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Competitive Interactions between Four Foliose Lichen Species With and Without Nutrient Enrichment

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Abstract

Competition between four foliose lichen species, common on slate rock surfaces in South Gwynedd, Wales, UK, was studied in experimental plots with and without nutrient enrichment by bird droppings. Fragments of the four lichens were glued to pieces of slate on horizontal boards in monoculture and in two-, three- and four-species mixtures in a factorial experimental design. In monoculture, nutrient enrichment increased thallus area of *Parmelia conspersa* (Ehrh. ex. Ach.)Ach., decreased thallus areas of *Parmelia saxatilis* (L.)Ach. and *Parmelia glabratula* ssp. *fuliginosa* (Fr. ex. Duby)Laundon, and did not affect thallus area of *Phaeophyscia orbicularis* (Necker)Moberg compared with untreated thalli. In the mixtures, *P. conspersa* and *Ph. orbicularis* were equally effective competitors in plots with and without nutrient enrichment. Addition of bird droppings, however, altered the ability of *P. saxatilis* and *P. glabratula* ssp. *fuliginosa*, to compete with the other species, the competitive ability of both species being reduced in some mixtures but increased in others. The results suggest that nutrient enrichment may alter the competitive balance between the four lichen species and this may be a factor determining their relative abundance on rock surfaces in South Gwynedd.

Keywords: Lichen, competition, nutrient enrichment, bird droppings, factorial experimental design

1. Introduction

Previous experiments have suggested that competition between foliose lichen species may be an important factor determining their relative abundance on slate rock surfaces in south Gwynedd, Wales, UK (Armstrong, 1982, 1985, 1986, 1991). Competition has been variously defined as the tendency of neighbours to use the same resource such as light, water, mineral or space (Grime, 1973), an interaction resulting from two or more organisms seeking a common resource when supply falls below their combined demands (Donald, 1963) or the means by which the environment regulates the components of a mixture (Hill and Shimamoto 1973). Lichens often grow horizontally on a substratum and, when the margins of thalli meet, overgrow each other suggesting competition for space is an important mechanism of competition. Experiments suggest that competitive ability of a lichen varies with rock surface aspect. Hence, *Parmelia conspersa* (Ehrh. ex Ach.)Ach. is a strong competitor on north and south facing rock surfaces and *Phaeophyscia orbicularis* (Necker) Moberg a weaker competitor on south facing rock surfaces.

By contrast, *Parmelia saxatilis* (L.) Ach. is a stronger competitor on north facing rock surfaces while *Parmelia glabratula* ssp.*fuliginosa* (Fr. ex Duby) Laundon is a weak competitor on both south and north facing rock surfaces (Armstrong, 1991). The success of a lichen thallus in competition with its neighbours may be dependent on a number of factors including radial growth rate (Armstrong, 1982), the height of lobes at the margin (Harris, 1996) and the biomass of the thalli (John, 1992). In foliose species which have flat lobes closely appressed to the substratum, however, a rapid radial growth rate may be the most important factor (Armstrong, 1991).

Nutrient enrichment by bird droppings can have a significant effect on the composition of lichen communities (Barkman, 1958; Jaggard et al., 1974; James et al., 1977; Armstrong, 1984). In addition, experiments suggest that the radial growth of foliose lichens is markedly affected by the addition of bird droppings to thalli (Armstrong, 1984, 1994); the radial growth of *P. conspersa* and *Ph. orbicularis* being increased and *P. glabratula* ssp. *fuliginosa* and *P. saxatilis* decreased by the addition of bird droppings compared with untreated thalli. Hence, if competition for space is partly dependent on radial growth rate, nutrient enrichment by bird droppings could increase the competitive ability of some species and reduce it in others and result in a different combination of species achieving competitive dominance. The objective of this study was to test this hypothesis experimentally by growing fragments of four, foliose lichen species alone in monoculture and in two-, three-, and four species-mixtures in plots with and without the addition of bird droppings.

2. Materials and Methods

Site

The experiments were carried out at a site in South Gwynedd, Wales, U.K. (SN 6193) in an area of Ordovician slate described previously (Armstrong, 1974).

Lichen species

The four most common foliose lichen species on slate rock surfaces at the site were studied (Armstrong, 1974): 1) *Parmelia conspersa* occurs on well-lit, slightly to markedly nutrient-enriched siliceous rocks, 2) *P. saxatilis* is frequent at two contrasting sites, viz., vertical hard rock surfaces at shaded humid sites which are not subject to direct rain and exposed, well-lit rock outcrops or boulders which are not nutrient-enriched, 3) *P. glabratula* ssp. *fuliginosa* is frequent on nutrient-poor siliceous rock outcrops and also occurs at shaded and maritime sites and 4) *Phaeophyscia orbicularis* is characteristic of nutrient-enriched sites and is believed to be less specific to rock type. On 1 April 1993, large healthy thalli of the four species were collected on portions of slate and the slate pieces were attached to horizontal boards in a private garden to equilibrate with the garden environment for a year before the start of the experiment (Armstrong, 1994).

Experimental design

The experiments were conducted over a period of three years in 3×3 cm plots marked out on flat pieces of roofing slate, without lichen thalli, at least 1200 cm^2 in size. Four or five plots were located on each piece of slate spaced as widely apart as possible. Fragments of each species were cut from the perimeters of large thalli and glued (Bostik adhesive) in random orientations to the plots. Previous experiments indicated that gluing does not affect the radial growth of lichen fragments (Armstrong, 1982). Each fragment was c. 13–15 mm^2 in area with at least three actively growing lobes. Previous studies showed that such fragments form new lobes within a few months and grow into a circular thallus within a three year period (Armstrong, 1992). In addition, three years is usually sufficient for the lichen thalli to grow to fill the experimental plots and hence, compete for space. Two sets of experimental plots were set up. Each comprised three replicates of 15 treatments arranged in a factorial experimental design (Clatworthy, 1960; Mahmoud and Grime, 1976; Ridgman, 1975; Wellbank, 1963): a monoculture of each of the four species comprising four fragments per plot; six two-species mixtures comprising eight fragments per plot; four three-species mixtures of 12 fragments per plot and one four-species mixture with 16

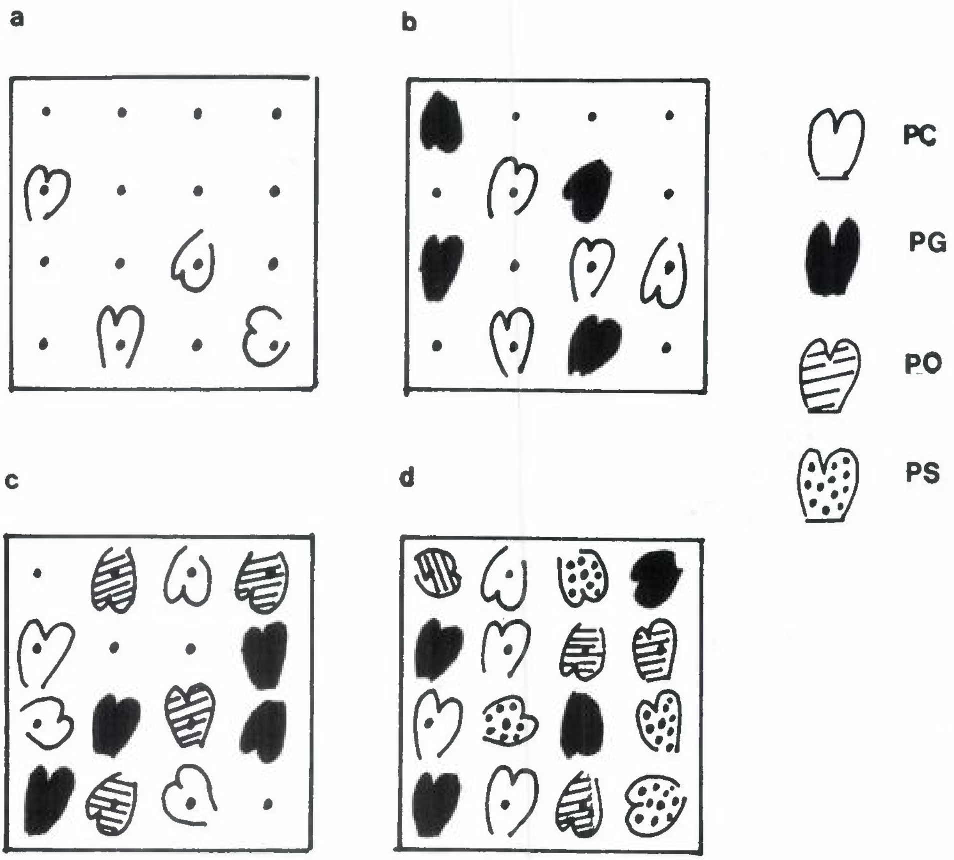

Figure 1. Examples of the arrangement of lichen fragments within the experimental plots: a) a monoculture of *Parmelia conspersa*, b) a two-species mixture of *P. conspersa* and *Parmelia glabratula* ssp. *fuliginosa*, c) a three-species mixture of *P. conspersa*, *Parmelia glabratula* ssp. *fuliginosa* and *Phaeophyscia orbicularis*, d) a four-species mixture. Lichen fragments were glued at random locations within the plot grid and at random orientations.

fragments per plot. An example of the pattern of gluing of the lichen fragments in each type of mixture is shown in Fig. 1. During the first 3 months, six fragments became detached from the plots (two *P. glabratula* ssp. *fuliginosa*, two *P. saxatilis* and one *Ph. orbicularis*) and were replaced. Particular combinations of species were assigned at random to the experimental plots. In each plot, the lichens were glued in a 4 × 4 grid approximately 3 mm apart and the fragments were assigned to random locations within the plot. In the monocultures and two- and three-species mixtures the remaining spaces were left unoccupied.

One set of experimental plots was left untreated, but in the other set, the plots were treated with bird droppings. Accumulations of fresh bird droppings, originating from a variety of birds common at the site (Armstrong, 1984), were collected from boards placed on a flat roof. The bird droppings were homogenised with a pestle and mortar and with a few drops of deionised water to give a paste. The thallus fragments in the plots received a thin smear of the paste at three-monthly intervals commencing on 1 April 1994 until 1 January 1997 (a total of 12 applications). The paste moistens the thalli and growth may depend on the degree of hydration of the thallus. Hence, after treatment, all the thallus fragments were wetted with distilled water until saturated and remained in the laboratory at the site for 24 hours to protect them from rain. All rock fragments were then placed in random locations on flat boards in the garden away from bird perching sites. No bird droppings were observed in contact with untreated thallus fragments during the course of the experiment.

Data collection and analysis

On 1 April 1997 the visible outline of each thallus was traced onto 'clingfilm' and the area of each thallus estimated by superimposing the traces onto 1 mm graph paper. Total area (mm^2) of each species in each plot and the means of the three replicates were calculated. Analysis of variance (ANOVA) (SuperANOVA software, Abacus Concepts Inc., Berkeley, CA 1989, USA) was the statistical method used. First, thallus areas of the four species in monoculture were compared using a two-factor, split-plot ANOVA. Second, for each species, thallus areas in the treated and untreated plots were analysed separately by three-factor ANOVA with the treatment sums of squares partitioned into main effects and two-and three-factor interactions (Ridgman, 1975). Third, to test whether there was an interaction between competition and nutrient enrichment, data from the treated and untreated mixtures were compared using two-factor ANOVA. The two-species mixtures were analysed separately from the three/four-species mixtures.

3. Results

Thallus areas of the four species, averaged over the three replicates, in monoculture at the end of three years are shown in Table 1. The data indicate that addition of bird droppings increased the thallus area of *Parmelia conspersa*, decreased thallus areas of *Parmelia saxatilis* and *Parmelia glabratula* ssp. *fuliginosa* but had no significant effect on thallus area of *Phaeophyscia orbicularis* compared with untreated plots.

Table 1. Thallus area (mm^2), averaged over three replicates, of four saxicolous lichens (PC = Parmelia conspersa, PS = *Parmelia saxatilis*, PG = *Parmelia glabratula* ssp. *fuliginosa*, and PO = *Phaeophyscia orbicularis* after three years in monoculture with (+) and without (–) the addition of bird droppings.

Treatment	Species tested PC	PS	PO	PG
– Bird droppings	444 (108)	200 (38)	526 (11)	159 (15)
+ Bird droppings	638 (91)	152 (15)	548 (39)	107 (7)

Analysis of variance: Species F=100.51 (P<0.001), Treatment F=1.68 (P>0.05), Interaction F=6.74 (P<0.01).

Thallus areas in the experimental plots at the end of the experimental period are shown in Figs. 2–5. In many plots, there were reductions in the area of thalli in the mixtures compared with the monocultutres consistent with interference between thalli. In *P. conspersa* (Fig. 2), thallus area in the treated and untreated plots was unaffected by the three competitors whether present individually or in combination. In addition, no significant interactions between competition and nutrient enrichment were observed in the two-species mixtures (F=3.50, P>0.05) or the three/four-species mixtures (F=0.60, P>0.05) suggesting that the addition of bird droppings did not affect the competitive ability of *P. conspersa*.

In *P. saxatilis*, in the untreated plots (Fig. 3), thallus area was reduced in the presence of each competitor compared with the areas in monoculture, the greatest reductions being observed in the presence of *Ph. orbicularis* and *P. conspersa*. In addition, thallus area of *P. saxatilis* in the three-species mixtures with *P. conspersa* and *P. glabratula* ssp. *fuliginosa* and *P. conspersa* and *Ph. orbicularis* was greater than suggested by performance in the two-species mixtures. In the treated plots, there was a greater reduction in area in the presence of *P. conspersa* and *Ph. orbicularis* compared with the untreated plots. In addition, thallus area was greater than expected in the three-species mixture with *Ph. orbicularis* and *P. glabratula* ssp. *fuliginosa* mixture and *P. saxatilis* was completely eliminated from the three-species mixture with *P. conspersa* and *Ph. orbicularis* and from the four-species mixture. Significant interactions between competition and nutrient enrichment were observed in the two-species mixtures (F=19.86, P<0.001) and the three/four-species mixtures (F=11.75, P<0.001) suggesting that the competitive ability of *P. saxatilis* was affected by the addition of bird droppings.

In *Ph. orbicularis*, in the untreated plots (Fig. 4), thallus area was reduced in the presence of *P. saxatilis* and *P. conspersa* compared with areas in monoculture but not in the presence of *P. glabratula* ssp. *fuliginosa*. In addition, the reduction in

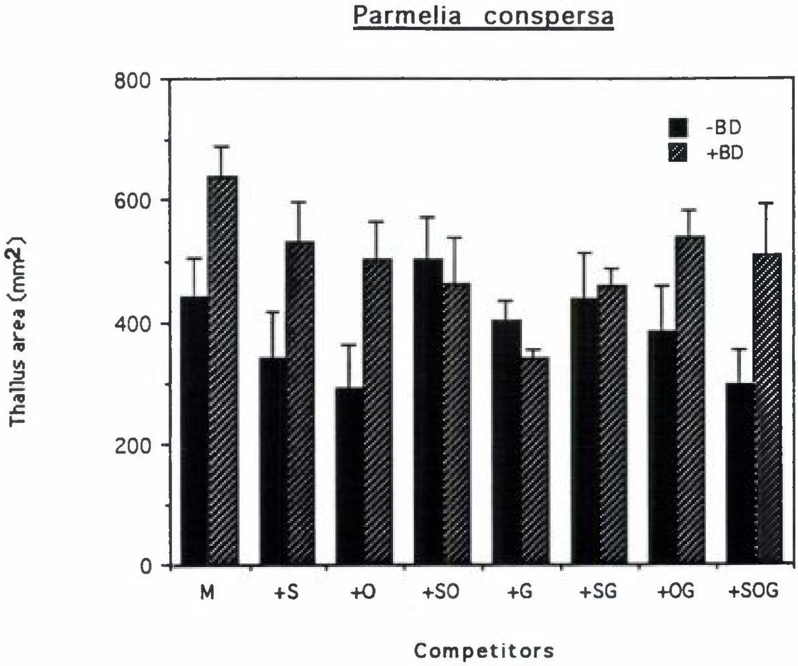

Figure 2. Thallus areas (mm^2), averaged over three replicates, after three years of *Parmelia conspersa* in monoculture (M) and two-and three-species mixtures (+) with and without the addition of bird droppings (BD), S = *Parmelia saxatilis*, O = *Phaeophyscia orbicularis*, G = *Parmelia glabratula* ssp. *fuliginosa*. Analysis of variance: no significant effects were observed.

area in the three-species mixture with *P. saxatilis* and *P. glabratula* ssp. *fuliginosa* was less than expected from the two-species mixtures. In the treated plots, there was less effect of each individual competitor in the two-species mixtures and the reduction in area in the three-species mixture with *P. conspersa* and *P. glabratula* ssp. *fuliginosa* was greater than expected from the two-species mixtures. No significant interactions between competition and nutrient enrichment were observed, however, in the two-species mixtures ($F=1.55$, $P>0.05$) or the three/four-species mixtures ($F=2.70$, $P>0.05$).

In untreated *P. glabratula* ssp. *fuliginosa* plots (Fig. 5), thallus area was reduced by all three competitors compared with area in monoculture, the greatest reduction being observed in the presence of *P. conspersa*. In addition, thallus areas were greater than predicted in the three-species mixtures with *Ph. orbicularis* and *P. saxatilis* and with *P. conspersa* and *Ph. orbicularis*. *P. glabratula* ssp. *fuliginosa* was eliminated in the three-species mixture with *P. conspersa* and *P. saxatilis* but thallus area was greater than expected in the four-species mixture.

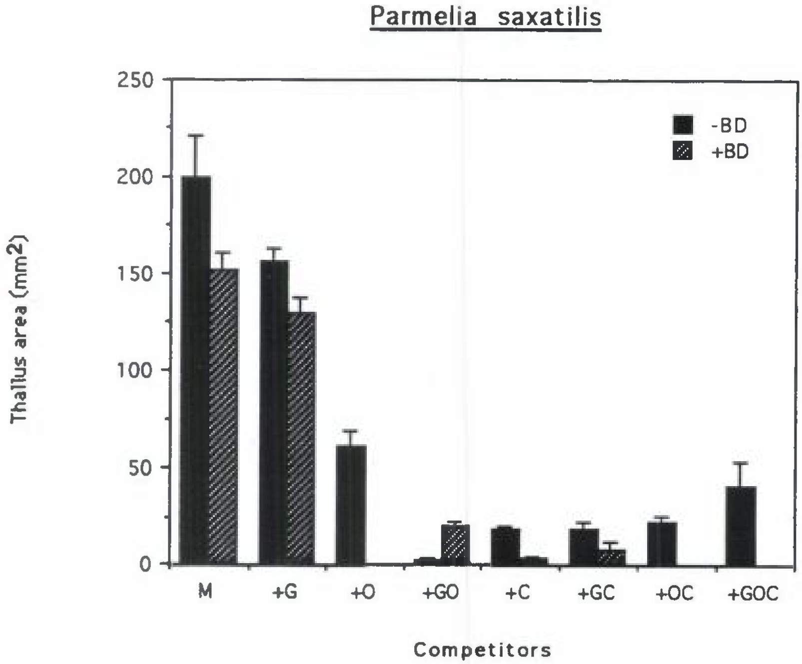

Figure 3. Thallus areas (mm^2) after three years, averaged over three replicates, of *Parmelia saxatilis* in monoculture (M) and two-and three-species mixtures(+) with and without the addition of bird droppings (BD), C = *Parmelia conspersa,* O = *Phaeophyscia orbicularis,* G = *Parmelia glabratula* ssp. *fuliginosa*. Analysis of variance (significant effects only): –BD Main effects PC F=139.78 (P<0.001), PO F=93.66 (P<0.001), PG F=11.15 (P<0.001), Two-factor interactions PC x PO F=130.71 (P<0.001), PC x PG F=21.67 (P<0.001); +BD Main effects PC F=696.98 (P<0.001, PO F=607.74 (P<0.001), Two-factor interactions PC x PO F 519.11 (P<0.001), PO x PG F=10.99 (P<0.001), Three-factor interaction F=17.80 (P<0.001).

In the treated plots, thallus area was reduced by *Ph. orbicularis* and *P. conspersa* but not by *P. saxatilis*. In addition, thallus area in the treated plots was reduced in the three-species mixture with *Ph. orbicularis* and *P. saxatilis* and completely eliminated in the remaining three-species and four-species mixtures. A significant interaction between competition and nutrient enrichment was observed in the two-species mixtures (F=27.86, P<0.001) and in the three/four-species mixtures (F=5.20, P<0.05) suggesting that the competitive ability of *P. glabratula* ssp. *fuliginosa* was influenced by bird droppings.

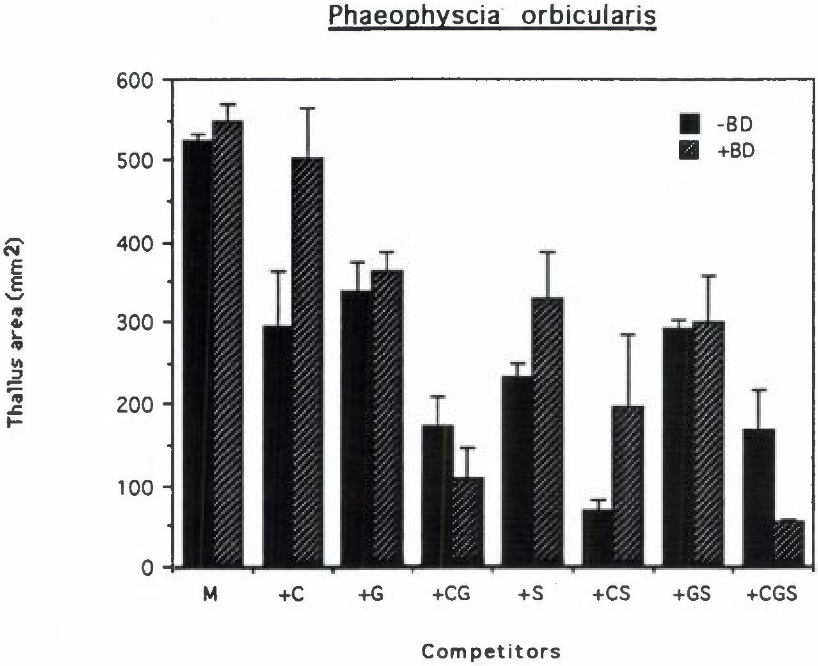

Figure 4. Thallus areas (mm^2) after three years, averaged over three replicates, of *Phaeophyscia orbicularis* in monoculture (M) and two-and three-species mixtures (+) with and without the addition of bird droppings (BD), C = *Parmelia conspersa*, S = *Parmelia saxatilis*, G = *Parmelia glabratula* ssp. *fuliginosa*. Analysis of variance (significant effects only): –BD Main effects PS F=29.99 ($P<0.001$), PC F=42.82 ($P<0.001$), Two-factor interactions PS x PG F=22.37 ($P<0.001$); +BD Main effects PS F=20.06 ($P<0.001$), PG F=27.03 ($P<0.001$), PC F=22.33 ($P<0.001$), Two factor interactions PS x PG F=8.01 ($P<0.01$), PG x PC F=5.02 ($P<0.05$).

4. Discussion

Competition experiments involving lichens have a number of limitations. First, similarly sized perimeter fragments were glued to pieces of slate in random locations and located on horizontal boards. However, the outcome of competition between two species may be affected by the age structure of the thalli and the spatial pattern of the competitors. Second, an additive experimental design was employed in which there is variation in density of lichen fragments between the monocultures and the various mixtures. Lichen thalli may not dry out as rapidly when in close contact with other thalli (Hestmark et al., 1997) and since growth is dependent on moisture status, competition in more complex

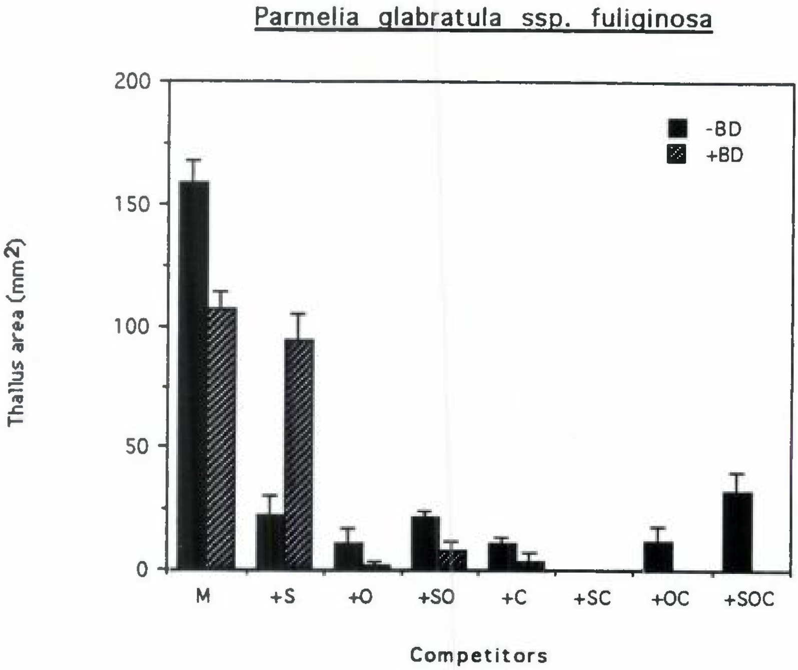

Figure 5. Thallus areas (mm^2) after three years, averaged over three replicates, of *Parmelia glabratula* ssp. *fuliginosa* in monoculture (M) and two-and three-species mixtures (+) with and without the addition of bird droppings (BD), C = *Parmelia conspersa*, O = *Phaeophyscia orbicularis*, S = *Parmelia saxatilis*. Analysis of variance (significant effects only): –BD Main effects PS F=45.19 (P<0.001), PO F=42.67 (P<0.001), PC F=80.22 (P<0.001), Two-factor interactions PS x PO F=101.86 (P<0.001), PS x PC F=61.16 (P<0.001), PO x PC F=107.28, Three-factor interaction F=43.17 (P<0.001); +BD Main effects PO F=189.26 (P<0.001), PC F=213.11 (P<0.001), Two-factor interactions PO x PC F=175.39 (P<0.001).

mixtures may not be predictable from performance of the lichen fragments in monoculture. Third, bird droppings were added to the experimental plots intermittently over three years whereas some rock surfaces may be subjected to a more continuous regime of deposition (Armstrong, 1994).

Overgrowth of one species by another was observed in all the experimental mixtures consistent with competition between the lichens for space. In the absence of nutrient enrichment, *Parmelia conspersa* was the strongest and *Parmelia glabratula* ssp. *fuliginosa* the weakest competitor. These results are similar to those reported on north and south facing rock surfaces in south Gwynedd despite the differences in the environmental conditions between vertically oriented rock surfaces and the horizontal boards (Armstrong 1991). In addition, competitive effects observed in the three- and four-species mixtures were not predictable from examination of the two-species mixtures. First, *P. saxatilis* performed better in mixtures with *P. conspersa* and *P. glabratula* ssp. *fuliginosa* and in mixtures with *P. conspersa* and *Ph. orbicularis* than expected. Second, *Ph. orbicularis* performed better in the three-species mixture with *P. saxatilis* and *P. glabratula* ssp. *fuliginosa* than expected and third, *P. glabratula* ssp. *fuliginosa* performed better in mixtures with *Ph. orbicularis* and *P. saxatilis* and in mixtures with *P. conspersa* and *Ph. orbicularis* and in the four-species mixture than expected. Two factors may explain these results. First, the individual effect of a strong competitor such as *P. conspersa* can be reduced in a more complex mixture thus enabling more species to coexist (Armstrong, 1991). Second, some weaker species, e.g. *P. glabratula* ssp. *fuliginosa*, are able to colonise the spaces created by fragmentation of the centres of thalli of a more successful competitor (Pentecost, 1980; Armstrong, 1991; Armstrong and Smith 1997; Hestmark, 1997), thus enabling the species to survive in a more competitive environment.

In monoculture, nutrient enrichment increased thallus area of *P. conspersa*, reduced thallus areas of *P. saxatilis* and *P. glabratula* ssp. *fuliginosa* but had no significant effect on thallus area of *Ph. orbicularis*, compared with untreated thalli. With the exception of *Ph. orbicularis*, these results are similar to those reported previously (Armstrong, 1984, 1994). In previous experiments, *Ph. orbicularis* showed significantly increased growth rates when treated with bird droppings (Armstrong, 1994). Nutrient enrichment, however, also increased rates of thallus fragmentation in *Ph. orbicularis* (Armstrong, 1994) which could explain the reduced thallus areas observed in the present experiment.

The data suggest that *P. conspersa* is a strong competitor under nutrient poor and rich conditions which could explain the predominance of this species on a wide range of rock surfaces (James et al., 1977). Similarly, although a weaker competitor than *P. conspersa*, *Ph. orbicularis* competed equally well in nutrient poor and rich plots and this species often dominates south facing surfaces where *P. conspersa* is absent. By contrast, the competitive ability of *P. saxatilis* and *P. glabratula* ssp. *fuliginosa* was influenced by nutrient enrichment. In some mixtures, both species competed less well in treated compared with untreated plots and were eliminated from some of the mixtures. Additions of bird droppings decreased the growth of both species which supports the hypothesis that competitive ability may depend on growth rate. Hence, poor growth and competitive ability in the presence of bird droppings could explain the low frequency of these two species on nutrient enriched rocks and their preference for nutrient poor, siliceous rocks (James et al., 1977). In addition, *P. glabratula* ssp. *fuliginosa* is a poor competitor on most rock surfaces but this species survives better in nutrient enriched plots where *P. saxatilis* is present. This result may explain the prevalence of *P. glabratula* ssp. *fuliginosa* on some north facing rock surfaces where *P. saxatilis* is also abundant (Armstrong, 1991). In addition, in some of the three- and four-species mixtures, *P. saxatilis* performed better in treated plots than expected. A possible explanation is that bird droppings increased the growth rate of some of the competing species and hence, the intensity of competition. The individual effect of a strong competitor could then be reduced allowing a weaker competitor to co-exist. If this hypothesis is correct, *P. saxatilis* may be able to survive on nutrient enriched rocks within more diverse communities.

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