resource whose supply falls below that of their combined demands (Donald, 1963). Third, the medium through which the environment regulates the balance between the components of a mixture (Hill and Shimamoto, 1973). A particularly useful definition, however, is given by Keddy (2001) as “the negative effects that one organism has upon another by consuming or controlling access to a resource that is limited in availability”. This definition emphasises the two most important aspects of competition, viz., it occurs when a resource is limited and results in detrimental effects on one or more species.

The lichen symbiosis is unusual in that it often dominates communities in extremely harsh environments where vascular plants may be excluded. In these environments, lichens experience extremes of temperature, moisture supply, and low availability of nutrients (Grime, 1979). There is abundant evidence that under these conditions, lichens sequester a high proportion of photosynthate for stress resistance rather than growth (Farrer, 1973). Hence, whether or not competition is a significant factor in symbiotic lichen communities is controversial. First, competition has been relatively little studied in such communities (Berner, 1970; Grime, 1977). Second, lichens grow in many ‘open’ communities such as eroding slopes, creeping soil, and on relatively unstable substrata; environments in which competition is assumed not to have been a major force in structuring such communities (Poelt and Vezda, 1990). In addition, Grime (1979) divided plant communities into three groups according to whether a ruderal, competitive, or stress tolerant strategy predominated amongst the constituent species. In this scheme, lichens were considered to be stress tolerant organisms and therefore, to occur in communities in which it competition was unlikely to play a significant role.

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By contrast, descriptive and experimental studies of lichen communities often provide compelling evidence that competition is important in determining the distribution of individual species and the composition of communities (Barkman, 1958; James et al., 1977; Oksanen, 1984; Armstrong, 1982).

This review considers: 1) the ecological studies which suggest that competition between lichens is important in communities on rock and tree bark, 2) the methods that have been used to study lichen competition, 3) the results of marginal contacts between thalli, 4) the factors that may give a species a competitive advantage, and 5) the role of competition in structuring lichen communities.

## 2. Studies Implicating Lichen Competition

In a major survey of the lichen vegetation of the U.K. (James et al., 1977), it was concluded that within a climatically uniform region, each substratum developed a similar lichen community. Nevertheless, there were also variations within apparently uniform habitats that were assumed to be due, in part, to competitive effects (James et al., 1977). This conclusion was also supported by Oksanen (1984) who observed from extensive studies that lichens appeared to compete for space and light on a variety of substrata.

### *Saxicolous communities*

In communities on rock surfaces, evidence both for and against competition has emerged from studies of lichen succession. On rocks in New Zealand (Orwin, 1970), crustose species, in which the thallus comprises a thin crust more or less tightly appressed to the substratum, are the first colonisers of freshly deposited surfaces, usually within five years of exposure. Foliose species, i.e., species with leaf-like marginal lobes more loosely attached to the substratum, appear only after the 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 removed by competition. A similar pattern was observed on rocks in Ontario, Canada (Woolhouse et al., 1985) and resulted in an increase in species richness over time. Allogenic processes, such as the gradual physical weathering of the rock, often determine these types of succession.

A feature of many saxicolous communities is the proportion of the rock surface unoccupied by lichen thalli even at the oldest sites. As lichen thalli die, areas become available for colonization suggesting that the intensity of competition for space may be reduced in older more established communities. By contrast, John (1989, 1990) concluded from studies of the Jonas Rockslide in the Canadian Rocky Mountains, that competition played a

significant role in the patterning of the species. Reid (1960) and Yarranton and Green (1966) have both reported similar conclusions 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.

Studies of the distributions of lichens in relation to rock aspect have also provided indirect evidence for the presence of competitive effects. The growth of foliose lichen species transplanted to north and south-facing rock surfaces was studied in north Wales by Armstrong (1977). The growth of *Parmelia conspersa* (Ehrh. Ex Ach.) Ach. and *Physcia orbicularis* (Neck.) Poetsch. was significantly reduced when transplanted to north-facing surfaces compared with south-facing surfaces consistent with their distributions, both species being characteristic of well-lit rock surfaces. By contrast, thalli of *Parmelia saxatilis* (L.) Ach. 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. These observations suggest that *P. saxatilis* may have been eliminated on south-facing surfaces due to competition from faster growing foliose species (Armstrong, 1977). Similarly, the crustose lichen *Rhizocarpon geographicum* (L.) DC. is abundant on south-facing rock surfaces at the site but also occurs on a small number of north-facing surfaces (Armstrong, 1974). Significantly more associated lichen species were present on the north-facing surfaces where *R. geographicum* was present (Armstrong, 2002). The mean frequency of these associated species, however, was significantly lower on the surfaces where *R. geographicum* was present. This suggests that the intensity of competition within a multi-species community may have been greater on some north-facing surfaces, thus reducing the effectiveness of the stronger competitors, and allowing *R. geographicum* to survive at the more unfavourable north-facing sites (Armstrong, 2002).

Competition has also been observed in supralittoral communities on the seashore (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 addition, 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 *Xanthoria parietina* (L.) Th. Fr. (which only reproduces sexually) parasitizes the algal symbiont of *Physcia* species in an effort to promote its dispersal (Ott, 1987). Such competition effectively removes some *Physcia* species from substrata colonised by *X. parietina*.

### *Corticolous communities*

Tree bark is a less stable substratum for lichen growth

than many rock surfaces, but nevertheless, the structure and diversity of vascular and non-vascular epiphyte communities may be influenced by interactions between the constituent species (Callaway et al., 2001). Barkman (1958) was one of the first lichenologists to systematically investigate corticolous lichen communities and concluded that epiphytic lichens and bryophytes were subjected to a number of different competitive interactions including competition for light and chemical interference (allelopathy). Studies of the succession of lichens on bark have also suggested competition may be important. Degelius (1964) found that the early crustose phase on ash trees endured for several years until overgrown by foliose species. There was also evidence that the 'stronger' foliose competitors such as *Parmelia acetabulum* (Neck.) Duby and *Anaptychia ciliaris* (L.) Korb could overgrow 'weaker' competitors such as *X. parietina* and *Parmelia sulcata* T.Tayl. Furthermore, there was evidence that some crustose species, e.g., members of the genus *Pertusaria*, were able to outcompete *X. parietina*. By contrast, Welch (2002), who studied intraspecific and interspecific competition on the boles of beech trees in Cornwall, found that crustose species never outcompeted foliose species. In fact, there was evidence that some foliose species tended to occupy sites where crustose species were predominant presumably because the crustose species were less effective than other foliose species as competitors of foliose lichens (Welch, 2002).

Some studies have suggested that the relative intensity of competition may vary with height on the tree. Giersberg (1981), for example, found that the distribution of *Ramalina farinacea* (L.) Ach. on beech was influenced by competition with *Evernia prunastri* (L.) Ach., *P. sulcata*, and *Hypogymnia physodes* (L.) Nyl. lower down the trunk but at higher locations, wind velocity and exposure were the most important factors. In addition, Harris (1971) demonstrated that *Parmelia caperata* (L.) Ach. and *P. reddenda* Stirt. had different patterns of zonation on trees with the former having an optimum cover approximately one-third of the way up the trunk while the latter occurred mainly in the middle regions of the trunk. Competitive effects were assumed to have had an important influence on these distributions. Hence, many lichenologists who have observed and studied saxicolous and corticolous communities have concluded that competition occurs between lichen thalli and that these interactions may be important in determining the distribution of individual species and the structure of lichen communities.

### 3. Methods of Studying Lichen Competition

Lichen communities on rock and tree bark offer a simple model system in which competition for space and light on a

substratum can be studied essentially in two dimensions. As a consequence, a number of specific methods have been developed to study lichen competition in these communities.

#### *Non-random associations and neighbourhood models*

Competitive effects between lichens are likely to lead to non-random distributions of individual species and changes in community structure within the immediate vicinity of lichen thalli ('neighbourhoods'). Hence, lichen competition has been studied by investigating non-random associations or by studying the immediate neighbourhoods of thalli. John and Dale (1995) studied the lichen vegetation on oak trees in Michigan and found numerous non-random associations at all scales. Some species were rarely neighbours while others appeared to coexist and to interact more consistently. Within the group of lichens that had an epiphytic foliose growth form, some species formed exclusive patches with few interspecific contacts while other species were more widely dispersed and showed many such contacts (John, 1992). Closer observations of these communities suggested that the 'heavier' more robust species were able to overlap or overgrow less robust species. Ramstad and Hestmark (2000) studied different neighbourhood models to predict the fate of an individual thallus of *Lasallia pustulata* (L.) Merat. in relation to its surrounding neighbours. Three models were fitted to the data, viz., the polygon model, the neighbourhood with fixed radius model, and the nearest neighbour model. The mean distance to nearest neighbours provided the best prediction of individual performance and is the most direct measure of the degree of competition in crowded communities. The nearest neighbour model uses actual distances to neighbours, a fairly direct measure of the degree of competition under crowded conditions (Ramstad and Hestmark, 2000).

#### *Study of contacts and overlaps*

A more direct method of studying lichen competition is to examine the points of marginal contact between adjacent thalli in a community and to determine the frequency of overlaps between individuals. This method was used to study competition at two sites in Wales by Pentecost (1980). At one site, *Caloplaca heppiana* (Mull. Arg.) Zahlbr. and *C. aurantia* (Pers.) Hellb. were equally matched and neither exclusively overgrew the other. At the second site, *Aspicilia calcarea* (Massal.) Sommerf. usually overgrew *C. heppiana* at the margins of the thalli but *C. heppiana* was able to colonise the fragmented centres of *A. calcarea* thalli and overgrew *A. calcarea* at 'window' contacts. Pentecost (1980) concluded that rate of colonization, thallus density, radial growth rate, type of contact between species, and rate of fragmentation were all variables influencing the outcome of competition between crustose species.

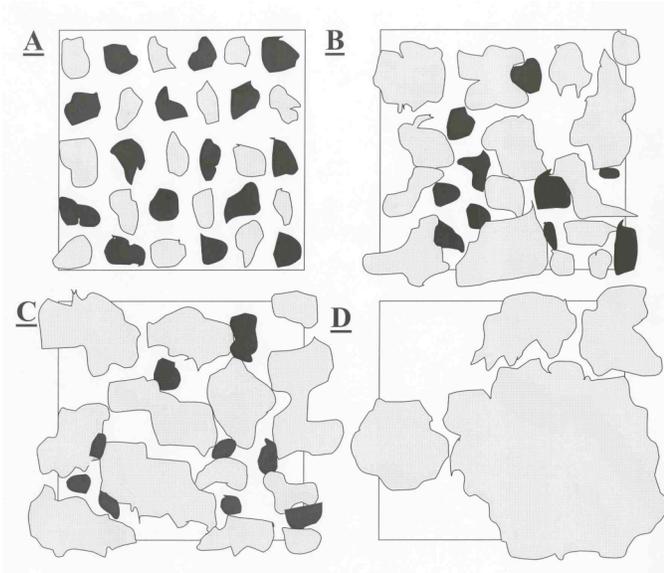


Figure 1. Competition between two foliose saxicolous lichens *Parmelia conspersa* (light coloured thalli) and *Parmelia glabratula* ssp. *fuliginosa* (dark coloured thalli) studied in experimental plots on pieces of smooth slate (A = start of experiment, B = 12 months later, C = 18 months later, D = 30 months later). Based on data from Armstrong (1982).

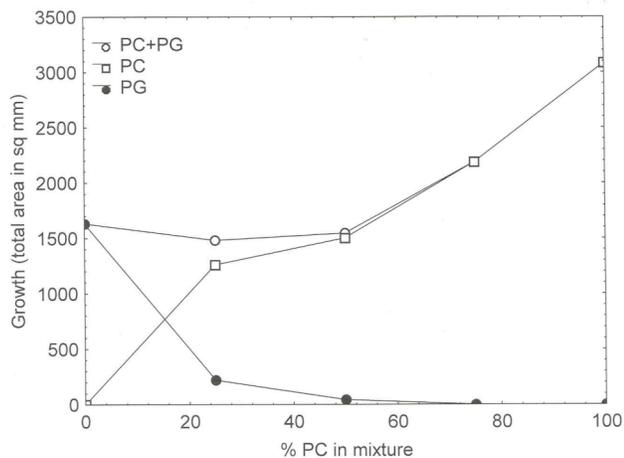


Figure 2. Competition between two foliose saxicolous lichens *Parmelia conspersa* (PC) and *Parmelia glabratula* ssp. *fuliginosa* (PG) studied using the replacement series design. PC grown in replacement series with PG showed non-linear responses curve for the total (PC + PG) and individual growth in area (PC, PG) of the species. Thalli of PC consistently overgrew those of PG. Based on data from Armstrong (1985).

### Experimental studies

Experimental approaches have been particularly useful in studying competition between higher plants (Mahmoud and Grime, 1976; Hall, 1974). Two types of experimental

design have been commonly used and both have been applied to the study of lichen competition (Armstrong, 1982; 1985). First, in additive designs, each species is grown in monoculture and paired in 1:1 mixtures with each of the other species (Clatworthy, 1960; Wellbank, 1963; Mahmoud and Grime, 1976). In this type of design, the density varies between monocultures and mixtures. This design was used to study competition between three species of foliose lichens in north Wales (Armstrong, 1982). The lichens were glued as fragments in experimental plots marked out on pieces of slate that were placed on horizontal boards in the field. Fig. 1 shows the results of one of the species combinations in a single plot, viz., competition between fragments of *P. conspersa* and *P. glabratula* ssp. *fuliginosa* (Fr. Ex Duby) Laund. After 12 months (Fig. 1B) fragments of *P. conspersa* had increased in area while several fragments of *P. glabratula* ssp. *fuliginosa* had disappeared. In addition, thalli of *P. conspersa* were observed to overgrow those of *P. glabratula* ssp. *fuliginosa* more frequently than vice versa. After 18 months (Fig. 1C), most fragments of *P. conspersa* were still present while there were fewer surviving fragments of *P. glabratula* ssp. *fuliginosa*, most of which were being overgrown by *P. conspersa*. After 30 months (Fig. 1D), *P. glabratula* ssp. *fuliginosa* had completely disappeared from the plot and a small number of large *P. conspersa* thalli were present, the large thallus at bottom right of the plot being the result of the coalescence of several smaller thalli. At no time during the experiment was the surface of the plot completely covered by lichens. The results for all three species in this experiment suggested that the three lichens competed in the following order of competitive ability: *P. conspersa* > *P. saxatilis* > *P. glabratula* ssp. *fuliginosa* (Armstrong, 1982).

Second, in substitutive designs, two species are grown in monoculture and are also grown in mixtures in differing proportions, the density remaining constant throughout (Hall, 1974; Wade, 1981). This type of design, also known as a 'replacement series' design, has the advantage that several different types of interaction may be inferred from the results and also enables a prediction to be made as to whether a particular binary mixture of species is likely to be stable. Armstrong (1985) used this method to study competition between three foliose species in north Wales. The result of one of the species combinations, viz., competition between fragments of *P. conspersa* and *P. glabratula* ssp. *fuliginosa* is shown in Fig. 2. The response curve for the combined growth of the two species is non-linear indicating that growth in the mixtures is less than that expected from growth in the monocultures. In addition, as in the additive experiment, growth of *P. conspersa* is greater than that of *P. glabratula* ssp. *fuliginosa* and the latter was virtually eliminated in the mixtures in which the proportion of *P. conspersa* was 50% and 75%. The data for all three combinations suggested that *P. conspersa* should predominate in communities with either *P. orbicularis* or *P.*

*glabratula* ssp. *fuliginosa* but that mixtures dominated by *P. orbicularis* and *P. glabratula* ssp. *fuliginosa* should be more stable.

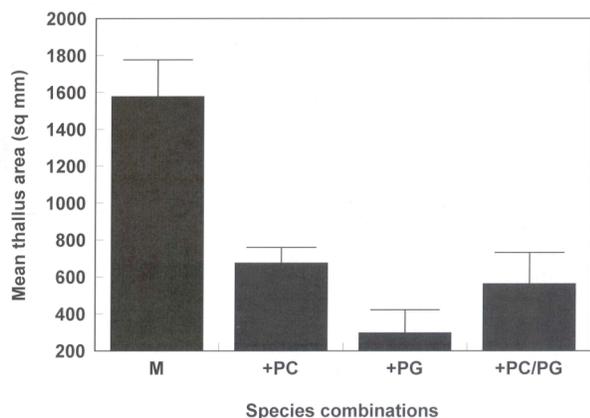


Figure 3. In this competition experiment, *Physcia orbicularis* was grown in monoculture (M) and in two-species mixtures with either *Parmelia conspersa* (PC) or *P. glabratula* ssp. *fuliginosa* (PG) and in a three-species mixture with both competitors (PC/PG). Based on data from Armstrong (1986).

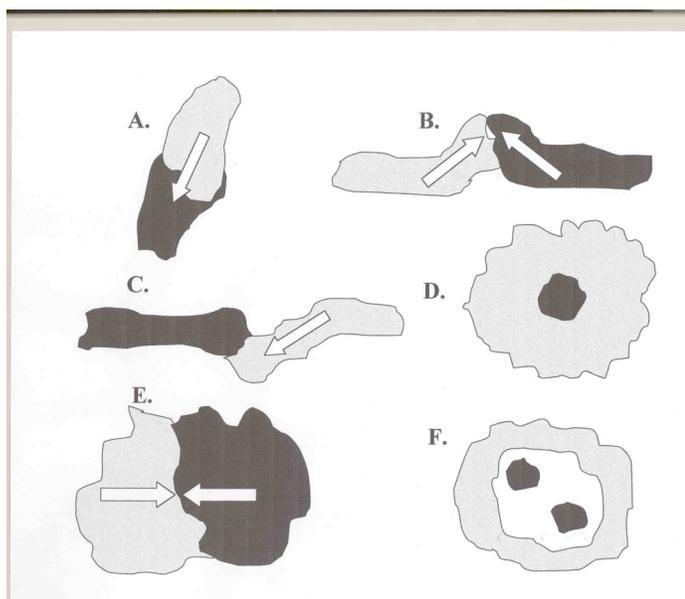


Figure 4. The possible outcomes of marginal competition between lichen thalli: A) the lighter thallus lobe overgrows the darker lobe, B) the two lobes push against each other causing elevation of both lobes, C) the lighter thallus lobe grows beneath and undermines the darker lobe, D) the poorer competitor grows as an epiphyte on the more successful thallus, E) growth ceases at the point of contact resulting in a 'truce' condition, and F) the poorer competitor grows in the 'windows' caused by degeneration of the centre of a more successful competitor.

In early experiments, both additive and substitutive designs were used to study competition between pairs of species. Lichen communities, however, comprise large numbers of species and methods are required for studying competition between several species simultaneously. A method based on a factorial experimental design and using analysis of variance (ANOVA) for estimating competitive effects was developed by Armstrong (1986). The lichens were glued in experimental plots as before but in multispecies mixtures corresponding to their factorial combinations as well as the conventional monocultures and two-species mixtures. Hence, in a study of three foliose species, significant two-factor interactions indicated that the results within a three-species mixture could not be predicted from those of the two-species mixtures (Armstrong, 1986).

Fig. 3 shows the result of growing fragments of *P. orbicularis* in two-species mixtures with either *P. conspersa* or *P. glabratula* ssp. *fuliginosa* and in a three-species mixture with both competitors. The data suggest that *P. orbicularis* thalli grew better in the presence of two competitors than would have been expected from their growth in the two-species mixtures. Hence, a mixture of the three species may be more stable than the two-species mixtures and therefore, the three species could co-exist on well-lit rock surfaces at the site. Differences in competitive behaviour between two and three-species mixtures were also observed by Welch (2002) who showed that *P. caperata*, *P. saxatilis*, and *X. parietina* all grew equally well in two-species mixtures but in three-species mixtures, *P. caperata* grew significantly better than *P. saxatilis*.

#### Competitive hierarchies

Studies of lichen competition enable species to be arranged in order of competitive ability known as a 'competitive hierarchy' (Tilman, 1982; Tilman and Kareiva, 1997). The competitive hierarchy model makes three basic assumptions. First, that all species exhibit their best performance in terms of size and growth rate at the same end of the resource gradient. This is a common situation for plants and lichens, all of which share a requirement for light, water, and nutrients. Second, that species vary in competitive ability in a predictable way as a result of resource acquisition or ability to interfere with neighbours. Third, that competitive ability is negatively correlated with the ability of a species to efficiently disperse its propagules and to colonise new sites. In a competitive hierarchy, the dominant species occupies the preferred end of the gradient and the subordinate species are displaced down the gradient at a distance determined by their position in the hierarchy. Hence, the competitive hierarchy model is predictive and may be used to determine the order in which species will be displaced along a gradient.

#### 4. Marginal Contacts Between Lichens

When lichens colonise a substratum they grow radially and ultimately the margins of thalli come into contact with each other. The processes that occur when two thalli meet are crucial in understanding the outcome of lichen competition. In his study on rocks in Wales, Pentecost (1980) listed several possible outcomes of lichen competition: 1) one species overgrows another, 2) neither species grows at the point of contact ('truce' condition), and 3) one species may grow epiphytically on the other. The actual outcome of contact may depend on the growth form of the lichen, marginal contacts between crustose species being more likely to result in 'truce' conditions than between foliose species (Pentecost, 1980). Dale (1985) also studied lichen contacts and concluded that when contact occurs between two thalli, one species will outcompete the other either by overgrowth or by the production of allelochemicals. The various possible outcomes of marginal interactions in lichens are illustrated in Fig. 4.

Published studies provide considerable evidence for lichen overgrowth especially in relatively undisturbed communities (Lawrey, 1991). Instances of thallus overgrowth were first observed by Malinowski (1912) who commented on the importance of this process in the dynamics of lichen communities. In a photographic study of a saxicolous lichen community, Hawksworth and Chater (1979) found that *Ochrolechia parella* (L.) Massal. overgrew thalli of *Rhizocarpon obscuratum* (Ach.) Massal. but reached equilibrium with *Lecanora gangaleoides* Nyl. Similarly, Pentecost (1980) found that in a community dominated by *C. heppiana* and *C. aurantia*, the 'truce' condition was the commonest outcome; whereas in communities of foliose species and foliose/crustose species, overgrowth was more likely to occur. In addition, umbilicate species such as *L. pustulata* are frequently successful because the thallus is attached at a single point and the margins are raised above the surface of the substratum (Harris, 1996). Species such as *L. pustulata* can also attach themselves to the surface of other thalli essentially growing as an epiphyte and shading portions of the host thallus. In the study of Armstrong (1982), in which a competitive hierarchy between three foliose species was established on slate rock in Wales, the ability of a species to overgrow its competitors was an important attribute predicting the outcome of competition. Overgrowth may also be important in lichen communities on soil dominated by branched fruticose species. For example, Frey (1959) carried out transplant experiments in Switzerland involving various species of *Cladonia* and found that transplanted mat-forming species frequently overgrew other types of soil *Cladonia*.

Two further processes may occur when foliose thalli meet. First, one thallus may undermine another by growing beneath the lobes of its competitor. This process may

elevate the competing lobe above the substratum and could result in cessation of lobe growth. Second, two lobes may push against each other elevating them both and resulting in both lobes dying back. Both these phenomena can be observed in lichen communities but there are few quantitative data at present to determine the frequency of these types of interactions.

In conclusion, there appears to be considerable evidence for thallus overgrowth, especially in interactions involving foliose species. It is likely that light fails to reach lobes that have been overgrown leading to a significant reduction in photosynthesis and termination of growth in the region of overlap (John, 1992). Nevertheless, there is also evidence for cessation of growth when two lichen thalli meet, especially in crustose communities, leading to a 'truce' condition. In addition, a poorer competitor may establish and grow within the fragmenting centres of a more successful competitor (Armstrong and Smith, 1997). Hence, despite the apparent prevalence of overgrowth observed in lichen communities, it is possible that such interactions do not lead inevitably to the elimination of a lichen species on a substratum (Armstrong, 1982).

#### 5. Competitive Attributes of Lichens

Various aspects of lichen biology may determine the success or failure of a competitive interaction. Four factors were listed by Pentecost (1980) as important in saxicolous communities, viz., colonisation rate and density, radial growth rate, type of contact between species, and rate of thallus senescence. Lawrey (1984) also listed the competitive attributes of lichens and considered growth rate, growth form, lichen chemistry, thallus size, and herbivore palatability to be important factors.

##### *Radial growth rate*

In experiments in which fragments of foliose lichens are grown in binary mixtures, the species with the faster radial growth rate is usually the most successful competitor (Armstrong, 1982). Hence, when three foliose species were grown in paired mixtures, *P. conspersa*, which has the fastest growth rate of the three, outcompeted both *P. glabratula* ssp. *fuliginosa* and *P. saxatilis* (Armstrong, 1982). A species with a fast rate of radial growth is able to colonise the available space on a substratum more efficiently than its competitors and may be able to overgrow neighbouring thalli more effectively if thallus morphology permits. In complex mixtures, however, it is more difficult to predict the competitive outcome of a mixture from the growth rates of the constituent species. Armstrong (1986) found that *P. glabratula* ssp. *fuliginosa* and *P. saxatilis* grew better in a three-species mixture with the faster growing *P. conspersa* than either did in two-species

mixtures with this species. It is possible that *P. conspersa* competes less efficiently when two competitors are present, a process that may allow the three species to coexist. Hence, although radial growth rate may be an important competitive attribute, it becomes less useful as a predictor of the outcome of competition in more diverse communities.

#### *Thallus senescence*

As many lichen thalli age, the central portions degenerate creating a space or 'window' in the centre of the thallus (Pentecost, 1980; Armstrong and Smith, 1997). This space can be exploited by lichen thalli of the same or a different species and this may be an important factor determining the outcome of competition on a surface. Hence, exclusion of a weak competitor may be prevented if the thalli are able to colonise the windows formed in the centres of a more successful competitor (Pentecost, 1980; Armstrong, 1982). In addition, Hestmark (1997) showed on coastal cliffs in southern Scandinavia, that *L. pustulata* was subject to considerable disturbance that created gaps in the community. These areas of disturbance were major sites of establishment and it was concluded that the age structure of the population was spatially structured by the pattern of gap recruitment. Hence, species able to take advantage of the creation of gaps and windows could be at a competitive advantage at disturbed sites despite slower growth rates.

#### *Growth form*

The growth form of a lichen and the morphology of the individual lobes could be important competitive attributes. In various experiments (Armstrong, 1982; 1985, 1986), the faster growing *P. conspersa* was often the most successful competitor especially in two-species mixtures. This species, however, also possesses lobes which are wider and thicker than most of its competitors (Armstrong, 1991b; Armstrong and Smith, 1999). Lobe morphology is also intimately associated with growth rate, wider lobes growing faster than narrower lobes (Hill, 1981; Armstrong, 1991b). The importance of growth form has also been demonstrated in umbilicate species, their competitive success being based, at least in part, on the morphological characteristics of the species and especially margin height (Harris, 1996). Hence, in foliose-foliose interactions, the mass and relative heights of the opposing lobes may be an important predictor of competitive success.

#### *Thallus chemistry and allelopathy*

The importance of lichen chemistry and allelopathic effects in lichen competition is controversial. Over 500 secondary metabolites have been reported in lichens of which 350 are unique to the symbiosis (Lawrey, 1995). Most of these metabolites are weak phenolic compounds

produced by the fungal partner and which accumulate in the outer walls of the hyphae. For many years there have been claims that such compounds, when leached from the thallus, may suppress neighbouring lichens and mosses (Lawrey, 1995).

Most evidence for allelopathy in lichen communities is based on observational studies and few experiments have been carried out. Beschel (1965) studied various slow growing crustose species and found that bare areas a few centimetres wide surrounded thalli of *R. geographicum*. Faster growing species that invaded this space disintegrated on the outer rim of the bare area and it was concluded that a 'diffusing antibiotic' may have been responsible. Subsequently, various experiments have demonstrated the allelopathic potential of lichens. Hence, alcohol extracted usnic and physodic acids have both demonstrated antimicrobial action. For example, experiments carried out by Whitton and Lawrey (1982, 1984) have demonstrated inhibitory effects of lichen compounds on spore germination. Ascospore germination of the lichen *Caloplaca citrina* (Hoffm.) Th. Fr. was inhibited by vulpinic, evernic, and atranoric acids while that of *Graphis scripta* (L.) Ach. was severely inhibited by vulpinic and evernic acids but was unaffected by atranoric acid. Neither species was affected by stictic acid (Whitton and Lawrey, 1984). In addition, whereas spore germination in *Cladonia cristatella* Tuck. was only slightly inhibited by lichen compounds, the fungus *Sordaria* was severely affected (Whitton and Lawrey, 1982). These experiments demonstrate the allelopathic potential of lichen compounds and also indicate that the lichenised fungi may be able to tolerate the inhibitory effects more readily than the non-lichenised fungi.

Studies that suggest allelopathic effects occur between lichens in the field are rare. Culbertson et al. (1977) studied the morphologically similar but chemically distinct species *Parmelia loxodes* Nyl. and *P. verruculifera* Nyl. A crustose species *Lepraria* grew epiphytically only on the latter species and it was concluded that this effect reflected the disparate medullary chemistries of the two *Parmelia* species. The study of Lawrey (2000) suggests that certain lichen fungi are strongly inhibited by some allelopathic compounds in lichens. For example, the phenolic defence compound lecanoric acid may prevent the growth of the symbiotic fungus *Nectria parmeliae* (Berk & Curtis) Hawksw.

Not all studies have found evidence to support allelopathy in lichens. Kaitera et al. (1996) found that neither internal nor external extracts of three lichen species or usnic acid inhibited the growth of *Gremmeniella abietina* (Lagerb.) Morelet *in vitro*, although some stimulatory effects were reported. In addition, the allelopathic potential of lichen compounds has been tested over a range of pH values (Gardner and Mueller, 1981). Vulpinic acid appeared to be the most toxic and stictic acid the least toxic of the

substances tested and it was concluded that compounds requiring the greatest number of steps in biosynthesis are energetically the most costly to produce. This conclusion raises the question whether lichens, that partition the products of photosynthesis largely for stress resistance (Farrar, 1973), would have the resources to produce significant quantities of effective allelochemicals.

A prediction of the strategy theory of Grime (Grime, 1979) is that the production of secondary compounds is a defence against generalist herbivores. In addition, Rogers (1990) concluded that competitors produce offensive allelochemicals while stress tolerant organisms produce defensive (antimicrobial) allelochemicals. From a review of 34 lichen species, production of allelochemicals appeared to be positively correlated with the presence of K-strategy and inversely correlated with r-strategy. In addition, Hilmo (1994) and Glenn et al. (1995) reported that the presence of usnic acid and other secondary compounds may reduce grazing by microarthropods and generalist herbivores while John (1989) suggested that crustose lichens use allelochemicals as a contact avoidance strategy.

A useful concept in discussions of lichen allelopathy is the 'optimal defence theory' (ODT) (Hyvarinen et al., 2000) which states that the tissues most closely related to plant fitness will be the most defended. The concentration of lichen compounds is often highest in structures that confer reproductive fitness as suggested by the theory and is strong evidence that the secondary compounds in lichens are essentially defensive. Nevertheless, the differential distribution of compounds among species could determine competitive outcome especially between species with otherwise similar competitive attributes.

## 6. The Significance of Competition in Lichen Communities

There is evidence from both observational and experimental studies that lichens compete with each other for space and light on various substrata. Nevertheless, the significance of these interactions in determining the structure and composition of symbiotic lichen communities is unclear. This section considers the evidence that competition can result in the exclusion of individual lichen species and bring about alterations in the composition of lichen communities.

### *Competitive exclusion*

It has been argued that two or more species cannot coexist on a single resource without the species forming a 'competitive hierarchy' which results in poor competitors being replaced by superior ones (Tilman, 1982). In the study of Armstrong (1982), however, no species was excluded from a binary mixture in all three replicate plots after a

three-year study period even though significant overgrowth had clearly taken place. The survival of 'poorer' competitors was enhanced in some plots by small variations in the aspect, slope, and microtopography of the substratum as well as by the formation of 'windows' due to thallus degeneration. In addition, when three foliose species were grown over three years using a substitutive design (Armstrong, 1985), *P. orbicularis* and *P. glabratula* ssp. *fuliginosa* showed similar growth in monoculture. In mixtures, the growth of each species was linearly related to its proportion in a mixture suggesting little effective interaction had taken place. Moreover, the growth of *P. conspersa* was greater than that of *P. orbicularis* and *P. glabratula* ssp. *fuliginosa* and the latter two species were substantially reduced in mixtures with *P. conspersa*; with *P. glabratula* being eliminated in mixtures where it was the minority species. Hence, stability and coexistence appear to be more likely outcomes when the constituent species have similar competitive attributes.

Coexistence is also more likely to occur in complex communities (Armstrong, 1986). Tilman and Kareiva (1997) demonstrated that multispecies coexistence occurs because species at the top of the hierarchy cannot occupy all sites simultaneously. Local displacement is never permanent so that when the better competitors die, sites become available for colonisation by less efficient competitors (Armstrong, 1982). In addition, competitive interactions in three-species mixtures cannot always be predicted from two-species mixtures (Armstrong, 1986; Welch, 2002). Hence, *P. glabratula* ssp. *fuliginosa* and *P. orbicularis* actually grew better in three than in two-species mixtures with *P. conspersa* suggesting that the three foliose species are able to coexist on well-lit rock surfaces at the site. These results suggest that although competition between neighbouring lichen thalli may be intense, the process may not necessarily lead to competitive exclusion in more complex communities.

### *Alterations in community structure and diversity*

Few studies have examined the role of competition in structuring more complex lichen communities. Armstrong (1991a) studied competition between four foliose lichen species in experimental plots facing north and south (Fig. 5). In south-facing plots, the growth of *P. glabratula* ssp. *fuliginosa*, *P. orbicularis*, and *P. saxatilis* was significantly reduced by *P. conspersa* and *P. glabratula* ssp. *fuliginosa* by *P. saxatilis*. Hence, *P. conspersa* is a characteristic species of well-lit, south facing rock surfaces at the site (Armstrong, 1974). By contrast, on north-facing plots, the growth of *P. conspersa* is reduced by *P. saxatilis*, reducing the competitiveness of the former and allowing *P. glabratula* ssp. *fuliginosa* to coexist with *P. conspersa*.

In a further experiment (Armstrong, 2000), the same four species were grown in well-lit plots with and without

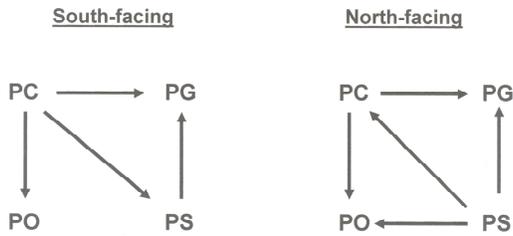


Figure 5. Effect of rock surface aspect on competition between four saxicolous lichens in experimental plots on slate (*Parmelia conspersa* (PC), *Parmelia glabratula* ssp. *fuliginosa* (PG), *Physcia orbicularis* (PO), *Parmelia saxatilis* (PS)). Presence of an arrow indicates a competitive interaction is present between two species. The arrow points to the species detrimentally affected by the interaction. Based on data from Armstrong (1991b).

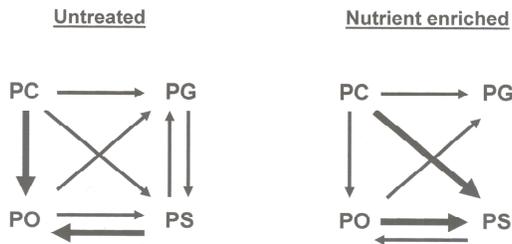


Figure 6. Effect of nutrient enrichment on competition between four saxicolous lichens in experimental plots on slate (*Parmelia conspersa* (PC), *Parmelia glabratula* ssp. *fuliginosa* (PG), *Physcia orbicularis* (PO), *Parmelia saxatilis* (PS)). The presence of an arrow indicates a competitive interaction between two species and width of the arrow the intensity of competition. The arrow points to the species detrimentally affected by the interaction. Based on data from Armstrong (2000).

nutrient enrichment by bird droppings (Fig. 5). 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 untreated plots, *P. conspersa* has a strong competitive influence on all three competitors and especially on *P. orbicularis*. There is also mutual competition between *P. orbicularis* and *P. saxatilis* and between *P. glabratula* ssp. *fuliginosa* and *P. saxatilis*. Under conditions of nutrient enrichment, *P. conspersa* is a stronger competitor against *P. saxatilis* but a weaker competitor against *P. orbicularis*. Hence, nutrient enrichment alters the competitive balance between the four species suggesting that a different combination of species would occur on nutrient rich and poor rocks.

Hence, 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 and Kinder, 1999).

By contrast, Welch (2002) showed that under conditions of nutrient application, symmetrical competition prevailed between *P. caperata* and *X. parietina* and also between *P. reddenda* and *P. caperata*. Where no nutrients were added, competition between these pairs of species was asymmetrical with *P. caperata* outcompeting *X. parietina* and *P. reddenda* outcompeting *P. caperata*. Hence, nutrient additions may not always reduce species diversity of a lichen community.

Another effect that can be observed in lichen communities is that of 'competitive release', i.e., an advantage to a poorer competitor due to a reduction in the intensity of competition. On two islands in the Potomac river, *P. conspersa* and *Pseudoparmelia baltimorensis* (Gyel. & For.)Hale dominated communities on both islands with *P. conspersa* being more frequent at high light environments and *P. baltimorensis* at low light environments. However, *P. conspersa* was able to occupy intermediate light intensity habitats in species poor environments where presumably the intensity of competition was substantially reduced. This study provides yet further evidence of the importance of competition in structuring lichen communities.

## 7. Symbiosis and Competition

Symbiotic organisms are often dominant in stressful environments and this phenomenon is exemplified by the dominance of lichens on rock surfaces and tree bark. In managed agricultural systems in South Australia, if the soil environment is not stressful to root nodule bacteria, it then becomes a competitive environment for nodulation soon after introduction of the inoculated legume (Howieson and Ballard, 2004). These results reinforce the view that there may be little competition under conditions of stress (Grime, 1977).

There may be parallels between lichen dominated systems and other ecosystems in which symbioses involving fungi are present. Many trees and shrubs, for example, develop a thick layer of fungal hyphae (ectotrophic mycorrhiza) which connect root cells with the external soil environment. These types of interaction are abundant near the soil surface and enable nutrient elements formed during the decomposition of litter to be effectively reabsorbed. This type of symbiotic community is strongly associated with mineral nutrient stress, e.g., on heathlands and certain scrub communities in temperate and tropical regions (Grime, 1979). As in lichen dominated systems, the symbiotic communities appear to be long-lived and this may enable the plants to exploit the limited number of periods when nutrients become available. It would appear quite plausible that competition between symbiotic fungi could occur in these communities. Moreover, there is direct evidence for competition among arbuscular mycorrhizal fungi (Cano and

Bago, 2005). Studies of three fungal isolates indicated a lack of antagonism when hyphae were exploring beyond the root tip but growth limitations were observed due to competition closer to the growth tip. This experiment emphasises that competition may be more important than previously thought in stressful environments involving symbiotic organisms.

## 8. Future Research

Many observational studies have concluded that competition is important in symbiotic lichen communities in determining the distribution of individual lichen species and therefore, the composition of lichen communities. This conclusion is further supported by studies that have investigated the interface between neighbouring lichen thalli (Pentecost, 1980) and experimental studies in which fragments of lichen thalli are grown in monocultures and in mixtures (Armstrong, 1982; 1985; 1986; Welch, 2002). Interactions commonly occur when lichen thalli meet often resulting in the overgrowth of one individual by another. Although some of the factors determining the outcome of this type of interaction such as thallus morphology and growth rate have been studied, the competitive attributes of lichens remain relatively little known. In particular, the role of secondary lichen compounds and allelopathy in lichen competition remains to be established. Experimental studies also support the hypothesis that competitive exclusion may occur in lichen communities. In addition, interactions among organisms take place within a complex environment consisting of both abiotic and biotic processes (Callaway and Walker, 1997). Hence, competition may be best studied by comparative studies of competitive interactions along gradients of abiotic stress.

Future descriptive and experimental studies of competition in lichens should focus on a number of areas. First, competitive effects should be studied along environmental gradients in which there is variation in the level of abiotic stress such as supralittoral environments on the sea shore or with increasing height on trees. Second, the role of competition in structuring and determining the stability of multi-species communities should be studied experimentally employing factorial experimental designs. Third, the complex interactions that occur between life cycle stage, indirect interactions, facilitative effects and competition in lichen communities should be studied (Callaway and Walker, 1997). Fourth, those aspects of lichen morphology, growth, and physiology that confer a competitive advantage on individual lichen species should be studied.

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