

## Effect of nutrient application on growth rate and competitive ability of three foliose lichen species

A. R. WELCH, M. P. GILLMAN and E. A. JOHN

**Abstract:** A field experiment was established to examine the effect of nutrient addition on the growth and competitive abilities of *Parmelia caperata*, *P. saxatilis* and *Xanthoria parietina*. Thallus fragments were attached to roofing slates in a split-plot experimental design in monospecific and multispecific mixtures and sprayed with nutrient solution at application frequencies representing a range of nutrient enrichments. Growth rates were measured as change in thallus diameter and the strength of competition determined by counting the number of thallus overlaps. Nutrient application significantly affected thallus growth with medium application rates promoting more thallus growth than controls (distilled water) or higher application rates in all three species. Nutrient addition at medium applications significantly increased the number of thallus overlaps made by all three species compared with controls, suggesting that competition became more intense. Although symmetrical competition was observed between all three species it was noted that growth and competition of thalli in two-species mixtures could not be used to predict the result in three-species mixtures. These results suggest that elevated nutrient levels can affect lichen growth rates and competition between thalli, leading to alterations in lichen community structure.

**Key words:** competition, fertilizer experiment, growth, lichen, nutrient enrichment, split-plot.

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### Introduction

Nitrogen and phosphorous are the plant nutrients most likely to limit primary production in natural, semi-natural and artificial ecosystems. Over recent decades, anthropogenic activities have resulted in a 6.87 and a 3.48-fold increase for fixed nitrogen (N) and phosphorus (P), respectively, added to the environment (Tilman 1999), both introduced deliberately, as a stimulant to plant growth in agriculture and forestry, and inadvertently, as a by-product of industrial and combustion processes. When these inputs reach natural and semi-natural terrestrial, freshwater and marine ecosystems via

run-off or aerial redistribution, they often have important consequences for the structure and function of those ecosystems, frequently resulting in dramatic shifts in species composition and a decline in species-richness (Tilman 1982; Marschner 1995), in addition to a range of other effects (Mason 1991). The impacts of nutrient addition on growth and structure of flowering plant communities are well documented (Austin & Austin 1980), but the effects of nutrient addition on communities of lower plants and lichens are less well studied, but likely to be equally dramatic, and crucial for the maintenance of biodiversity.

Lichenologists have long been aware of a suite of nitrophilous lichen species that are associated with nutrient-rich (and usually base-rich) habitats, such as rocks used as bird-perches, the 'canine zone' at the base of urban tree boles, and farmland. A number of lichenologists have observed a positive correlation between proximity to livestock farms and the abundance of nitrophilous

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A. R. Welch: Department of Biology, University College School, Frogna, London NW3 6XH, UK.

M. P. Gillman: Open University, Ecology and Conservation Research Group, Walton Hall, Milton Keynes, MK7 6AA, UK.

E. A. John: School of Life Sciences, John Maynard Smith Building, University of Sussex, Falmer, Brighton, East Sussex BN1 9QG, UK.

lichen species (Crittenden *et al.* 1994; Sanchez-Hoyos & Manrique 1995; Pitcairn *et al.* 1998; van Herk 1999; Ruoss 1999). Conversely, other lichen species are associated with less nutrient-rich habitats, and acidophytic species distributions are typically negatively correlated with nutrient enrichment (Gaio-Oliveira *et al.* 2004).

Experimental studies have shown that nitrophilous species such as *Xanthoria parietina* (L.) Th. Fr. thrive at eutrophicated sites and may grow poorly when transplanted away from them (Armstrong 1984). Provision of additional nutrients increases the radial growth rate of nitrophilous lichen species (Armstrong 1984; Crittenden *et al.* 1994; Sanchez-Hoyos & Manrique 1995; Miller & Brown 1999) by as much as 15–32% per year (Lewis-Smith 1995), while inhibiting growth in acidophytic species (Vagts & Kinder 1999). Armstrong (2000) found that nutrient enrichment reduced the thallus area of the acidophytic *Parmelia saxatilis* which possibly explains its low frequency on nutrient enriched rocks. However, all lichens require plant growth nutrients to maintain photosynthetic capability, and even acidophytes might be expected to show enhanced growth when exposed to sub-toxic doses of essential nutrients.

Lichen responses to nutrients are complicated due to their extreme sensitivity to the nature of their ionic environment. Therefore, the impact of nutrient enrichment on the pH of their substratum may be as critical as the increased availability of the nutrients themselves. While nitrogen enrichment in the form of nitrate and nitrite can acidify the substratum in an untreated non-chelated form (Bull *et al.* 1995), addition of ammonium ( $\text{NH}_4^+$ ) results in elevated (alkaline) pH levels, and there is evidence to suggest this is a factor leading to the loss of acidophytes such as *Parmelia saxatilis* (L.) Ach. (van Herk 1999) from affected substrata. Furthermore, nutrient enrichment can stimulate the growth of free living algae on the surface of lichen thalli (Scott 1960), resulting in a reduction of thallus photosynthetic ability. There is also evidence to suggest that nutrient enrichment may cause

a breakdown in the lichen symbiosis (Scott 1960; Nash 1996).

Nutrient enrichment of lichen communities will lead to changes in species composition where less N-tolerant species are replaced by more N-tolerant species (van Dobben & De Bakker 1996). This could happen in part as a result of changed competitive dynamics, a phenomenon reported from higher plant communities (Levine *et al.* 1998; Hartley & Amos 1999). Less is known about competitive exclusion in lichen communities which are less amenable to experimental manipulation, but observational studies have suggested that it can occur after environmental perturbation (Lawrey 1981; Vagts & Kinder 1999) therefore leading to a reduction in species diversity.

During interspecific competition between lichens the morphological characteristics of the two competing thalli are important (Pentecost 1980; Harris 1996) since species that possess a raised thalline edge enabling them to rise above the substratum, are more likely to overgrow more addressed neighbouring thalli. Furthermore, heavier thalli appear to have a distinct advantage when attempting to overgrow lighter thalli (Armstrong 1982; John 1992). Since light fails to reach an overgrown thallus its ability to photosynthesise would be compromised, leading to a reduction or termination of growth in the region of overlap (John 1992; Harris 1996). Other factors that might ultimately determine the success of a competitive interaction between two thalli include a faster rate of lobe regeneration, faster radial growth rate and the presence of allelochemicals (Armstrong 1986). We propose that moderate levels of anthropogenic nutrient enrichment will increase lichen growth rates and in turn reduce the time required for neighbouring thalli to contact each other, leading to increased competition intensity within lichen communities.

In this paper we report on experiments designed to assess the impact of nutrient addition, at a range of application frequencies, on lichen growth rates and competition by determining how three common lichens with distinct ecologies respond when

grown alone and in two- and three-species mixtures using a split-plot experimental design. The species selected were *Parmelia caperata* (L.) Ach., (neutrophytic), *P. saxatilis* (acidophytic) and *Xanthoria parietina* (nitrophilic). Such information could help determine how lichen community structure might change in response to anthropogenically-elevated nutrient levels. To this end three hypotheses were tested. First, the addition of nutrients across a range of application frequencies would increase lichen growth rates, as measured by changes in their thallus diameters, up to an optimum application frequency. Such changes in thallus diameter may well be species and dose specific with nitrophilous species such as *X. parietina* predicted to exhibit a more positive response to nutrient enrichment at higher doses than acidophytic species such as *P. saxatilis*. Neutrophytic species such as *P. caperata* were predicted to exhibit intermediate responses to nutrient application. Second, nutrient addition in the sub-toxic range would increase thallus growth and reduce the time taken for neighbouring thalli to make contact therefore leading to an increased number of thallus overlaps compared with controls receiving no added nutrients. Differences in thallus morphology would be critical in determining dominance, illustrated by species with more adpressed thalli being less successful at overtopping those with less adpressed thalli in two- and three-species mixtures. Third, thalli in monospecific mixtures will show fewer overlaps than those in multispecific mixtures since there should be no clear dominance hierarchy.

## Materials and Methods

### Lichen material and experimental substrata

Thalli of *Parmelia caperata*, *P. saxatilis* and *Xanthoria parietina* were collected from specimens having a diameter greater than 5 cm to ensure transplants were taken from healthy individuals whose radial growth rate was in the constant or linear phase (Hale 1967; Armstrong 1973). All thalli were collected within north Cornwall from saxicolous substrata (granite, slate and granitic schists) in areas with a mean winter SO<sub>2</sub> level less than 30 µg m<sup>-3</sup> (Dobson 1992). Within 24 hours of

Xp/Pc/Ps	Pc/Pc/Pc	Xp/Xp/Xp	Xp/Ps/Xp
Ps/Xp/Pc	Pc/Pc/Pc	Xp/Xp/Xp	Ps/Xp/Ps
Pc/Ps/Xp	Pc/Pc/Pc	Xp/Xp/Xp	Xp/Ps/Xp
Ps/Xp/Pc	Pc/Pc/Pc	Xp/Xp/Xp	Ps/Xp/Ps
Xp/Pc/Xp	Ps/Ps/Ps		Ps/Pc/Ps
Pc/Xp/Pc	Ps/Ps/Ps		Pc/Ps/Pc
Xp/Pc/Xp	Ps/Ps/Ps		Ps/Pc/Ps
Pc/Xp/Pc	Ps/Ps/Ps		Pc/Ps/Pc

FIG. 1. Split-plot experimental design showing a typical arrangement for *Parmelia caperata* (Pc), *P. saxatilis* (Ps) and *Xanthoria parietina* (Xp). Sub-plots provide three monospecific and four multispecific species combinations. One vacant sub-plot provides space for any natural colonization. Slate dimensions are approximately 21 cm (W) by 17 cm (H), with sub-plots of 5 cm (W) by 7 cm (H).

collection transplants were glued to an experimental substratum with Bostik® all purpose clear adhesive which has been shown not to adversely affect lichen growth (Armstrong 1982).

Smooth uncolonized roofing slate was used as the experimental substratum in order to reduce the influence of microtopography and to simplify thallus measurements. On each slate an area of 20 × 15 cm was clearly etched and sub-divided into eight equal areas (sub-plots) of 7 × 5 cm (Fig. 1). Since the rate of thallus growth is a function of the original size of the thallus (Hale 1967) all thalli were cut into 0.5 × 0.5 cm<sup>2</sup> (± 1 mm) fragments and glued in specific arrangements approximately 5 mm apart within seven of the eight sub-plots on each slate. The remaining sub-plot was left vacant for observation of any natural colonization that might occur.

Two factors were tested in this experiment, a nutrient addition (diluted Hoagland's Solution) factor with six levels (× 0; × 1; × 2; × 4; × 8 and × 16 frequencies of application) and a lichen interaction factor (species mixture) with four levels (one monospecific and three multispecific). The treatments were laid out in a randomised block split-plot design where frequency of application was assigned to the main plots (individual slates) and lichen interaction to sub-plots (within slates).

Ten replicates for the control treatment (× 0 frequency of application of Hoagland's Solution) and six replicates for the remaining treatments (× 1; × 2; × 4; × 8 and × 16) were established. The 40 slates were placed on a horizontal flat roof of a garden shed (c. 2 m wide × 3 m long × 2.5 m high) in an unshaded location. Garden netting was suspended 15 cm above the slates to reduce disturbance by animals.

The experiment was located at Trenance, north Cornwall (928709, SW 87/97; alt. 60 m), an undisturbed location (situated at the far end of a large garden

away from pedestrian access) in zones 9 and 10 of the 'Hawksworth and Rose' scale where mean winter SO<sub>2</sub> levels were less than 30 µg m<sup>-3</sup> (Hawksworth & Rose 1976).

The experimental set up was completed by mid June 1994. One month was allowed before spraying with Hoagland's Solution in order for species to acclimatize to the new environmental conditions and furthermore to reduce physiological stress (increased respiration) arising from transplantation and fragmentation (M. R. D. Seaward, personal communication).

### Chemical treatment

Freshly prepared Hoagland's Solution (Hoagland 1948; Keddy *et al.* 2000) of pH 6.5 diluted to 10% original strength was used to saturate the transplanted thalli. This provided a solution with the following concentrations of ions (mM) K<sup>+</sup>, 3.83; N as NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>, 6.06; Mo<sub>7</sub>O<sub>24</sub><sup>6-</sup>, 0.71; NH<sub>4</sub><sup>+</sup>, 0.09. This closely approximates to organic fertilizer in mineral nutrient composition and therefore reproduces the type of nutrients lichens may become exposed to in the field. Other fungal and algal nutrient media are available but these are seldom used outside the laboratory. Furthermore, numerous other authors (e.g. Keddy *et al.* 2000) have used Hoagland's Solution in fertilizer experiments, or modified versions of it, therefore allowing comparative studies to be made.

At monthly intervals 25 cm<sup>3</sup> of solution was administered to each isolated slate using a plastic spray bottle, with the nozzle set to cover a spray area of approximately 10 cm<sup>2</sup> from a height of 50 cm above the slate. This method produced a range of spray-droplet sizes which, according to Larson (1984), increases the efficiency of thallus water imbibition and wetting. Nutrient solution was applied once, twice, four, eight or sixteen times in 16 days. The control slates and slates not receiving nutrient solution on a particular day were sprayed with an equal volume of distilled water, administered at the same application frequencies as the nutrient solution, to ensure similar states of thallus hydration amongst treatments. In order to prevent dilution or spread of the nutrient solution, treatments were not applied during periods of strong wind which could result in chemical drift, or wet weather which would result in a dilution effect.

### Analysis of growth rates

Photographs of each slate were taken in July 1994, December 1994, April 1995 and May 1995. A specially constructed camera stand was used to ensure a constant focal length when photographing each slate. The maximum diameter of each thallus was measured on the photograph using a digital vernier gauge and representative measurements were taken from the photographs for all thalli within each sub-plot. This provided an indication of growth rate throughout the experiment for each species under different application frequencies and species mixtures.

Change in thallus diameter over the course of the experiment was determined by subtracting the initial thallus diameters from the final thallus diameters collected in May 1995. Changes in thallus diameter for *P. caperata*, *P. saxatilis* and *X. parietina* (four species mixtures per species) were summed for each of the six application frequencies. This provided six single values for each species ( $n=24$ ) which represented the changes in thallus diameter, regardless of species mixture, at each application frequency. The mean of the three values at each application frequency was used to represent the mean total change in thallus diameter ( $n=72$ ).

Where monospecific and multispecific mixtures are compared the sum of the change in thallus diameter from the six replicates at each of the six application frequencies is used to represent the total change in thallus diameter ( $n=36$ ).

### Analysis of competitive interactions

Competition between species was evident when thalli overgrew each other. The numbers of thallus overlaps were counted for each species mixture at each nutrient solution application frequency. The total number of overlaps a species could make in a particular mixture was determined by the number of neighbouring thalli (possible number of overlaps). The ratio of observed overlaps to potential overlaps provided a means of analysing competitiveness between the three lichen species. This provided six ratios (one per mixture) for each species. Summing the ratio of the observed overlaps made to possible overlaps that could be made for each species across all mixtures provided a single value for each application frequency ( $n=72$ ). This gave an indication of how application frequency affected competitive ability—primarily as a function of thallus growth rate.

### Statistical analysis

A two-way split-plot ANOVA was used to investigate whether application frequency and lichen interaction (species mixture) affected thallus growth rates and the number of thallus overlaps made by *P. caperata*, *P. saxatilis* and *X. parietina*. Application frequency was the major factor and lichen species mixture the sub-plot factor. Tukey (Honestly Significant Difference) multiple means test (Zar 1996) was used to determine which means differed significantly. All calculations were performed using Statistica<sup>®</sup> 5.5 (Statsoft Inc., Tulsa, USA).

## Results

### Missing thalli

During the course of the experiment some thalli were lost from individual slates under each application frequency (Table 1). Missing thalli were not used in data analysis.

TABLE 1. Lichen thalli lost (actual number and percentage) from all slates for each treatment between July 1994 and May 1995

Treatment (App. Freq.)	Number of thalli		Thalli lost for each species*			Total thalli lost (%)
	(Present)	(Lost)	Pc	Ps	Xp	
0	840	166	9	49	41	19.8
1	504	122	11	35	53	24.2
2	504	114	7	36	56	22.6
4	504	125	7	46	46	24.8
8	504	104	13	38	48	20.6
16	504	103	20	47	32	20.4

\*Pc=*Parmelia caperata*; Ps=*P. saxatilis*; Xp=*Xanthoria parietina*. 'Present' represents the initial number of thalli at the start of the experiment.

TABLE 2. Two-way split-plot ANOVA for the effect of application frequency (App. Freq.) (factor one) and species mixture (Sp. Mixt.) (factor two) on change in thallus diameter and number of thallus overlaps

	Effect	DF	MS	F	P
Change in thallus diameter	(1) App. Freq.:	5	0.285	59.31	<0.001
	(2) Sp. Mixt.:	11	0.061	12.76	<0.001
	Interaction:	55	0.012	2.60	<0.001
	Error:	360	0.005		
Number of thallus overlaps	(1) App. Freq.:	5	0.36	5.16	<0.001
	(2) Sp. Mixt.:	11	0.40	5.62	<0.001
	Interaction:	55	0.06	0.89	0.693
	Error:	360	0.07		

\*Species mixture represents all species combinations (see Fig. 1).

## Growth rates

Two-way split-plot ANOVA indicated that growth (thallus diameter) was affected by both application frequency and species mixture (Table 2). In addition there was a significant interaction effect. Regardless of individual species mixture effects, Tukey (HSD) analysis indicated that the control treatment ( $\times 0$ —no nutrient addition) was significantly different from all other application frequencies (Fig. 2). Greatest thallus growth occurred up to  $\times 4$  with decreased growth, compared with controls, occurring at higher application frequencies ( $\times 8$  and  $\times 16$ ). Thallus growth was affected significantly by species mixture regardless of application frequency (Table 2). In monospecific mixtures *P. saxatilis* grew less than either *P. caperata* ( $P < 0.01$ ) or *X. parietina* ( $P < 0.01$ )

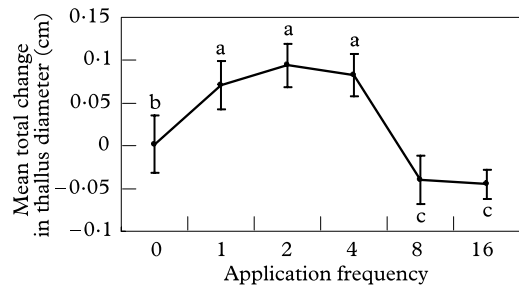


FIG. 2. The effect of application frequency of Hoagland's Solution on the mean total change in thallus diameter for *Parmelia caperata*, *P. saxatilis* and *Xanthoria parietina*. Data not sharing a common letter differ significantly (Tukey HSD test  $P < 0.05$ ). Bars are SEM,  $n = 72$ .

(Fig. 3). In two-species mixtures thallus growth for all three species was similar. However, in three-species mixtures growth



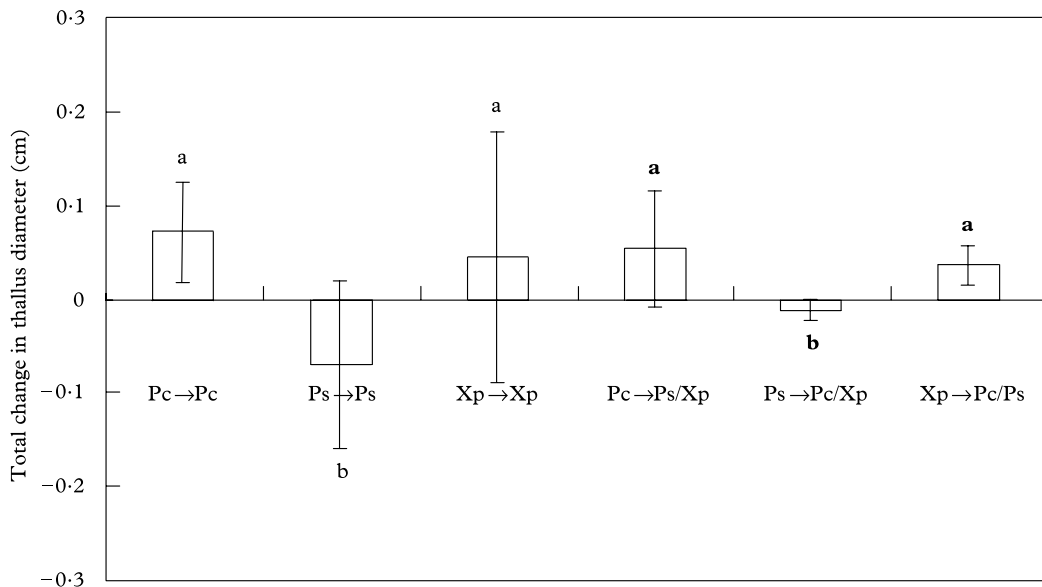


FIG. 3. Total change in thallus diameter for mono and multispecific mixtures of *Parmelia caperata* (Pc), *P. saxatilis* (Ps) and *Xanthoria parietina* (Xp) at all six application frequencies. Data not sharing a common letter differ significantly (Tukey HSD test,  $P=0.05$ ; monospecific data in normal type and multispecific data in bold type). Bars are SEM,  $n=36$ . Arrows ( $\rightarrow$ ) indicate the direction of competition, e.g. Pc $\rightarrow$ Pc indicates *P. caperata* overlapping *P. caperata* in a monospecific mixture and Ps $\rightarrow$ Pc/Xp indicates *P. sulcata* overlapping *P. sulcata* and *X. parietina* in a multispecific mixture.

of *P. caperata* and *X. parietina* was greater than *P. saxatilis* ( $P<0.01$ ) (Fig. 3).

### Competitive relationships (thallus overlaps)

Two-way split-plot ANOVA indicated that the number of thallus overlaps made by each species was affected by both application frequency and species mixture (Table 2), but there was no interaction effect. The number of thallus overlaps made during the course of this experiment were affected significantly by species mixtures, regardless of application frequency (Table 2).

Regardless of species mixture, Tukey (HSD) analysis showed that the  $\times 0$  treatment was significantly different from the  $\times 1$ ,  $\times 2$  and  $\times 4$  application frequencies (Fig. 4B). However, some species mixtures showed significant differences between the number of thallus overlaps being made on neighbouring thalli. *Parmelia caperata* overlapped its own thalli significantly less than

it overlapped neighbouring thalli of *X. parietina* ( $P<0.001$ ). This was also true when grown in three-species mixtures ( $P<0.001$ ). Also *P. caperata* made significantly fewer overlaps when grown with *P. saxatilis* as a neighbour compared with the number it made in three-species mixtures ( $P<0.001$ ) (Fig. 5).

*Parmelia saxatilis* made significantly fewer overlaps on its own thalli than on neighbouring thalli in three-species mixtures ( $P=0.05$ ) (Fig. 5). No significant differences in the number of thallus overlaps were observed for *X. parietina* in any species mixture.

### Discussion

Nutrient addition led to an increase in lichen thallus growth rate compared with control applications where no nutrients were supplied, suggesting that in the control treatments, thallus growth was limited by nutrient availability. Growth rate of lichen thalli was positively correlated with nutrient

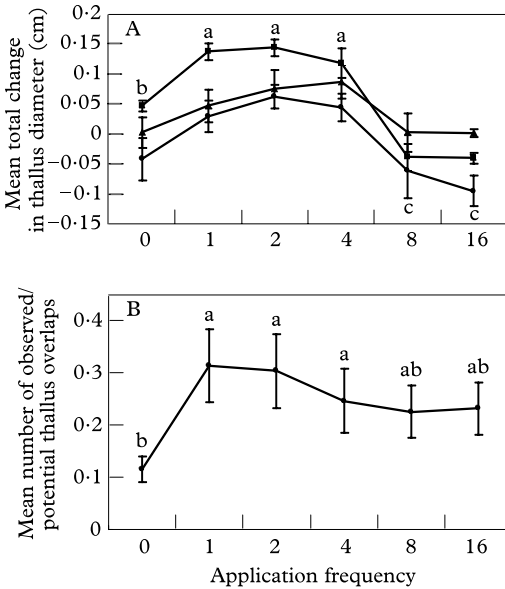


FIG. 4. The effects of application frequency of Hoagland's Solution. A, mean total change in thallus diameters for *Parmelia caperata* (■,  $n=24$ ), *P. saxatilis* (●,  $n=24$ ) and *X. parietina* (▲,  $n=24$ ); B, number of thallus overlaps (all species mixtures). Data not sharing a common letter differ significantly (Tukey HSD test  $P<0.05$ ). Bars are SEM,  $n=72$ .

application rate up to moderate ( $\times 1$ ,  $\times 2$  and  $\times 4$ ) application frequencies but at higher nutrient applications ( $\times 8$  and  $\times 16$ ) reduced thallus growth occurred, perhaps as a result of nutrient toxicity (Nash 1996) or other ionic imbalance.

It was predicted that under the relatively high pH regime of Hoagland's solution (pH 6.5) *P. saxatilis*, an acidophytic species, would grow less than either *P. caperata*, a neutrophytic species, or *X. parietina*, a nitrophilous species. However, the performance of *P. saxatilis* was only below that of the other species in monospecific mixtures (Fig. 3). In multispecies pair-wise mixtures growth of *P. saxatilis*, *P. caperata* and *X. parietina* were similar, suggesting that *P. saxatilis* may be able to tolerate elevations in pH and grow as well as neutrophytic and nitrophilous species, at least in the short term (one year).

Although growth of *X. parietina* was less than predicted at higher nutrient levels ( $\times 8$

and  $\times 16$ ) it was still significantly more than either *P. caperata* or *P. saxatilis* (Fig. 4A). The lower growth rate observed for *X. parietina* could be a consequence of the high N content of Hoagland's Solution. Since *X. parietina* is abundant near bird perching sites and in areas where eutrophication from animals occurs, it may follow that nitrogenous compounds associated with fecal deposits are necessary to increase thallus growth in this species (Armstrong 1984). Alternatively *X. parietina* may require an elevated pH or perhaps a specific nutrient/pH combination (A. R. Welch, unpublished). Recent studies suggest that *X. parietina* has a high tolerance to N pollution but excessive N exposure can damage both photobiont and mycobiont particularly in acidophytic and neutrophytic species by reducing chlorophyll *a* and ergosterol concentrations (Gaio-Oliveira *et al.* 2004). At high nutrient application frequencies ( $\times 8$  and  $\times 16$ ) thallus growth rates of all three species were significantly lower than at  $\times 0$ ,  $\times 1$ ,  $\times 2$  and  $\times 4$  (Fig. 2). This might suggest that nutrient toxicity reduces thallus growth, perhaps as a result of a breakdown in the symbiosis (Nash 1996) or that build-up of the components of the nutrient solution within the thallus were generating large osmotic potentials in the fungal apoplast resulting in the loss of cellular water and leading ultimately to plasmolysis (Gaio-Oliveira *et al.* 2004).

When these three species were each placed in monospecific mixtures fewer overlaps were observed (as predicted) than when in two- and three-species mixtures. This might have arisen as a consequence of reduced growth along the points of contact between neighbouring thallus margins resulting in a 'truce' situation. This is common among crustose species (Pentecost 1980) but observed on fewer occasions in foliose species since the less addressed thalli are not restrained by the substratum and are therefore able to make overlaps more easily. Instead the leading edges of foliose thalli tend to make contact and the resultant compressional forces serve to raise both thalli further above the substratum (A. R. Welch, personal observation).

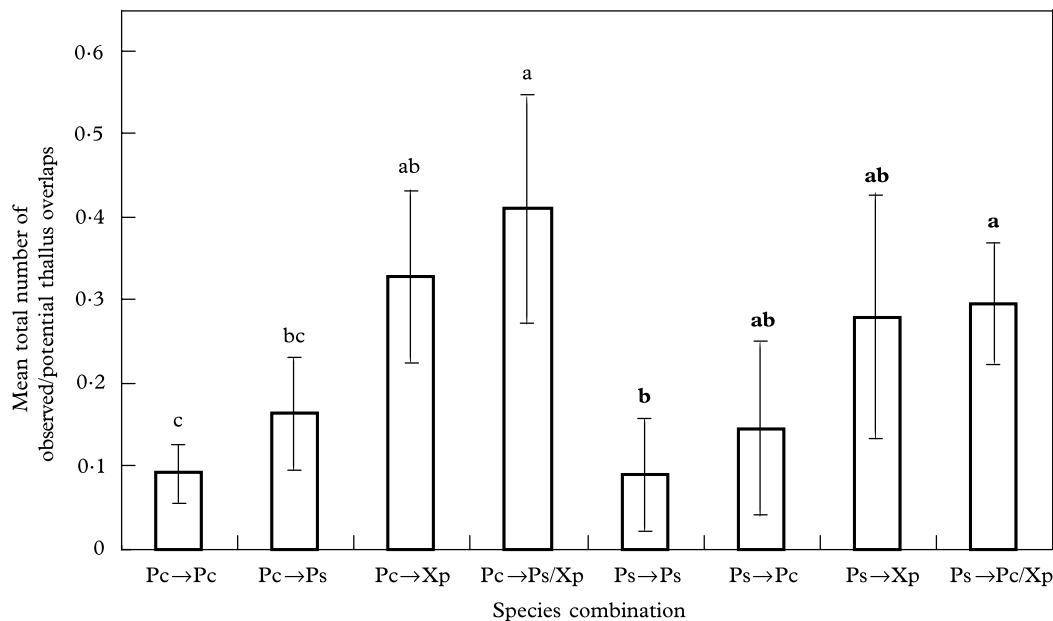


FIG. 5. The mean number of thallus overlaps made, regardless of application frequency of Hoagland's Solution, for *Parmelia caperata* (Pc) and *P. saxatilis* (Ps) at each species mixture. Data not sharing a common letter differ significantly (Tukey HSD test  $P=0.05$ ; Pc data in normal type and Ps data in **bold** type). Bars are SEM,  $n=36$ . For notation see Figure 3.

All pair-wise combinations of *P. caperata*, *P. saxatilis* and *X. parietina* produced similar thallus growth at all nutrient applications although in three-species mixtures *P. caperata* and *X. parietina* grew significantly more than *P. saxatilis* (Fig. 3). This suggests that the growth rates of thalli in three-species mixtures cannot be predicted from growth in two-species mixtures, possibly a result of inter-species differences in thallus morphology. Since the thalli of all three species are elevated above the substratum it is possible that contact between neighbouring thalli results in a reduction in thallus growth rate and that this is simply more pronounced in *P. saxatilis*. However, a comparison of two species mixtures does not support this hypothesis, as *P. saxatilis* did not show greater growth in the presence of the addressed *X. parietina*. This suggests that although thallus morphology is an important attribute it may not be solely responsible in determining the success of a species. It is likely that thallus chemistry plays a

significant role with the production of offensive and defensive secondary compounds contributing to the ecological success (distribution) of a species (Rogers 1990). Although the growth of *X. parietina* was similar when in combination with either *P. caperata* or *P. saxatilis*, it was being compromised by the less addressed thalli of these species. However, its ability to tolerate an elevated nutrient status may be one method by which it could compensate, particularly if the growth of *P. saxatilis* was being compromised by the elevated pH. That all three species demonstrated increased growth at medium nutrient applications ( $\times 1$ ,  $\times 2$  and  $\times 4$ ) than at  $\times 0$  suggests nutrients were limiting lichen growth.

The growth rate of a species ultimately determines the time taken for neighbouring thalli to make contact and nutrient application frequency had a significant effect on the number of thallus overlaps made during the course of the experiment (Table 2). As predicted, moderate nutrient applications ( $\times 1$ ,



$\times 2$  and  $\times 4$ ) led to significantly more thallus overlaps being recorded than in the control treatment (Fig. 4B).

Whether one thallus successfully overgrew another appeared to be determined by differences in thallus morphology, with the less addressed thallus usually overgrowing the more addressed one. For instance, *P. caperata* overgrew *X. parietina* significantly more often than it overgrew its own thalli (Fig. 5). Since the degree of thallus adpression among conspecifics would be similar, any morphological advantage between individuals of the same species would reflect minor genetically and environmentally induced differences in growth form. In this experiment, the morphologically similar *P. saxatilis* and *P. caperata* did not show any strong tendency to dominate each other, although previous field research (John 1992) had led us to predict that *P. caperata*, with thicker thallus lobes, would dominate *P. saxatilis*. However, when *P. caperata* and *P. saxatilis* were placed in three-species mixtures with *X. parietina* significantly more overlaps were observed than in monospecific mixtures (Fig. 5), despite densities of thallus fragments remaining constant in all treatments. This might be attributed to both species overgrowing the more addressed thalli of *X. parietina* more easily than their own or each others thalli. However, when *P. saxatilis* was grown with *X. parietina* similar numbers of thallus overlaps to those made in monospecific mixtures were observed (Fig. 5). This could be explained if thalli of *P. saxatilis* and *X. parietina* are competitively similar, and a competitive advantage is only seen when a third species (*P. caperata*) is present. However, this is unlikely since the thallus margin of *P. saxatilis* is considerably less addressed than that of *X. parietina*.

Similar species interactions have been observed by Armstrong (1986) between other lichens, namely *Parmelia glabratula* and *Physcia orbicularis*, which tended to grow better in the presence of two competitors than one. In addition, the growth of the competitively dominant *Parmelia conspersa* was reduced in the presence of two species (Armstrong 1986). Such competitive

interactions may allow lichen species to coexist on the same substratum.

Alternatively it might be more realistic to assume that the ability of *X. parietina* to tolerate elevated nutrient levels and/or its calcicolous nature (R. A. Armstrong, personal communication) provides a small competitive advantage when placed in multispecies mixtures with thalli of *P. saxatilis*. It is also possible that an elevated pH compromised the growth of *P. saxatilis* and therefore reduced its competitive ability. This could account for the similarity between the number of thallus overlaps made by *P. saxatilis* on *X. parietina* and on its own thalli.

Although nitrophilous species such as *X. parietina* might have the ability to utilize additional nutrients and/or an elevated pH to promote growth rates, this could only prove a competitive advantage if other lichen species did not colonize and dominate substrata rapidly and their thallus morphology permits sufficient overlaps.

The results outlined in this paper are in broad agreement with the work of Armstrong (1984, 1986, 2000). It appears that several factors might dictate the ability of a lichen species to compete. In addition, any naturally selected advantage, such as the ability to reduce herbivore grazing by the production of allelochemicals, could be significant in determining the competitiveness of a species (Armstrong 1986; Rogers 1990) since grazing by microarthropods reduces the thallus area and consequently decreases photosynthetic ability.

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