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The effect of anthropogenic nutrient addition on the growth and competitive abilities of selected lichen species

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The effect of anthropogenic nutrient addition on the growth and competitive abilities of selected lichen species.

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Welch, A.R. (2002) The effect of anthropogenic nutrient addition on the growth and competitive abilities of *Parmelia caperata, P. reddenda, P. saxatilis* and *Xanthoria parietina* in Cornwall. Ph.D Thesis, The Open University, U.K.

Abstract: The effects of anthropogenic nutrient addition and species combination on the growth and competitive abilities of four widespread foliose lichens was investigated using two replicated factorial nutrient addition experiments conducted in conjunction with field studies.

The first was carried out on thallus fragments of *P. caperata* (Pc), *P. saxatilis* (Ps) and *X. parietina* (Xp) transplanted onto a saxicolous substrate (roofing slate). Thallus growth rates were dependent on lichen species (F=12.76; $P<0.001$) and application frequency (F=59.31; $P<0.001$) with low (x1) to medium (x2 & x4) applications significantly increasing growth (increase in final thallus diameter), compared with control treatments (no nutrients). At higher (x8 & x16) applications a significant reduction in growth occurred compared with controls.

Competition (number of thallus overlaps) was also dependent on both lichen species (F=5.62; $P<0.001$) and application frequency (F=5.16; $P<0.001$). All three species exhibited symmetrical competition under experimentally elevated nutrient conditions.

In the second transplant experiment using *P. caperata* and *P. reddenda* (Pr), growth rates were again dependent on lichen species (F=8.31; $P<0.001$) and application frequency (F=112.17; $P<0.001$). Both species exhibited symmetrical competition under experimentally elevated nutrient conditions.

Field studies suggest asymmetrical competition occurs between *P. caperata* & *X. parietina* (Pc→Xp) where no experimentally elevated nutrient conditions exist. However,

competition between *P. caperata* & *P. saxatilis* and *P. saxatilis* & *X. parietina* remains symmetrical (Pc↔Ps; Ps↔Xp).

On beech, under conditions of no experimentally elevated nutrients, competition between *P. reddenda* and *P. caperata* was symmetrical (Pr→Pc). Furthermore there is evidence to suggest niche separation occurs between these two species and that this becomes less important under conditions of nutrient enhancement. These results suggest elevated nutrient levels alter growth rate and competition which affect lichen community structure.

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For Zara

21st June 1988 – 9th October 2000

Chapter One

Introduction

1.1 Introduction

Anthropogenic nutrient addition arising from the doubling of agricultural food production within the last 40 years has seen a 6.87-fold increase in nitrogen (N) addition and a 3.48-fold increase in phosphorus (P) addition (Tilman, 1999). Furthermore it is estimated that the next 50 years will see the final period of rapid agricultural expansion, accompanied by 2.4 to 2.7-fold increases in N and P-driven eutrophication (Tilman *et al.*, 2001).

Such high levels of N deposition can lead to hypertrophication where nutrient levels are greatly elevated above those found naturally. Freshwater and marine ecosystems suffer as a result due to run-off from agricultural fields which may ultimately lead to a decrease in species diversity, an increase in plant and animal biomass, increased water turbidity, increased rate of sedimentation and the promotion of anoxic conditions (Mason, 1991).

In addition, the aerial redistribution of various forms of N puts many terrestrial ecosystems at risk from the effects of eutrophication (Tilman, 1999). This is observed in environments where the nutrient supply is suboptimal. Here any increase in nutrient supply from the deficiency range causes an increase in plant growth rate and ultimately a reduction in species diversity (Tilman, 1982; Marschner, 1995).

Such changes in community composition may be easily recognised in the case of larger plant species like grasses where numerous experiments have been established to look specifically at the effects of nutrient addition on growth and changes in community composition (Austin & Austin, 1980). However, smaller plant species exhibit similar effects when placed under eutrophic or hypertrophic conditions but their changes in community composition may be easily overlooked. This is almost certainly the case with lichen communities despite being found on a wide variety of substrata across a broad range of ecological amplitudes.

Although lichens are often regarded as lower plants they are in fact 'composite organisms' consisting of a fungal (mycobiont) and an algal (photobiont) component living in symbiotic association. Such an association usually results in the formation of a stable body or thallus within which the fungal and algal components can be easily distinguished (Hale, 1967).

Studies of the impact of nutrient addition on lichen communities have revealed that some species show increased radial growth rates (Sanchez-Hoyos & Manrique, 1995; Miller & Brown, 1999; Armstrong, 2000) while other (acidophytic) species, like *Parmelia saxatilis*, show significantly reduced growth (Armstrong, 1984; Vagts & Kinder, 1999; Armstrong, 2000). This reduction in growth rate may be the direct result of nutrient toxicity which may ultimately affect a breakdown in the symbiosis (Nash, 1996) between algae and fungi. Furthermore, there is evidence to suggest that in 'stress' situations, arising through exposure to hypertrophic conditions, some foliose species like *Hypogymnia physodes* concentrate a higher proportion of the photosynthate within the fungal component, rather than expend it in thallus growth (Farrar, 1976).

The consequences of these changes in lichen growth may be a determining factor in community composition which is itself determined by competition intensity. Under oligotrophic or mildly eutrophic conditions the individual effects of all neighbouring lichen thalli may be similar with no single species being dominant. In such a situation diffuse competition is said to occur (Keddy, 2001). However, as nutrient status increases there tends to be a shift towards monopolistic competition where one of the neighbouring species is the primary contributor to competition intensity while the other species have a relatively minor effect (Keddy, 2001).

To this end the extent to which nutrient addition affects thallus growth in large foliose species like *Parmelia caperata* (L.) Ach., *P. reddenda* (Stirton), *P. saxatilis* (L.) Ach., and *Xanthoria parietina* (L.) Th. Fr., is examined in this thesis along with effects on their competitive abilities when placed in monospecific and multispecific mixtures. Nitrophilous species like *X. parietina* would be expected to demonstrate increased growth rates under enhanced nutrient conditions, quickly making contact with neighbouring thalli. Whether thalli are successful at overgrowing those of their neighbours may depend on the differences between the morphological characteristics of the competing thalli of these species.

Lacking the conventional root systems of vascular plants, most species depend on atmospheric sources of nutrients which are taken up across the whole surface of the thallus. The rates of absorption and loss of these nutrients are determined by the anatomical and morphological characteristics of individual thalli along with the prevailing environmental conditions.

Dissolved nutrients may contact the thallus through precipitation, sedimentation and impaction. Alternatively they may be taken up by gaseous absorption which, due to a lack of stomata, occurs across the entire thallus surface. Many species colonise soil and rock substrata and nutrient uptake from soil pools can occur in some species as demonstrated by *Peltigera canina* (Goyal & Seaward, 1982).

Lichens exposed to lithic nutrient sources are able to break down the substrate mechanically if they possess rhizines (root-like fungal outgrowths from the lower cortex which serve to provide attachment), and chemically, using secondary compounds to dissolve nutrients which, once solubilised, may be absorbed.

On trees nutrient streaks may be exploited by some epiphytic species while other lignicolous species obtain nutrients directly from the bark. Furthermore terricolous and saxicolous species collect dust particles in their intracellular spaces resulting in the accumulation of high concentrations of nutrients within the thallus. The efficiency of this accumulation is related to thallus morphology and shows much variation between species. However, some species like *Xanthoria parietina* contain large intracellular spaces which can make up 18% of the thallus. These may serve as very efficient nutrient stores (Nash, 1996).

The importance of nutrients for plant growth has long been recognized. In environments where N is limited, increases in N availability result in a significant increase in photosynthetic rate and leaf biomass (Shangguan *et al.*, 2000; Kao *et al.*, 2001). Such increases occur until another factor becomes limiting or until N concentrations become toxic, whereupon reductions in growth are observed.

Different concentrations of N application promote different growth responses within plants. For example, experiments with the growth of Whitegrass (*Cortaderia pilosa*) indicate that root growth occurs preferentially at low N levels (1-3 mg l^{-1}) while green shoot material grows more at higher levels (10 mg l^{-1}) (Wilson *et al.*, 2001). Such information has been used in intensive farming practices in order to maintain and increase crop yields through the application of N.

Increased use of N based fertiliser has led to the suggestion that European ecosystems may be at serious risk from eutrophication (Emmett *et al.*, 1995; Eugster *et al.*, 1998). This is particularly evident in the Netherlands which has high levels of N deposition estimated to be 40 Kg N ha^{-1} yr^{-1} (Van Der Eerden *et al.*, 1998).

There is much evidence to suggest that nutrient addition causes changes in the floristic composition (Wilson & Tilman, 1991; Schellberg *et al.*, 1999) and species diversity of plant communities. Furthermore, fertiliser addition experiments have shown that the competitive balance between plants can be altered by increasing the competition between species which may become more intense as soil nutrient levels increase (Gerdol *et al.*, 2000).

In heathland ecosystems *Nardus stricta* is being replaced by *Calluna vulgaris* in areas where nutrient inputs have increased significantly (Hartley & Amos, 1999). Similar effects have been found in salt marshes where a nutrient-induced reversal in the competitive dynamics among salt marsh perennials was observed (Levine *et al.*, 1998) which could ultimately change the patterns of plant zonation in these habitats. Furthermore, changes in the rankings of relative competitive performance have been shown to exist between shoreline plant species when different concentrations of a modified Hoagland's Solution were applied (Keddy *et al.*, 2000). Intertidal community structure may also be affected by nutrient addition from seabird guano which may result in the elevated vertical distribution of the lichens *Caloplaca marina* and

Xanthoria elegans at the expense of *Physcia* species, which in the supralittoral fringe, may be completely removed (Wootton, 1991).

Such eutrophic conditions promote algal growth (O'Dare, 1990) and in the supralittoral fringe seabird guano appears to increase the abundance of the green alga *Prasiola meridionalis* and *Mastocarpus papillatus*, which in turn reduces the abundance of the lichen *Verrucaria mucosa* as a direct result of increased competition with *Prasiola meridionalis* in the splash zone (Wootton, 1991).

Resource enrichment can also lead to habitat invasion by non-native plant species, thereby changing community composition (Davis *et al.*, 2000). Such changes in competitive dynamics between plants have also been observed for lichens and it is proposed that nutrient addition alters the competitive balance between species which in turn determines their relative abundance (Armstrong, 2000). This may ultimately result in the competitive exclusion of some lichen species (Lawrey, 1981; Vagts & Kinder, 1999) therefore leading to a reduction in diversity.

Early models of competition made the assumption that two or more competing species could not coexist on a single resource without the species forming a competitive hierarchy which resulted in poor competitors being replaced by superior ones (Tilman, 1982). When two species do compete for the same resource that is in short supply they may evolve differences that could reduce competition. For example, lichen thalli that are less adpressed are able to overgrow more adpressed neighbouring thalli.

The concept of r- and K-selection (MacArthur & Wilson, 1967) allows species to be characterised by the relative importance of r (rate of increase) and K (saturation density) in their life cycles. During the initial colonisation of a habitat r-selection predominates followed ultimately by K-selection. Species that are r-selected rarely suffer much pressure from interspecific competition (although this is dependent upon where they grow) and tend to evolve few, if any, mechanisms for strong competitive ability. This arises from the fact that ruderals under stresses such as those that develop under competition tend to reduce growth and invest in reproduction (Grime – personal communication). Alternatively, K-selected species are able to exist under great interspecific competitive pressures that operate within, as well as between, the species (Krebs, 1994).

According to Grime (1979) three primary plant strategies exist along the r-K continuum with ruderals (R) and stress-tolerant (S) strategies corresponding respectively to the extremes of r- and K-selection, while competitors (C) occupy an intermediate position.

Lichens demonstrate the main characteristics of stress tolerance (S) by having a slow rate of growth, being long-lived and, in some cases, responding well to physiological change (fluctuations in the environment due to seasonality). Grime (1979) characterises lichens as being stress-tolerant organisms which are adapted to relatively undisturbed conditions experiencing moderate intensities of stress. However, it is not realistic to categorise all lichens in the same way since their rates of growth and competitive abilities are extremely variable.

Furthermore, it is difficult to predict the outcome of competition due to competition coefficients (Krebs, 1994) which describe the ability of a species to prevent a competitor from gaining access to limited resources. The competition coefficients are represented for the two species as α and β in the Lotka-Volterra equations. An example of such interference competition would be the use of allelopathic chemicals by plants to keep competing species from gaining access to resources (Krebs, 1994).

Gill (1974) argues that a species can evolve competitive ability through α-selection. Therefore any mechanism that successfully prevents a competitor from gaining access to limiting resources will increase α-selection (or β-selection) and improve the competitive ability of that species. Such a mechanism of interference competition may be used by some lichens since many species are able to produce a wide variety of allelopathic compounds. This would act to increase α-selection in some species and increase their competitive ability.

As previously mentioned some species may show a reduction in thallus growth rate due to concentrating photosynthate within the fungal component (Farrar, 1976) when placed under stress conditions. This may allow the synthesis of secondary allelopathic compounds thus increasing their competitive ability through α-selection. In this way some species are able to tolerate prolonged periods of stress therefore justifying Grime's characterisation of lichens as being stress-tolerant organisms.

Competitive interactions can be complex and an understanding of the mechanisms underlying the survival of one species at the expense of the other or the ability of two species to coexist is essential (Tilman, 1987) particularly since the impact of nutrient-driven competitive change is becoming increasingly widespread. Therefore careful monitoring of nutrient additions and the assessment of the effects these have on the growth and competition of species is of much importance.

1.4 The effect of nutrient addition on lichen community structure

It is proposed that nutrient addition will increase lichen growth rates at certain concentrations and decrease them at others. Where increased growth rates are observed there will be a reduction in the time taken for neighbouring thalli to make contact. The resulting overlaps may provide relevant information through changes in the competitive dynamics between species which could be subsequently used to make predictions on the effect of nutrient addition on lichen community composition. Whether species in these experiments are removed through nutrient toxicity or directly through competition from neighbouring thalli is fundamental to our understanding of the way in which anthropogenic nutrient addition affects community composition and species diversity.

Therefore, in situations where N is limiting, any disturbance in the N cycle, which ultimately increases the availability of mineral N, will result in an increase in growth followed by changes to community structure brought about by intra- and interspecific competition. Careful observation of the growth and competition of indicator species may, as in SO_2 pollution monitoring, prove to be a useful tool in recognising ecosystems that are being subjected to a slowly increasing nutrient status. Although this would be regarded by some as having limited use, due to lichens having slow growth rates (Table 1) and therefore a correspondingly slow response to change, it could nevertheless prove valuable in long-term pollution studies and could perhaps be used in conjunction with diffusion tubes as a means of monitoring N pollution.

Hale (1967) reviewed work on thallus growth rates and observed that data for some species like *Parmelia conspersa* and *P. sulcata* had widely ranging values. Armstrong and Smith (1992) looked at the variation in the growth of individual lobes of *P. conspersa* and reported similar results. This may well reflect inaccuracies incumbent in the various methods by which growth rates were measured, for example, tracing thallus outlines onto acetate sheets or taking measurements from photographed thalli, or alternatively these changes in thallus growth may be a product of the environment in which these species are growing. If the latter is the case then it suggests, as with all plants, that these species are able to grow at different rates when placed under different environmental constraints.

Species	Mean growth rate (mm) with SE in parentheses
Parmelia caperata	4.5 (0.68)
P. conspersa	4.19 (1.39)
P. reddenda	3.72 (0.64)
P. saxatilis	2.25 (1.75)
P. sulcata	1.71 (0.29)
Xanthoria parietina	2.5 (0.43)

Table 1. Average annual radial thallus growth rates of some common foliose lichens.

There are many important questions regarding the effect of nutrient addition on lichen growth rates and intra- and interspecific competition. For example, do growth rates increase and if so do they increase uniformly? Evidence put forward by Armstrong and Smith (1992) suggests that thallus growth is influenced by several causes, namely the genetic origin of lobes comprising the thallus, lobe width (wide lobes growing faster than narrower ones), differences in behaviour of the photobiont or mycobiont and variations in the levels of secondary compounds within thallus lobes.

Whether some species utilise nutrients better than others is a fundamental consideration when attempting to rationalise the impact anthropogenic nutrient addition may have on the competitive dynamics between large foliose species. This is important since it has been shown that nutrient addition can alter the competitive balance between species and that this in turn determines their relative abundance (Armstrong, 2000). Therefore increasing our awareness of the impact that anthropogenic nutrient addition has on lichen growth and competition may allow a better understanding of the underlying causes that determine lichen community structure.

1.5 Format of the thesis

In order to address the issues previously outlined species surveys were carried out on saxicolous (Chapter Two) and corticolous (Chapter Four) substrata in order to determine the abundance and competitive interactions that occur naturally (without any anthropogenic nutrient addition from dilute Hoagland's Solution). The influence of aspect on abundance and competitive ability was also noted. Furthermore, the effect of height (between 1.0m – 2.0m) on corticolous substrata was recorded to determine any vertical zonation.

Two field experiments were also set up to determine the effect of nutrient addition using dilute Hoagland's Solution on growth rate and competitive ability (intra- and interspecific competitive interactions). Hoagland's Solution was chosen as it closely approximates to organic fertilisers in mineral nutrient composition (Appendix-Table 4). Therefore, lichens may be exposed to these nutrients under conditions of fertilisation near farms and from seabirds near coastal locations.

It could be argued that since lichens consist of a fungal component (95%) and an algal component (5%) it would have been appropriate to use a specialised fungal nutrient media. However, fungal nutrient media are rarely used outside the laboratory and lichens would not normally become exposed to them.

In addition, Hoagland's Solution, or modified forms of it (Keddy, 2001), has been used by many previous authors therefore allowing comparative studies with other work to be made.

Chapter Two

A survey of three large foliose lichens, *Parmelia caperata*, *P. saxatilis* and *Xanthoria parietina* was carried out on north, south, east and west facing saxicolous substrata (granite and slate) to determine their natural abundance. This was represented using three measurements of thallus area (dominant, subordinate and overlap) taken from photographs of these species in pair-wise interactions.

Competition between *Parmelia caperata*, *P. saxatilis* and *Xanthoria parietina* at each aspect was determined by observing the frequency of thallus overlaps made by each species during pair-wise interactions. This provided an insight into whether any dominance hierarchy existed between them and to what extent this might change with addition of nutrient solution in Chapter Three.

Chapter Three

A field experiment was established to look specifically at the effect of nutrient addition (dilute Hoagland's Solution) administered at six different concentrations on the growth and competitive abilities of *P. caperata, P. saxatilis* and *X. parietina*, using thalli transplanted to a slate substrate.

Growth rates were represented as a change in thallus diameter while competitive ability was determined by comparing the actual number of overlaps made with the total number of potential overlaps that could have been made. This provided an indication of the effect nutrient addition might have on changing the competitive dynamics between these three species.

Chapter Four

A species survey carried out within the Lanhydrock Estate detailed the epiphytic lichen cover found on beech trees (*Fagus sylvatica*) at each of four aspects (N, S, E and W). Particular emphasis was placed on the abundance and intra- and interspecific competitive abilities of *P. caperata* and *P. reddenda*. Abundance was represented as the number of thalli of both species present at each aspect. Competitive interactions were represented as either a scaled or unscaled (1:1) ratio of the number of overlaps made to those not made between thalli in pair-wise interactions.

This provided an insight into whether any dominance hierarchy might exist between *P. caperata* and *P. reddenda* and whether any vertical zonation could be determined between 1.0m – 2.0m on the boles. Furthermore, an indication of how competition might change under experimental nutrient addition in Chapter Five could be established.

Chapter Five

Chapter Five considers the effect of four nutrient solution applications on the growth (change in thallus diameter) and competitive abilities (frequency of thallus overlaps) of *P. caperata* and *P. reddenda*, using a reciprocal transplant experiment conducted on the boles of beech trees. This provided an indication of how nutrient addition might alter the competitive dynamics between these two species and in turn determine lichen community structure.

Chapter Six

The final chapter summarises the findings of this thesis with respect to the effects of anthropogenic nutrient addition on lichen growth rates and competitive ability. In addition the wider implications of how changes in growth rate and competitive behaviour may affect lichen community structure are also discussed.

Nutrient levels within the environment continue to rise steadily and this has led to eutrophic and hypertrophic conditions being reported. Such increases have resulted in the publication of the 1991 Nitrates Directive (91/676/EEC) which aimed to reduce water pollution from nitrates and to prevent further increases in nitrate pollution by setting maximum nitrate levels at 210 Kg N ha^{-1} from 1998 with a further reduction to 170 Kg N ha^{-1} from 2002 (European Report, 1998).

It is hoped that this thesis will provide some insight into the impact nutrient addition has on lichen growth and competition and how this in turn may determine lichen community structure.

1.6 Ecology of the species

Four species of common and widely distributed lichens were used in this study; *Parmelia caperata*, *P. reddenda*, *P. saxatilis* and *Xanthoria parietina* all of which colonise a wide range of substrata (Figure 1).

On nutrient-rich and enriched substrata *X. parietina* is often abundant and grows well under near neutral pH conditions while *P. caperata* and *P. saxatilis* prefer neutral and slightly acidic substrata respectively. *P. reddenda* is a rather local ancient woodland indicator species occurring mainly in the South and West of the British Isles, Southern Scandinavia, France, North and South America and East and South Africa (Purvis *et al.*, 1992).

In well lit unpolluted environments each species is capable of forming large rosettes with thallus diameters up to 20 cm for *P. caperata* and *P. saxatilis*, 10 cm for *P. reddenda* and 15 cm for *X. parietina*.

In SO_2-polluted environments *P. caperata* survives SO_2 levels of approximately 70 μm m^{-3} while *P. reddenda*, *P. saxatilis* and *X. parietina* are only able to tolerate SO_2 levels below 70 μm m^{-3} (Purvis *et al.*, 1992).
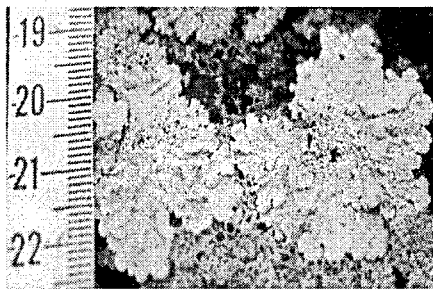
(a). *Parmelia caperata*
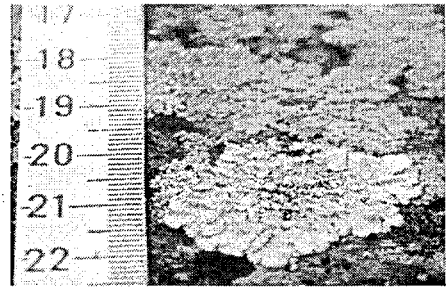
(b). *Parmelia reddenda*
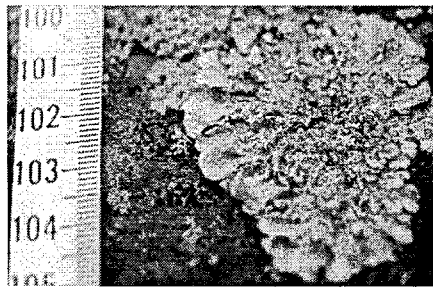
(c). *Parmelia saxatilis*
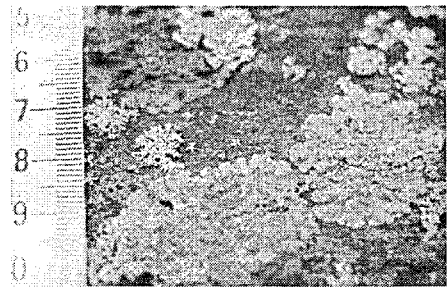
(d). *Xanthoria parietina*

Figure 1. The four lichen species used in this thesis photographed at field sites in Cornwall between 1992 and 2002.

Chapter Two

Competitive interactions of *Parmelia caperata*, *P. saxatilis* and *Xanthoria parietina* on saxicolous substrata

2.1 Introduction

It has been suggested that lichens are likely to compete for space and light (Oksanen, 1984) on a variety of substrata. Species with large thallus areas are able to absorb more light and available nutrients than their neighbours, possibly giving them a competitive advantage.

Other factors such as substrate pH, the water retentive capacity of both substrate and thalli and substrate stability are also important in determining competition, since the requirement for specific microenvironmental factors may be critical in determining the outcome of a particular competitive interaction and therefore the position and abundance of thalli on a particular substrate.

Of the many factors that affect the wetting and drying cycles of individual lichen thalli aspect is perhaps the most important. In northern temperate latitudes experiments have shown that north facing thalli dry out more slowly than south facing thalli (Armstrong, 1975). The net carbon assimilation rate (NCAR) of the thallus increases as thallus water content increases until an optimum is reached, usually between 65-90% thallus saturation depending on individual thallus morphology. The NCAR then declines when thallus saturation is reached resulting in a reduction in thallus growth.

Differences in the rate of thallus drying on north and south facing aspects results in the latter being able to achieve an optimum thallus water content for longer periods than the former since thalli on north facing aspects may have a thallus water content in excess of the optimum. The consequence of this is that efficient photosynthetic activity is maintained for longer periods while thallus saturation is at or near the optimum (Armstrong, 1976a). Furthermore there is evidence to suggest that wetting and drying of the thallus facilitates nutrient flow from the mycobiont to the phycobiont (Smith, 1975).

The rate of thallus growth determines the frequency with which neighbouring thalli make contact. When contact between two thalli occurs one may out-compete the other by overgrowth or by the production

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of allelochemicals (Dale, 1985). Alternatively, a 'truce' may develop in which radial growth of both species is terminated at the points of contact along the thalline margins (Pentecost, 1980). This is particularly evident during intra- and interspecific competitive interactions between saxicolous crustose species. The competitive interactions of foliose species result in a 'truce' situation occurring less frequently since the thalline margins are not restrained by the substrate and are therefore free to overlap neighbouring thalli (Pentecost, 1980).

The morphological differences between thalli of neighbouring species may be very different, with one species being less adpressed than the other. This may provide a competitive advantage allowing one thallus to grow over the top of another. The study of competitive interactions between species provides an indication of how lichen community composition may change over time. Such studies are particularly important for saxicolous lichen communities, whether foliose or crustose, since the predominantly greater substrate stability of undisturbed rock may result in higher frequencies of observed thallus overgrowth (Lawrey, 1991) compared with terricolous and epiphytic lichen communities where there is a greater chance of abiotic and biotic disturbance. Therefore, competition would be predicted to have a large role in organising the community.

By recording observations of thallus overlaps this study aims to determine whether a competitive hierarchy exists between *P. caperata*, *P. saxatilis* and *X. parietina* as they compete with themselves and each other for space on the substrate. The extent to which this competition is affected by aspect will also be investigated.

Where neighbouring thalli make contact and an overlap is observed, the surface areas of the overlapping (dominant thallus area) and overlapped (subordinate thallus area) thalli may be calculated and related to aspect. Similarly, the area of the subordinate thallus that is actually being covered by the dominant thallus may be estimated (overlap area), assuming radially symmetrical growth from a central point on the subordinate thallus.

For example *X. parietina* may be expected to grow faster in areas of eutrophication since it is a nitrophilous species. Therefore it should cover large areas of the substrate under eutrophic conditions than neighbouring thalli of another species. This would be reflected by large thallus areas. Whether it overlaps neighbouring thalli would largely depend on the morphological differences between thalli of the two species.

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Here the following hypotheses will be tested:

(i).   Dominant, subordinate and overlap thallus areas are dependent on the competing species (*P. caperata*, *P. saxatilis* and *X. parietina*) and aspect (N, S, E and W).

(ii).   The frequency of thallus overlaps is assumed to be independent of lichen species and aspect. All foliose species are therefore expected to make similar numbers of overlaps under heterospecific pair-wise species combinations on neighbouring thalli.

Study area

      Cornwall occupies the South West peninsula of the British Isles. Lanhydrock Estate, owned by the National Trust, is situated approximately three miles south-east of Bodmin (SX085636). The Lanhydrock Estate is divided into several parkland areas containing a diverse lichen flora on predominantly oak, sycamore, ash, lime and beech substrata (Figure 2). In addition there are numerous natural and man-made saxicolous substrata composed mainly of granite and slate.
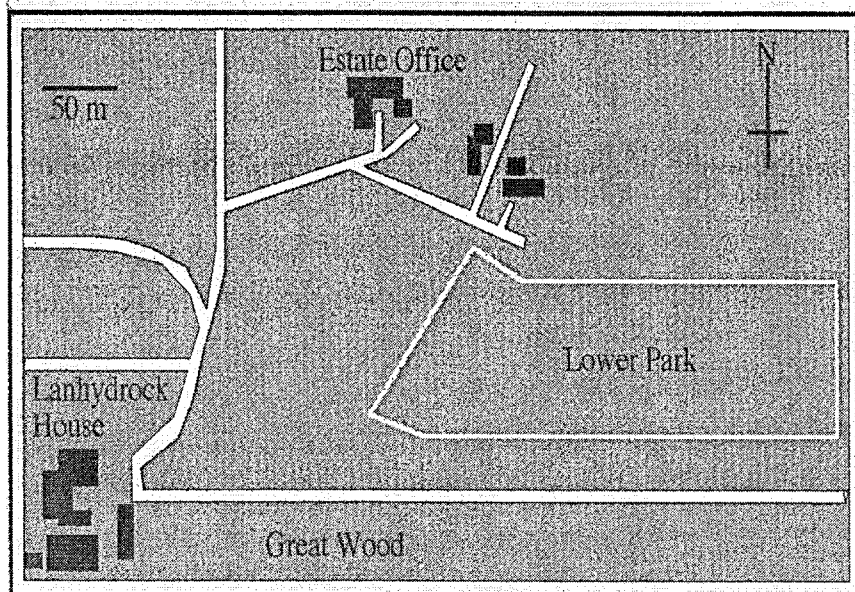
Figure 2. Map of the Lanhydrock Estate showing the location of parkland and buildings. Scale: 1 cm : 50 m.

Saxicolous substrata were examined for the presence of *P. caperata*, *P. saxatilis* and *X. parietina* between December 2000 and October 2001. Photographs were taken at locations (dry stone walls, gate posts, ornamental walls and buildings etc.,) within randomly chosen areas obtained from grid squares superimposed onto a large scale map (1 : 1250) of the Lanhydrock Estate. Individual grid squares were selected using the random number function on a scientific calculator (Sharp™ EL-9600). Photographs were taken at each location where thalli of these species contacted themselves or each other. Only thalli not shaded by vegetation (grasses, shrubs and bushes) or considered susceptible to adverse abiotic and/or biotic disturbance were selected. Photographs of competitive interactions were also taken at locations within randomly selected areas outside the estate, but within a 20 mile radius of it, and used for comparison.

Nine photographs (five within the estate and four outside) were taken for each of the nine species combinations (three intraspecific and six interspecific) at each of the four aspects (N, S, E and W). Aspect was recorded to within an accuracy of ± 20 degrees. Measurements of thallus area were taken from a total of 324 photographs (180 inside and 144 outside the estate).

Intra- and interspecific competition was evident where neighbouring thalli were observed to overlap at a point where they made contact (Figure 3).
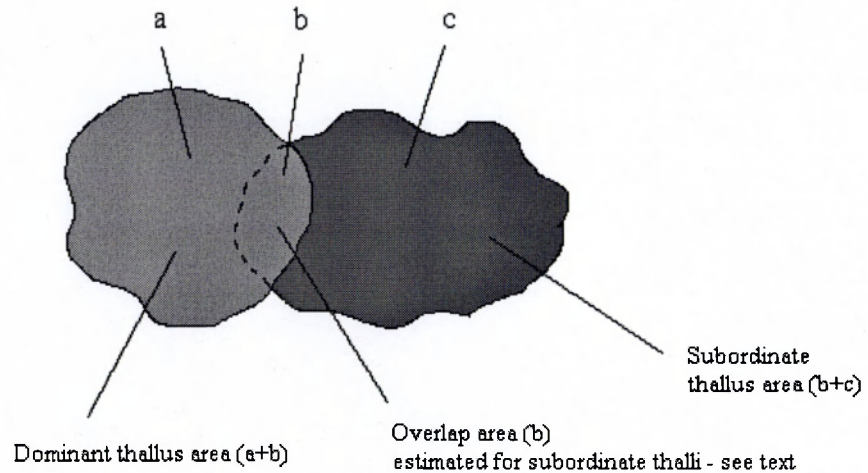
Figure 3. Diagram representing thallus 'A' (dominant) overlapping thallus 'B' (subordinate). The area of the subordinate thallus covered by the dominant thallus is represented as the overlap area.

Thallus overlaps were counted from photographs and then photocopied onto 2 x 2 mm^2 graph paper. Areas were calculated either using an image analyser or by counting whole squares covered by thalli and then summing partly covered squares. The accuracy of both procedures was checked using the paired samples t-test on thallus areas calculated from 50 photographs (25 using an image analyser and 25 by counting whole and part squares on graph paper) and found not to be significantly different ($t_{48} = 0.106$; $P = 0.916$) (Appendix-Table 1). Non-visible thallus areas were estimated based upon radially symmetrical growth of the thallus from a single point (Pentecost, 1980; Dale, 1985) with the assumption that growth rate of the thallus is uniform at all unimpeded points on the circumference. Data from subordinate thalli that had radial growth impeded by biotic sources (another neighbouring species not being studied) or abiotic sources (interference from chemicals (paint), rust (hinges on large granite gate posts) or chaffing from wire fences were not used. In addition the frequency with which overlaps were made between competing thalli was

recorded in order to determine whether a dominance hierarchy might exist. Due to low numbers, data from inside and outside the estate were combined (Table 8).

It is possible to have a situation where one thallus overlaps a neighbouring thallus while being simultaneously overlapped by the same neighbouring thallus. This was not observed in any of the photographs taken.

Statistical analysis

A nested design was used with three-way analysis of variance (ANOVA) (Zar, 1996) to determine the effect of site, aspect and species combination on dominant and subordinate thallus areas. An aspect factor with four levels (north, south, east and west) and a species combination factor with nine levels (three intraspecific and six interspecific) were nested with a site factor containing two levels (inside the estate and outside the estate). The area of subordinate thalli overgrown by dominant thalli (overlap area) was determined by the same method (Table 2). Tukey (Honestly Significant Difference) multiple means test (Zar, 1996) was used to determine significant difference between means. The frequency with which thallus overlaps were made by *P. caperata*, *P. saxatilis* and *X. parietina* was assumed to be independent of aspect and lichen species. This assumption was assessed using G-analysis for goodness of fit testing against the ratio of overlapped to non-overlapped thalli. The test was applied using the Yates correction since DF = 1 throughout (Table 9). All calculations were performed using Statistica™ 5.5 (Statsoft Inc., Tulsa, USA).

Factor	Levels			
Site:	1 (Inside estate);	2 (Outside estate)		
Aspect:	1 (North);	2 (South);	3 (East);	4 (West)
Sp. Comb.:	1 (Pc→Pc);	2 (Ps→Ps);	3 (Xp→Xp)	
	4 (Pc→Ps);	5 (Ps→Pc);	6 (Pc→Xp)	
	7 (Xp→Pc);	8 (Ps→Xp);	9 (Xp→Ps)	

Table 2. Three-way ANOVA layout for the effect of site, aspect and species combination (Sp. Comb.) on thallus area. The following notation is used throughout: *P. caperata* (Pc); *P. saxatilis* (Ps); *X. parietina* (Xp). The symbol '→' is used to represent a competitive interaction eg: Pc→Ps represents thalli of *P. caperata* overgrowing thalli of *P. saxatilis*.

Dominant thalli

A three-way nested ANOVA (aspect and species combination nested within site) indicated that site and aspect did not significantly affect the dominant thallus areas (DTA) of *P. caperata*, *P. saxatilis* and *X. parietina*. However, species combination was observed to have a significant effect. In addition, the effect of factor two (aspect) was modified by the effect of factor three (species combination) (Table 3).

Effect	DF	MS	F	P
(1) Site:	1	67938.9	1.57	0.210
(2) Aspect:	6	82174.4	1.91	0.080
(3) Sp. Comb.:	16	79606.8	1.85	0.026
Interaction 12:	-	-	-	-
Interaction 12:	-	-	-	-
Interaction 23:	48	64599.6	1.50	0.026
Interaction 123:	-	-	-	-
Error:	252	43112.24		

Table 3. Three-way nested ANOVA for the effect of site (factor one), aspect (factor two) and species combination (Sp. Comb.) (factor three) on dominant thallus area (DTA).

Since site and aspect had no effect on DTA a one-way ANOVA was used to determine more precisely the effect of lichen species on DTA. The results of this analysis indicated that the individual species significantly effected DTA (Table 4).

Effect	DF	MS	F	P
(1) Sp. Comb.:	8	115843.6	2.45	0.014
Error:	315	47215.9		

Table 4. One-way ANOVA for the effect of species combination (Sp. Comb.) on dominant thallus area (DTA).

However, Tukey HSD analysis indicated that significant differences in DTA only occurred between two non-pair-wise species combinations (Ps→Pc & Pc→Xp P = 0.035; Pc→Xp & Xp→Ps P = 0.02) (Figure 4).
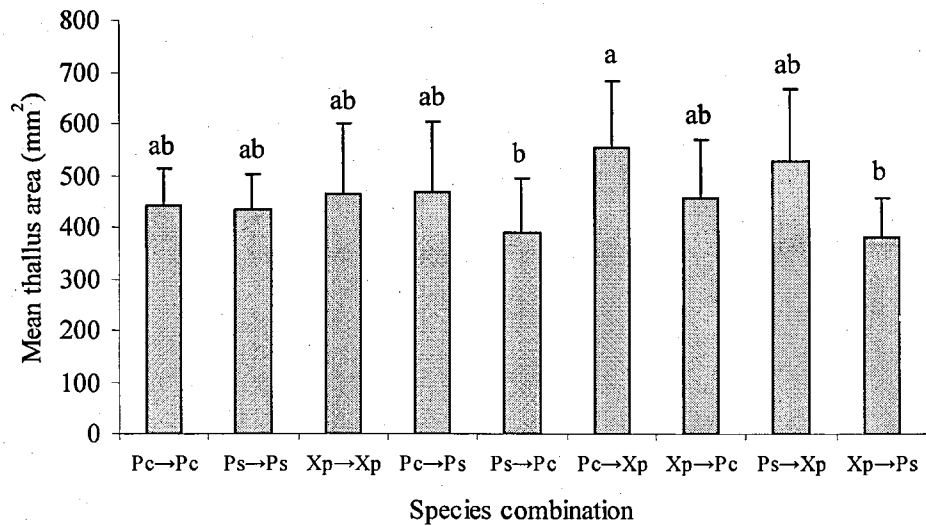
Figure 4. The effect of species combination on dominant thallus area (DTA) for all aspects. Data not sharing a common letter differ significantly (Tukey HSD test P = 0.05). Bars are SEM, n = 36.

Subordinate thalli

Three-way nested ANOVA indicated that site and aspect did not significantly affect the subordinate thallus areas (STA) of *P. caperata*, *P. saxatilis* and *X. parietina*. However, species combination did produce a significant effect (Table 5). Although all conspecific and heterospecific pair-wise combinations had similar subordinate thallus areas some significant differences were observed between non-pair-wise species combinations (Figure 5).

Effect	DF	MS	F	P
(1) Site:	1	77708.9	1.58	0.210
(2) Aspect:	6	97723.3	1.99	0.068
(3) Sp. Comb.:	16	128528.0	2.62	<0.001
Interaction 12:	-	-	-	-
Interaction 12:	-	-	-	-
Interaction 23:	48	41597.8	0.85	0.752
Interaction 123:	-	-	-	-
Error:	252	49119.8		

Table 5. Three-way nested ANOVA for the effect of site (factor one), aspect (factor two) and species combination (Sp. Comb.) (factor three) on subordinate thallus area (STA).

Since site and aspect had no effect on STA a one-way ANOVA was used to determine more accurately the effect of lichen species. The results of this analysis indicated that species combination had a significant effect on the area of the subordinate thalli of *P. caperata*, *P. saxatilis* and *X. parietina* (Table 6).

Effect	DF	MS	F	P
(1) Sp. Comb.:	8	212368.3	4.34	<0.001
Error:	315	48877.6		

Table 6. One-way ANOVA for the effect of species combination (Sp. Comb.) on subordinate thallus area (STA).

Tukey HSD analysis indicated that subordinate thallus areas of *X. parietina* were significantly larger when competing intraspecifically (Xp→Xp) than when competing interspecifically with neighbouring thalli of *P. caperata* (Xp→Pc) ($P = 0.005$) and *P. saxatilis* (Xp→Ps) ($P = 0.009$).

Significant differences occurred between two non-pair-wise species combinations (Ps→Pc & Xp→Xp $P = 0.001$ and Ps→Xp & Xp→Xp $P = 0.002$) (Figure 5).
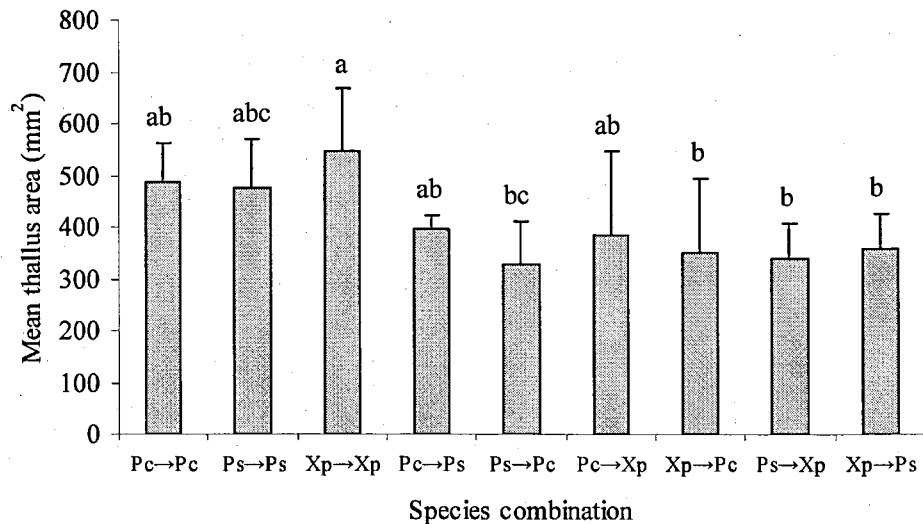
Figure 5. The effect of species combination on subordinate thallus area (STA) for all aspects. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$). Bars are SEM, n = 36.

Overlap area

The estimated area of overlap on subordinate thalli was not significantly affected by site, aspect or species combination (Table 7).

Effect	DF	MS	F	P
(1) Site:	1	429.9	0.10	0.746
(2) Aspect:	6	6006.8	1.47	0.188
(3) Sp. Comb.:	16	5367.9	1.31	0.188
Interaction 12:	-	-	-	-
Interaction 12:	-	-	-	-
Interaction 23:	48	3253.2	0.80	0.826
Interaction 123:	-	-	-	-
Error:	252	4081.3		

Table 7. Three-way nested ANOVA for the effect of site (factor one), aspect (factor two) and species combination (Sp. Comb.) (factor three) against estimated overlap area on subordinate thallus area for all intra- and interspecific competitive interactions.

2.4 Results – thallus competition

Frequency of thallus overlaps

It was predicted that all three species would have similar overlap frequencies. Combined data from both inside and outside the estate (Table 8) were tested using G-analysis testing against the ratio of overlapped to non-overlapped thalli at each aspect.

This indicated that competition between *P. caperata* and *P. saxatilis* was similar at all aspects except east (G = 4.12; P = 0.04) (Table 9). However, to reduce the possibility of obtaining a Type I error only $P < 0.05$ were accepted.

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P. caperata made significantly more overlaps on thalli of *X. parietina* on north (G = 14.45; *P* < 0.01), south (G = 4.97; *P* = 0.02) and east (G = 12.31; *P* < 0.01) facing aspects compared with the reciprocal (Table 9 and Figure 6).

No significant differences in the number of thallus overlaps were observed when *P. saxatilis* was competing with *X. parietina* under any aspect (Table 9).

Substrate effect

Granite and slate have considerably different microtopographies. The rougher surface of granite allows water to be retained for longer periods than would be expected for the smoother slate. This could affect the rate of thallus drying and consequently the NCAR of thalli.

One-way ANOVA for the effect of substrate (granite and slate) on thallus areas of *P. caperata*, *P. saxatilis* and *X. parietina* indicated that substrate did not significantly effect DTA (F = 3.33; *P* = 0.07); STA (F = 0.21; *P* = 0.65) or OA (F = 0.25; *P* = 0.62).

North	Sp. Comb	Inside	Outside	Total
	Pc→Ps	3	4	7
	Ps→Pc	3	2	5
	Pc→Xp	6	5	11
	Xp→Pc	1	1	2
	Ps→Xp	3	3	6
	Xp→Ps	2	3	5

South	Sp. Comb	Inside	Outside	Total
	Pc→Ps	4	2	6
	Ps→Pc	2	3	5
	Pc→Xp	4	4	8
	Xp→Pc	1	2	3
	Ps→Xp	4	2	6
	Xp→Ps	5	2	7

East	Sp. Comb	Inside	Outside	Total
	Pc→Ps	4	5	9
	Ps→Pc	3	1	4
	Pc→Xp	5	5	10
	Xp→Pc	1	1	2
	Ps→Xp	2	3	5
	Xp→Ps	3	4	7

West	Sp. Comb	Inside	Outside	Total
	Pc→Ps	5	3	8
	Ps→Pc	3	2	5
	Pc→Xp	3	4	7
	Xp→Pc	2	4	6
	Ps→Xp	3	1	4
	Xp→Ps	5	3	8

Table 8. The frequency of thallus overlaps by *P. caperata* (Pc), *P. saxatilis* (Ps) and *X. parietina* (Xp) in heterospecific species combinations (Sp. Comb.) for each aspect. Data for both inside and outside the estate are shown.

P. caperata overlapping *P. saxatilis*

	G	P
North	0.70	0.40
South	0.19	0.66
East	4.02	0.05
West	1.46	0.23

P. caperata overlapping *X. parietina*

	G	P
North	14.45	<0.01
South	4.97	0.02
East	12.31	<0.01
West	0.16	0.69

P. saxatilis overlapping *X. parietina*

	G	P
North	0.19	0.66
South	0.16	0.69
East	0.70	0.40
West	2.85	0.09

Table 9. G-analysis summary table showing the frequency of thallus overlaps made by *P. caperata*, *P. saxatilis* and *X. parietina* in pair-wise competition. $P = 0.05$, DF = 1 throughout. To allow for the possibility of a Type I error when making multiple tests only significant differences below $P = 0.05$ were accepted.
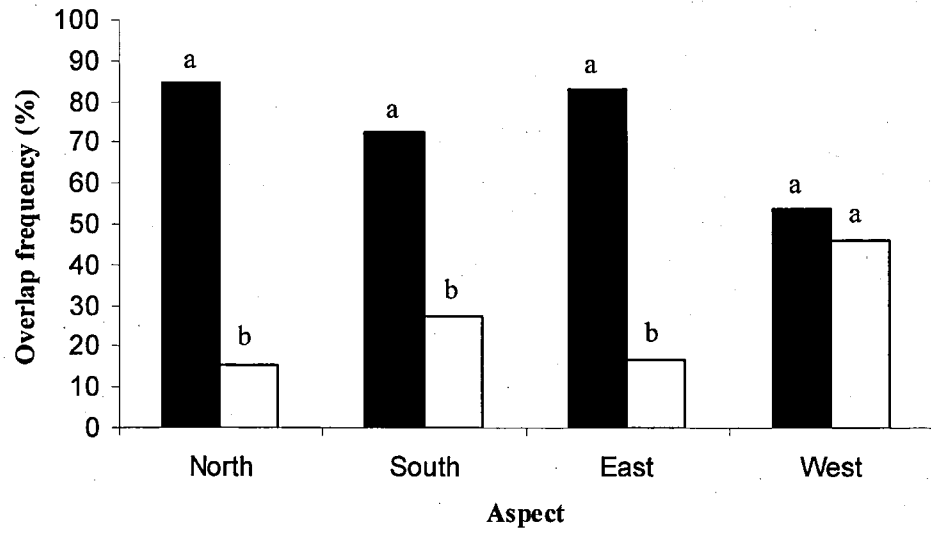
Figure 6. The frequency of thallus overlaps as a percentage of the total number made by *P. caperata* (shaded) and *X. parietina* (unshaded) on each others thalli at each aspect (Table 8). Bars not sharing the same letter differ significantly within an aspect ($P <$ 0.05) (Table 9).

Growth rate and competitive interactions

During the process of substrate colonisation neighbouring lichen thalli may make contact and a competitive interaction may result. The time taken for thalli to make contact is determined by the radial growth rate of the thallus which can show much variation between species (Table 1).

Thallus growth rates are also affected by the amount of light and precipitation since these factors determine photosynthetic and respiratory activity within the thallus which in turn affect the net carbon assimilation rate (NCAR) of a species, culminating in reduced or increased radial growth rates. This ultimately determines the time taken for neighbouring thalli to make contact and initiate competitive interactions.

Are dominant, subordinate and overlap thallus areas dependent on the competing species and aspect?

Results indicated that *P. caperata*, *P. saxatilis* and *X. parietina* had similar dominant, subordinate and overlap areas. Furthermore aspect had no effect on thallus areas (Tables 3, 5 and 7). Despite small variations in structure individuals of the same species have similar thallus morphologies. As a result, competing conspecific thalli should have similar lobe adpression, lobe mass and thickness and a similar resistance to dessication. This could explain why competition between conspecific thalli of these three species were similar (Figures 4 and 5).

Although it is regularly assumed that intraspecific competition is more intense than interspecific competition (Keddy, 2001) it would appear that for lichens where thalli are morphologically similar, as in conspecifics, single individual thalli are competitively equivalent. The fact that conspecific thalli do overlap each other suggests that some competitive advantage over neighbouring thalli has been gained.

This could be due to small variations in genotype which might result in a less adpressed thalline margin, random grazing by microarthropods, the presence of other competing lichen species and vegetation or numerous other biotic and abiotic factors acting individually or collectively.

Is the frequency of thallus overlaps independent of lichen species and aspect?

Competition between *P. caperata, P. saxatilis* and *X. parietina* appears to be similar and unrelated to aspect when looking only at areas occupied on the substrate. Such competitive equivalence would not have been predicted since *P. caperata* has visibly thicker thalline lobes than either *P. saxatilis* or *X. parietina*. Furthermore, *P. caperata* may be expected to out-compete *X. parietina* due to the latter possessing a more adpressed thallus than the former.

However, examination of the frequency of thallus overlaps made by these three species indicates that a dominance hierarchy exists. *X. parietina* was overlapped on north, south and east facing aspects significantly more frequently by *P. caperata* compared with the reciprocal (Figure 6). Although such competitive dominance by *P. caperata* over *X. parietina* is not consistent across all aspects the assumption that *P. caperata* is above *X. parietina* in a dominance hierarchy would appear to be correct (Figure 7).
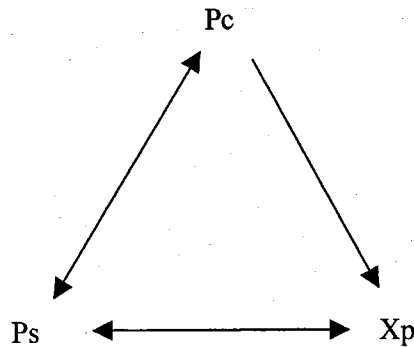
Figure 7. A proposed competitive hierarchical pyramid for *P. caperata* (Pc), *P. saxatilis* (Ps) and *X. parietina* (Xp) based on the frequency of thallus overlaps made by each species.

P. caperata and *P. saxatilis* appear to be competitively equivalent. Such symmetrical competition was not predicted due to the superior thallus morphology of *P. caperata* which possesses larger, less adpressed lobes than *P. saxatilis*. The symmetrical competition observed between these two species may be a consequence of diffuse competition (MacArthur, 1972), afforded by other neighbouring species competing with *P. caperata*. This would be advantageous to *P. saxatilis* since it would allow it to remain for longer periods on the substrate thus affording it a greater chance of reproductive success. However, diffuse competition could only be seen as an advantage if the other neighbouring thalli did not out-compete individual thalli of *P. saxatilis*.

Such species interactions have been observed between other lichens, namely *P. glabratula* and *Physcia orbicularis*, which tended to grow better in the presence of two competitors rather than one. In addition, the growth of the competitively dominant *Parmelia conspersa* was observed to be reduced in the presence of two species (Armstrong, 1986). Such competitive interactions may allow lichen species to coexist on the same substrate.

Armstrong (1974b) reported that *P. saxatilis* was frequently found on northwest facing saxicolous substrata, indicating that it competed well with other lichens at this aspect, but declined in abundance on southeast facing substrata due to competition with *P. conspersa*. This would place *P. saxatilis* below *P. conspersa* in a dominance hierarchy (Armstrong, 1982). The asymmetrical competition between *P.*

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conspersa and *P. saxatilis* is confirmed by transplant experiments which indicated that thalli of *P. saxatilis* were able to grow similarly at both northwest and southeast facing aspects (Armstrong, 1977).

Competition between *P. saxatilis* and *X. parietina* however appears to be symmetrical which is somewhat surprising since *P. saxatilis* has a visibly superior thallus morphology than *X. parietina* whose thalli are considerably more adpressed. The symmetrical competition may be a consequence of pH. The abundance of seabirds in coastal regions (Lanhydrock Estate is situated 15 miles from the coast) increases pH levels through the deposition of excreta which may compromise the competitive ability of acidophytics like *P. saxatilis* when competing with nitrophilous species. This could explain why thalli of *X. parietina* compete symmetrically with neighbouring thalli of *P. saxatilis*. Alternatively *X. parietina* may be a calcicole and require an elevated pH in order to survive (Armstrong – personal communication). However, this is only speculative since it would have been impossible to accurately determine the amount of seabird excreta to which each thallus was exposed. Therefore, in this context, any measurement of pH would have been meaningless. Consequently, further experiments are necessary in order to confirm the effect of seabird guano and pH on lichen growth and competition.

A clearer picture could be obtained if the ages of individual thalli were known. Thallus age has been shown to determine radial growth rate in the lichen *P. conspersa*. Juvenile thalli with a diameter less than 1.0 cm had significantly slower growth rates than older thalli of larger diameter (Hale, 1967). Furthermore, as the thallus matures the centre begins to fragment resulting in a reduction in the relative radial growth rate (Armstrong, 1973). However, radial extension at the lobe margins remains relatively constant and does not change significantly with fragmentation of the centre (Armstrong, 1974a).

It may be that these species are still in the process of establishing a dominance hierarchy, which, given their slow growth rates, is perhaps more likely. The need to pay particular consideration to the time taken for competitive interactions to occur has been stressed by Keddy (2001) since far too many competitive interactions are incorrectly predicted to react instantaneously (as assumed by the Lotka-Volterra model).

In addition it is important to remember that at the distributional limits of the dominant species a transition to the subordinate species may occur. This is based on the assumption that the dominant species may become so weakened by environmental effects (Keddy, 2001) that it becomes excluded by the subordinate lichen species. *P. caperata*, *P. saxatilis* and *X. parietina* are not near their respective

distributional limits in the areas of study, although it is clear that *P. caperata* and *P. saxatilis* do not thrive particularly well in eutrophic environments where an elevated pH is not uncommon.

Interference mechanisms in competition have been well documented (Krebs, 1994). The possession of a less adpressed thallus is an example of how one species might gain a competitive advantage over another. The use of allelochemicals provides a further example. Although this was not observed during the course of this study for *P. caperata*, *P. saxatilis* or *X. parietina* it is feasible that secondary compounds might be used to gain an advantage over neighbouring species (Armstrong, 1982) and so form a dominance hierarchy.

It is clear that several factors dictate the ability of a species to compete. Radial growth rate, thallus age and thallus morphology are clearly very important. Interference competition may also play a significant part since the ability to reduce herbivore grazing by the production of allelochemicals could be significant in determining the competitiveness of a species (Armstrong, 1979; Rogers, 1990).

Chapter Three

The effect of nutrient application on the growth rate and competitive abilities of lichens

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3.1 Introduction

There is much evidence to suggest 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).

However, when Armstrong (1984) applied bird droppings to lichen thalli and observed their growth rates he concluded that *P. saxatilis*, an acidophyte, grew well in the presence or absence of nutrients and was observed to be frequent on and off bird perching stones. The presence of *P. saxatilis* at locations where there is an elevated nutrient status could reflect differences in the nutrient composition between bird droppings and anthropogenic nutrient addition. In a later experiment, Armstrong (2000) states that nutrient enrichment reduced thallus areas of *P. saxatilis* which he claims could explain the low frequency of this species on nutrient enriched rocks. It is feasible that the chemical composition of fecal deposits may vary quite widely between birds, reflecting species, age and more particularly, individual dietary preferences (personal observation).

Although N supplementation in the form of nitrate and nitrite can acidify the substrate in an untreated non-chelated form (Bull *et al.*, 1995), the use of ammonium (NH_4^+) salts results in elevated (alkaline) pH levels, and there is evidence to suggest this has resulted in the removal of acidophytes like *P. saxatilis* (van Herk, 1999) from effected substrata.

Such elevated pH levels may occur, albeit patchily, in coastal regions where large gatherings of seabirds increase substrate pH through urine and fecal depositions. The pH of bird droppings ranges from 5.0 – 8.0 (Armstrong, 1984) and this may be sufficiently high to reduce the colonisation, growth and subsequent competition of acidophytics. In addition, an elevated nutrient status can cause excessive algal growth over the lichen thallus (Scott, 1960; O'Dare, 1990), resulting in a reduction of thallus photosynthetic

ability. Alternatively, there is evidence to suggest that eutrophic conditions may cause a breakdown in the symbiosis (Scott, 1960; Nash, 1996).

Lichens may become exposed to anthropogenically elevated nutrient levels from a variety of sources including waste (brewing, food processing etc.,), sewage, forest management, vehicle exhaust emissions and intensive agricultural practices.

Intensive farming dictates the use of additional N-based fertilisers (organic and inorganic) in order to maximise crop yields (Höglind & Frankow-Lindberg, 1998; Stoll *et al.*, 1998) and as a result may lead to areas of the environment receiving elevated nutrient levels.

Nitrophilous species like *X. parietina* thrive in nutrient-rich environments as seen near bird perching sites and farms. When transplanted away from areas of nutrient enrichment poor growth is frequently observed (Armstrong, 1984). This suggests a negative correlation exists between distance from livestock farms and the abundance of nitrophilous lichen species (Crittenden *et al.*, 1994; Sanchez-Hoyos & Manrique, 1995; Pitcairn *et al.*, 1998; van Herk, 1999; Ruoss, 1999).

The ability of a lichen to tolerate elevated nutrient levels could allow it to occupy environments where species have been removed through nutrient toxicity. Nitrophilous species that are capable of tolerating fluctuations in substrate pH would appear to have an advantage in such situations. Therefore, *X. parietina* may be expected to out-compete *P. saxatilis*, an acidophytic species and *P. caperata*, a predominantly neutrophytic species, where elevated pH levels arise under conditions of nutrient enrichment.

During interspecific competition the morphological characteristics of the two competing thalli become an important issue (Pentecost, 1980; Harris, 1996) since species that possess a raised thalline margin, enabling them to rise above the substrate, are more likely to overgrow more adpressed neighbouring thalli. Furthermore, heavier thalli appear to have a distinct advantage when attempting to overgrow lighter thalli (Armstrong, 1982; John, 1992). Since light, moisture and nutrients fail to reach an overgrown thallus, its ability to photosynthesise would be compromised, therefore leading to a reduction or termination of growth in the region of overlap (John, 1992; Harris, 1996).

Other factors which could ultimately determine the success of a competitive interaction between two thalli include a faster rate of lobe regeneration (particularly important in this experiment where thallus fragments are used), faster radial growth rate and the presence of allelochemicals (Armstrong, 1986).

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Furthermore, there is evidence to suggest that the provision of additional nutrients may reverse competitive dynamics and therefore alter the competitive balance between plants (Hartley & Amos, 1999) and consequently modify their zonation patterns (Levine *et al.*, 1998). Similar alterations to zonation have been observed for lichens and it is thought that nutrient application could result in the competitive exclusion of some species (Lawrey, 1981; Vagts & Kinder, 1999) therefore leading to a reduction in species diversity.

It is proposed that anthropogenic nutrient enrichment will increase lichen growth rates and in turn reduce the time for neighbouring thalli to contact each other. This will lead to increased competition for space, thus supporting Grime's theory that competition becomes more important as nutrient resource levels increase (Grime, 1979).

This chapter assesses the impact of nutrient addition on lichen growth rates and competition by determining how *P. caperata*, *P. saxatilis* and *X. parietina* behave in two and three species mixtures. Such information could help determine how lichen community structure might change in response to anthropogenically-elevated nutrient levels. To this end the following hypotheses will be tested:

(i). The addition of nutrients across a range of application frequencies will increase lichen growth rates, as measured by changes in their thallus diameters, up to an optimum frequency of application. Such changes in thallus diameter may well be species specific with nitrophilous species like *X. parietina* predicted to exhibit larger thallus diameters (increased growth rate) under conditions of nutrient enhancement than acidophytic species like *P. saxatilis*. Neutrophytic species like *P. caperata* are predicted to exhibit intermediate responses to nutrient application.

(ii). Nutrient addition across a range of application frequencies will 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. Competitively successful species would be expected to make significantly more overlaps than other species in pair-wise combinations.

(iii).   Conspecific thalli will show fewer thallus overlaps than heterospecific thalli since differences in thallus morphology will dictate the competitive success of a species and consequently determine its position in a dominance hierarchy.

Lichen material

Lobes of lichen thalli were collected for each of the three species from specimens having a diameter greater than 5 cm. This ensured that transplants were taken from individuals whose radial growth rate was constant or linear (Hale, 1967; Armstrong, 1973). All species were collected within Cornwall from saxicolous substrata (granite, slate and granitic schists) located in areas with mean winter SO_2 levels less than 30 μm m^{-3} (Dobson, 1992). Transplants were transported in specimen bags and glued to the substrate with Bostik™ all purpose clear adhesive (Armstrong, 1981) within 24 hours of collection.

Substrata

In order to reduce the influence of microtopography and to simplify thallus measurements, smooth uncolonised roofing slate was used as the substrate. Upon each slate an area of 20 x 15 cm was clearly etched and sub-divided into eight equal areas (sub-plots) of 7 x 5 cm (Plate 1 and Figure 8).
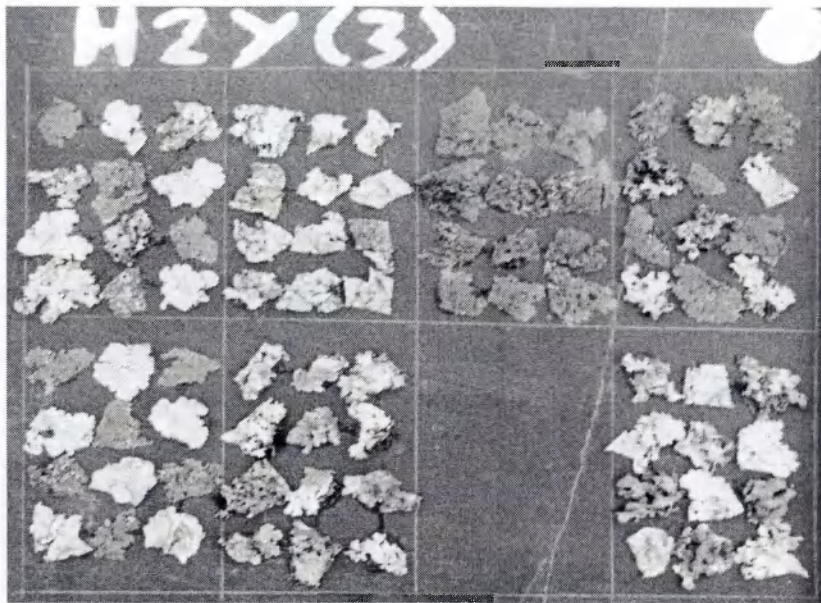
Plate 1. One of the 40 slates used in the transplant experiment (not to scale). Each of the seven sub-plots contains one species combination (see Figure 8 for detail).

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

Figure 8. A typical arrangement for the three lichen species under investigation, *P. caperata* (Pc); *P. saxatilis* (Ps) and *X. parietina* (Xp), after transplanting to a slate substrate. Sub-plots provide one conspecific and three heterospecific thallus combinations for each species. Vacant sub-plot provides space for any natural colonisation. Slate dimensions are approximately 21 cm (W) by 17 cm (H), with sub-plots of 5 cm (W) by 7 cm (H).

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 x 0.5 cm^2 (±1 mm) fragments and glued in specific arrangements approximately 5 mm apart (Figure 8) within seven of the eight sub-plots on each slate. The remaining sub-plot was left vacant for observation of any natural colonisation that might occur.

Two factors were tested in this experiment, a nutrient addition (diluted Hoagland's Solution) factor with six levels (x0; x1; x2; x4; x8 and x16 frequencies of application) and a lichen interaction factor (species combination) with four levels (one conspecific and three heterospecific). The treatments were laid out in a randomised block (Appendix – Figure 1) split-plot design where frequency of application was assigned to the main plots and lichen interaction to sub-plots.

Ten replicates for the control treatment (x0 frequency of application of Hoagland's Solution) and six replicates for the remaining treatments (x1; x2; x4; x8 and x16) were established. The 40 slates were placed on a horizontal flat roof of a garden shed (2 m (W) by 3 m (L) by 2.5 m (H) approximately) in an unshaded location (Appendix – Plate 1). Garden netting was suspended 15 cm above the slates to reduce animal disturbance. Using the layout in Figure 8 it was possible to investigate all intra- and interspecific interactions at each application frequency of Hoagland's Solution.

All slates were completed by mid June 1994. One month was allowed before spraying with Hoagland's Solution in order for species to acclimatise to the new environmental conditions and furthermore to reduce physiological stress (increased respiration) arising from transplantation and fragmentation (Seaward – personal communication).

Experimental site

The site for the experiment was located at Trenance (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_2 levels were less than 30 μm m^{-3} (Hawksworth & Rose, 1976).

Chemical treatment

Freshly prepared Hoagland's Solution (Hoagland, 1948; Keddy *et al.*, 2000) of pH 6.5 (Appendix – Table 4) diluted to 10% original strength was used to saturate the transplanted thalli. This provided a N concentration of 9.80 g dm^{-3} (Appendix – Table 5).

At regular intervals (approximately one month apart) 25 cm^3 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^2 from a height of 50 cm above the slate. This 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 and 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 to ensure similar states of hydration in all thalli. This was particularly important since evidence suggests that desiccated thalli fail to grow, even under conditions of nutrient enhancement, until sufficient thallus re-hydration occurs (Badacsonyi *et al.*, 2000) perhaps as a result of dehydrated thalli concentrating nutrient solutions near the upper surface which culminates in nutrient toxicity (Nash, 1996). 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.

Representative measurements were taken from the photographs for all thallus fragments within each sub-plot on four occasions. This provided an indication of growth rate throughout the experiment for each species under different application frequencies and species combinations.

Variations in thallus diameter at the beginning of the experiment (July 1994) were overcome by subtracting the initial thallus diameters from the final thallus diameters collected in May 1995. This provided an indication of the change in thallus diameter under each treatment and species combination.

The changes in thallus diameter for each species combination were summed for each of the six application frequencies. This provided six single values for each species (*P. caperata, P. saxatilis* and *X. parietina*) which represented the changes in thallus diameter, regardless of species combination, 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 conspecific and heterospecific species combinations 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 combination at each application frequency. Where the species overlapped neighbouring thalli each overlap was counted (actual number of overlaps) for each species combination at each application frequency. The total number of overlaps a species could make at a

particular species combination was determined by the number of neighbouring thalli (possible number of overlaps).

The ratio of actual overlaps to possible overlaps provided a means of analysing competitiveness between *P. caperata*, *P. saxatilis* and *X. parietina*. This provided six ratios (one per species combination) for each species.

Summing the ratio of actual overlaps made to possible overlaps that could be made for each species across all species combinations provided a single value for each application frequency (n = 72). This gave an indication of how application frequency effected competitive ability – primarily as a function of thallus growth rate.

Statistical analysis

Two-way ANOVA was used to investigate whether application frequency and lichen interaction (species combination) affected thallus growth rates and the number of thallus overlaps made by *P. caperata*, *P. saxatilis* and *X. parietina*. Tukey (HSD) multiple means test (Zar, 1996) was used to determine which means differed significantly. All calculations were performed using Statistica™ 5.5 (Statsoft Inc., Tulsa, USA).

During the course of the experiment thalli were lost from individual slates under each application frequency (Appendix – Tables 2 and 3). Missing thalli were ignored completely and not used in any calculations.

Student's t test indicated that thalli of *P. caperata* suffered significantly fewer losses than those of *P. saxatilis* (t_{10} = 9.51; P < 0.001) and *X. parietina* (t_{10} = 8.58; P < 0.001). There was no significant difference in the number of lost thalli between *P. saxatilis* and *X. parietina* (t_{10} = 0.96; P = 0.36).

3.3 Results – thallus growth rate

Growth rates

Two-way ANOVA indicated that growth (thallus diameter) was affected by both application frequency and lichen species combination (Table 10). In addition the effect of application frequency (factor one) was modified by the effect of species combination (factor two).

Effect	DF	MS	F	P
(1) App. Freq.:	5	0.285	59.31	<0.001
(2) Sp. Comb.:	11	0.061	12.76	<0.001
Interaction:	55	0.012	2.60	<0.001
Error:	360	0.005		

Table 10. Two-way ANOVA for the effect of application frequency (App. Freq.) (factor one) and species combination (Sp. Comb.) (factor two) on change in thallus diameter.

Application frequency

Regardless of the individual species combination effects, Tukey (HSD) analysis indicated that application frequency significantly affected thallus growth with x0 (control – no nutrient addition) being significantly different from all other application frequencies (Figure 9). Most thallus growth occurred up to x4 with decreased growth, compared with controls, occurring at higher application frequencies (x8 and x16). Individual species responses are shown in Appendix-Figure 2.
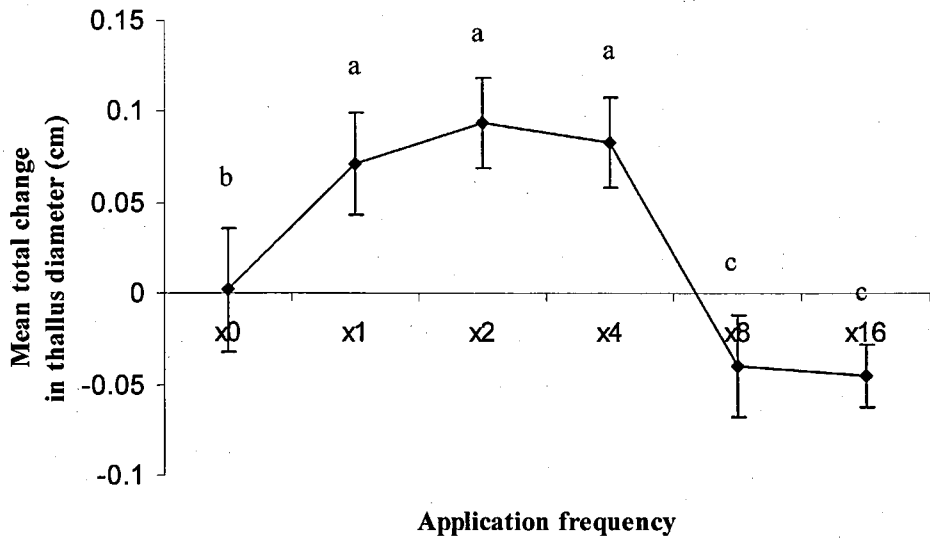
Figure 9. The effect of application frequency on the mean total change in thallus diameter for *P. caperata*, *P. saxatilis* and *X. parietina*. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$); (x0 & x1, $P < 0.01$); (x0 & x2, $P < 0.01$); (x0 & x4, $P < 0.01$); (x0 & x8, $P = 0.035$); (x0 & x16, $P < 0.01$). Bars are SEM, n = 72.

Species combinations

Thallus growth was affected significantly by lichen species combination regardless of application frequency (Table 10). When thalli were placed in conspecific species combinations Tukey (HSD) analysis indicated that *P. saxatilis* grew less than both *P. caperata* ($P < 0.01$) and *X. parietina* ($P < 0.01$) (Figure 10).

In two-species mixtures thallus growth of all three species was similar. However, when placed in three-species mixtures thalli of *P. caperata* grew significantly more than those of *P. saxatilis* ($P < 0.01$) (Figure 11).
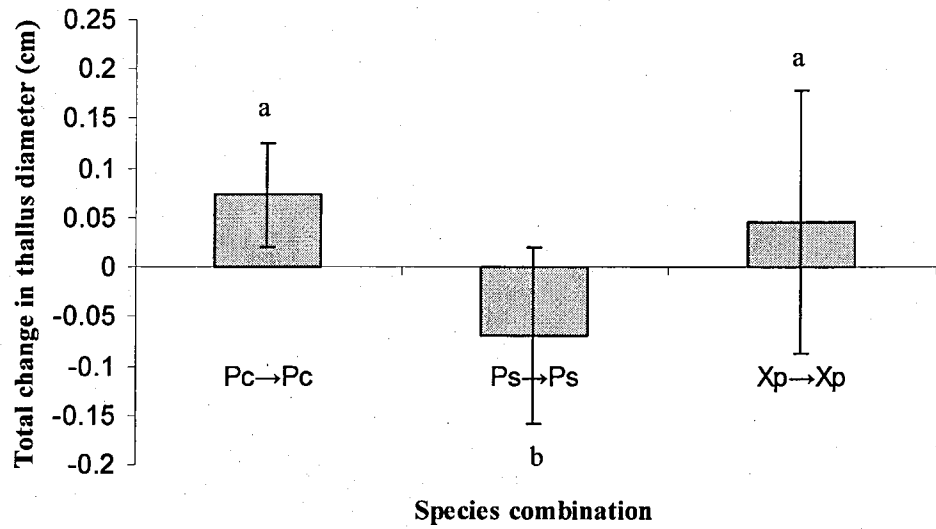
Figure 10. Total change in thallus diameter for conspecific species combinations of *P. caperata* (Pc→Pc), *P. saxatilis* (Ps→Ps) and *X. parietina* (Xp→Xp) for all six application frequencies. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$). Bars are SEM, n = 36.
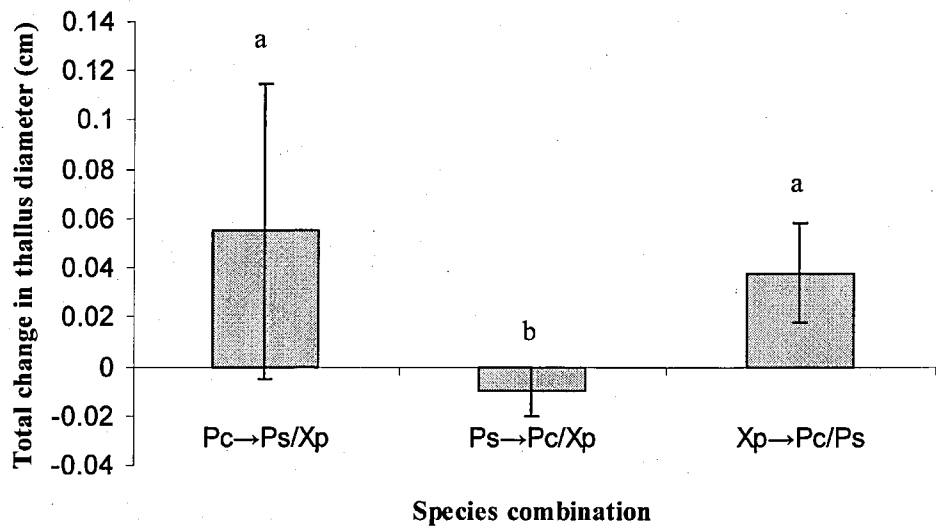
Figure 11. Total change in thallus diameter for all three-species combinations of *P. caperata* (Pc→Ps/Xp), *P. saxatilis* (Ps→Pc/Xp) and *X. parietina* (Xp→Pc/Ps) for all six application frequencies. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$). Bars are SEM, n = 36.

3.4 Results – thallus competition

Two-way ANOVA indicated that the number of thallus overlaps made by *P. caperata, P. saxatilis* and *X. parietina* were affected by both application frequency and lichen species combination (Table 11). There was no interaction between the two factors.

Effect	DF	MS	F	P
(1) App. Freq.:	5	0.36	5.16	<0.001
(2) Sp. Comb.:	11	0.40	5.62	<0.001
Interaction:	55	0.06	0.89	0.693
Error:	360	0.07		

Table 11. Two-way ANOVA for the effect of application frequency (App. Freq.) (factor one) and species combination (Sp. Comb.) (factor two) on the number of thallus overlaps.

Application frequency

Regardless of species combination, Tukey (HSD) analysis indicated that application frequency significantly affected the number of thallus overlaps, with x0 (control – no nutrients) being significantly different to x1, x2 and x4 application frequencies (Figure 12).

The number of thallus overlaps made during the course of this experiment were affected significantly by lichen species combination, regardless of application frequency (Table 11). Tukey (HSD) analysis indicated that when thalli were placed in conspecific species combinations similar numbers of thallus overlaps were made by all three species.

However, some heterospecific species combinations showed significant differences between the number of thallus overlaps being made on neighbouring thalli. *P. 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 combinations ($P < 0.001$). Also *P. caperata* made significantly fewer overlaps when grown with *P. saxatilis* as a neighbour compared with the number it made in three-species combinations ($P < 0.001$) (Figure 13).

P. saxatilis made significantly fewer overlaps on its own thalli than on neighbouring thalli in three-species combinations ($P = 0.05$) (Figure 14). No significant differences in the number of thallus overlaps were observed for *X. parietina* at any species combination.
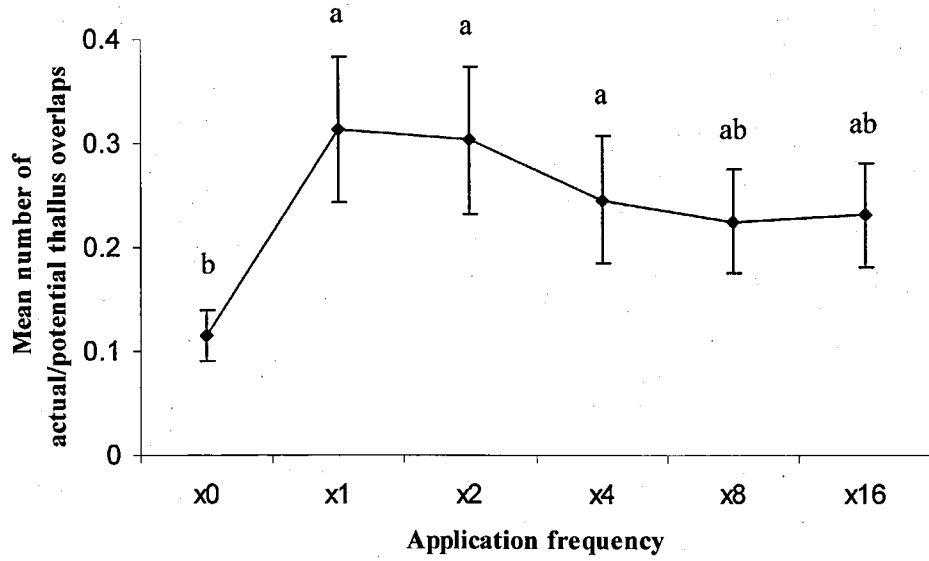
Figure 12. The effect of application frequency on number of thallus overlaps (all species combinations). Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$); (x0 & x1, $P < 0.01$); (x0 & x2, $P < 0.01$); (x0 & x4, $P = 0.036$). Bars are SEM, n = 72.
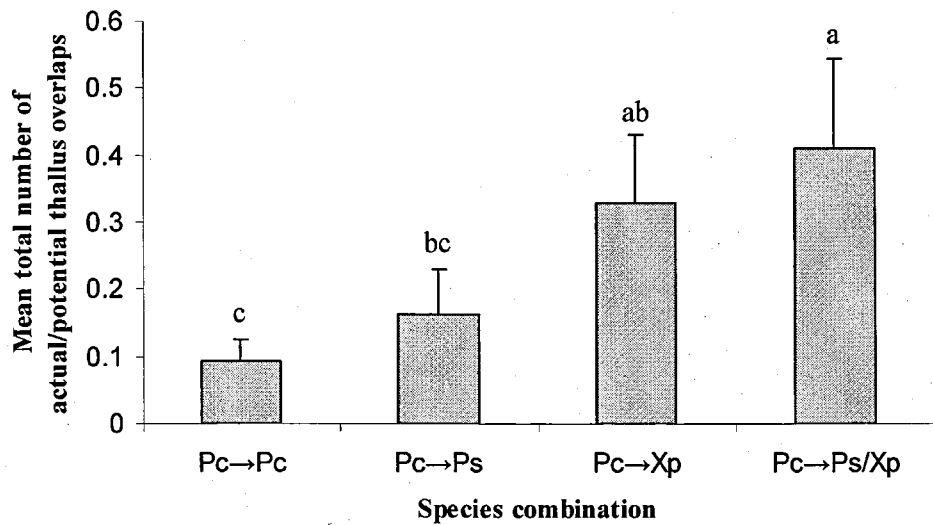
Figure 13. The mean number of thallus overlaps made, regardless of application frequency, for *P. caperata* at each species combination. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$). Bars are SEM, n = 36. Arrow ($\rightarrow$) indicates the direction of competition, eg. Pc→Ps indicates *P. caperata* overlapping *P. saxatilis*.
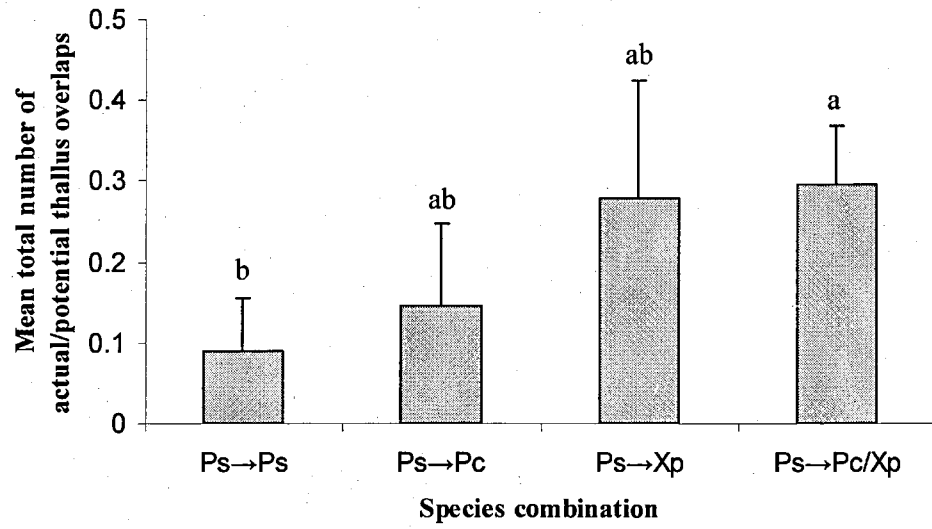
Figure 14. The mean number of thallus overlaps made, regardless of application frequency, for *P. saxatilis* at each species combination. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$). Bars are SEM, n = 36. For notation see Figure 13.

Nutrient addition to an ecosystem has wide ranging effects which depend upon the concentration, type of nutrient and duration of addition. One of the main effects on lichens observed here is the increase in thallus growth rate compared with control applications where no nutrients were supplied. This, in theory, could allow nutrient tolerant species to colonise areas of the substrate rapidly, perhaps at the expense of other species which may be removed through nutrient toxicity or as a direct result of competition. However, this was not observed during the course of the experiment for the nitrophilous species *X. parietina.*

Does the addition of nutrients across a range of application frequencies increase lichen growth rates up to an optimum frequency of application? Furthermore, are changes in growth rate species specific?

It would appear that nutrient application and growth rate of the lichen thallus are positively correlated up to moderate (x1, x2 and x4) application frequencies. However, when nutrient concentrations become too high (x8 and x16) reduced thallus growth was observed, perhaps as a direct result of nutrient toxicity (Nash, 1996) (Figure 9).

It was predicted that under nutrient enrichment *P. saxatilis*, an acidophytic species, would grow less than both *P. caperata*, a neutrophytic species, and *X. parietina*, a nitrophilous species. This would be due to the nutrient solution having a pH of 6.5 therefore sufficiently increasing substrate pH and resulting in the promotion of slower thallus growth in acidophytics. This was only true in conspecific species combinations (Figure 10). In heterospecific pair-wise species combinations growth of *P. saxatilis* was similar to that observed for *P. caperata* and *X. parietina*. This suggests that *P. saxatilis* may well be able to tolerate elevations in pH and grow as well as neutrophytic and nitrophilous species, at least in the short term (one year).

An equally surprising result was observed with the thallus growth of *X. parietina* which was predicted to out-grow both *P. caperata* and *P. saxatilis* in nutrient enriched situations since it is a

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nitrophilous species and thrives in situations where nutrient enhancement occurs. One explanation may be due to the nutrient composition of Hoagland's Solution which contains N compounds as potassium nitrate, ammonium hydrogen phosphate and ammonium molybdenum oxide (Appendix-Tables 4 and 5). 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. An alternative explanation is that the calcareous nature of *X. parietina* (Armstrong – personal communication) dictates a requirement for an elevated pH in order to survive. Such an elevation may be obtained from the fecal deposits of birds which can fall between the pH range of 5.0 – 8.0 (Armstrong, 1984). At high nutrient application frequencies (x8 and x16) thallus growth rates of all three species were significantly lower than controls, x1, x2 and x4 (Figure 9). This may suggest that nutrient toxicity reduces thallus growth, perhaps as a result of effecting a breakdown in the symbiosis (Nash, 1996).

When these three species were placed in conspecific species combinations fewer overlaps were observed than when in two and three-species mixtures as initially predicted. Also conspecific thalli of *P. saxatilis* grew significantly less than conspecific thalli of both *P. caperata* and *X. parietina* (Figure 10). The reason why this should occur significantly more in this species than in either *P. caperata* or *X. parietina* may be a consequence of an elevation in pH which compromised the growth of this particular acidophyte. Furthermore, the reduction of growth along the points of contact between neighbouring thalline margins may result in a 'truce' situation. This is common among crustose species (Pentecost, 1980) but observed on fewer occasions in foliose species since the less adpressed thalli are not restrained by the substrate 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 substrate (personal observation).

All pair-wise combinations of *P. caperata*, *P. saxatilis* and *X. parietina* produced similar thallus growth at all application frequencies. However, in three-species combinations *P. caperata* grew significantly more than *P. saxatilis* (Figure 11). This suggests that the growth rates of thalli in three-species mixtures cannot be predicted from growth in two-species mixtures. Again, one explanation may be due to thallus morphology. Since all three species have thalli that rise above the substrate 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*.

If morphological differences between lichen thalli are to account partially for the differences between growth rates it should follow that thallus growth of *P. saxatilis* would be larger in the presence of *X. parietina* than in the presence of *P. caperata* since *X. parietina* has more adpressed thalli than *P. caperata*. This was not supported by the results of this experiment.

Thallus growth of *X. parietina*, regardless of application frequency, was similar when grown with either *P. caperata* or *P. saxatilis*. This would appear to indicate that morphological differences between thalli of these three species did not compromise the growth of *X. parietina* at any application frequency. Alternatively, if thalli of *X. parietina* were being compromised by less adpressed neighbouring thalli of *P. caperata* and *P. saxatilis*, the ability to tolerate an elevated nutrient status may be one method by which this species could compensate, particularly if the growth of *P. saxatilis* is being compromised by an elevated pH.

Does nutrient addition lead to an increased number of thallus overlaps and do competitively successful species make significantly more overlaps than other species in pair-wise combinations? Do conspecific thalli show fewer thallus overlaps than heterospecific thalli?

At the start of the experiment thalli within each sub-plot were approximately the same distance apart (5 mm) so any change in the growth rate of a species ultimately determined the time taken for neighbouring thalli to make contact. Application frequency had a significant effect on the number of thallus overlaps made during the course of the experiment (Table 11).

Nutrient application at x1, x2 and x4 resulted in significantly more thallus overlaps being made on neighbouring thalli than those observed under control (x0) application frequencies (Figure 12). This could have been predicted from the thallus diameter measurements which indicated that nutrient applications x1, x2 and x4 produced significantly larger thallus growth than controls (Figure 9).

This increased growth rate resulted in a reduction in the time taken for neighbouring thalli to make contact. Whether one thallus successfully overgrew another appeared to be determined by differences in thallus morphology, with the less adpressed thallus usually overgrowing the more adpressed one. This was

seen to occur with *P. caperata* which overgrew thalli of *X. parietina* significantly more often than it overgrew its own thalli (Figure 13). Since the degree of thallus adpression among conspecifics would be similar, no two competing individuals would necessarily have a competitive morphological advantage. However, this would not always be the case in heterospecific species combinations. This could explain why *P. caperata* made significantly more overlaps on thalli of *X. parietina* than on its own thalli.

Therefore it may be expected that in a heterospecific species combination where competing neighbours have similar thallus adpression the number of overlaps would be similar to the number made when these species were placed in conspecific species combinations. This is supported by *P. caperata* which does not overgrow neighbouring thalli of *P. saxatilis* more than its own thalli (Figure 13). Furthermore, *P. saxatilis* overgrows its own thalli and those of *P. caperata* on a similar number of occasions (Figure 14). As a result it could be suggested that these two species are competitively equivalent. This is somewhat surprising since the visibly thicker thalline lobes of *P. caperata* should provide it with a competitive advantage when competing with the comparatively thinner lobes of *P. saxatilis*.

However, when *P. caperata* and *P. saxatilis* are placed in three-species mixtures with *X. parietina* significantly more overlaps are observed than in conspecific combinations (Figures 13 and 14). This may be attributed to both species overgrowing the more adpressed thalli of *X. parietina* in preference to their own or each others thalli. However, when *P. saxatilis* was placed in heterospecific species combination with *X. parietina* similar numbers of thallus overlaps to those made under conspecific combinations were observed (Figure 14). This may suggest that thalli of *P. saxatilis* and *X. parietina* are similar competitively speaking, and a competitive advantage is only seen when a third species (*P. caperata*) is present. However, this is unlikely since the thalline margin of *P. saxatilis* is considerably less adpressed than that of *X. parietina*.

Alternatively it may be more realistic to assume that the ability of *X. parietina* to tolerate elevated nutrient levels and/or its calcicolous nature (Armstrong – personal communication) may have provided a small competitive advantage when placed in heterospecific species combination 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 (Figure 14).

Although nitrophilous species like *X. parietina* have the ability to utilise additional nutrients to promote growth rates, this can only be seen to provide a competitive advantage if their thallus morphology permits sufficient overlaps of neighbouring thalli.

The results of this chapter are in broad agreement with the work of Armstrong (1984; 1986 & 2000). Furthermore it is clear that anthropogenic nutrient addition changes the competitive dynamics between species which may alter lichen community composition in the long term. This is illustrated by the findings of Chapter Two which indicated that asymmetrical competition occurred between thalli of *P. caperata* and *X. parietina*. The competition between these two species becomes symmetrical following anthropogenic nutrient addition (Figure 15).
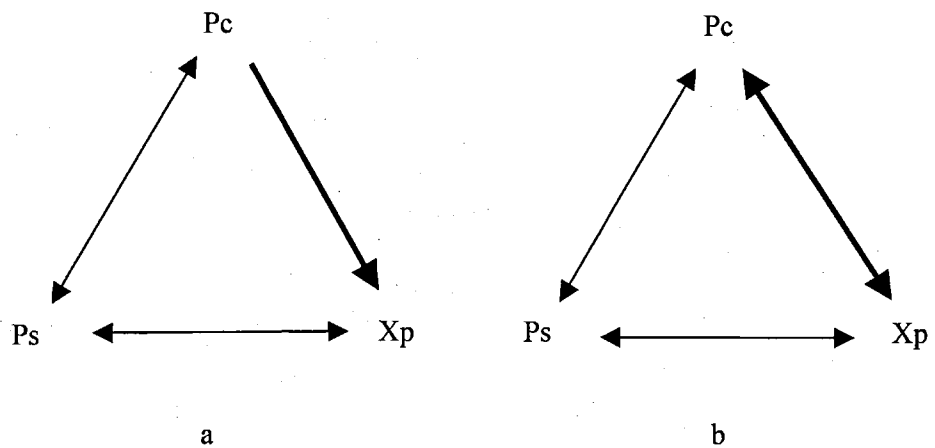
Figure 15. A competitive hierarchical pyramid for *P. caperata* (Pc), *P. saxatilis* (Ps) and *X. parietina* (Xp) under (a) no anthropogenic nutrient addition and (b) anthropogenic nutrient addition.

It is clear that several factors dictate the ability of a species to compete. Furthermore, 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, 1979; 1986; Rogers, 1990) since grazing by microarthropods reduces the thallus area and consequently decreases photosynthetic ability. In addition a thallus could become increasingly more adpressed as grazing from the lobe margin continues inwards towards the centre.

Chapter Four

The intra- and interspecific competitive interactions of *Parmelia caperata* and *P. reddenda* growing on beech (*Fagus sylvatica*).

4.1 Introduction

Lichens primarily compete on substrata for space and light and those species with larger, less adpressed, thalli will tend to overlap their neighbours more often during the process of substrate colonisation. Field experiments have indicated that some epiphytic foliose species are more likely to overlap some neighbouring thalli than others giving rise to a competitive hierarchy (John, 1992).

The speed with which dominance hierarchies are formed may be related to aspect since this is clearly an important factor in determining thallus growth rates (Armstrong, 1975) and therefore determines the time taken for neighbouring thalli to make contact (Chapter Two).

The aim of this study was to determine the intra- and interspecific competitive abilities between *P. caperata* and *P. reddenda* and to ascertain whether they occupy similar or different niches on the boles of beech (*Fagus sylvatica*). How these species competed within lichen communities on the boles was also investigated using circumferential point sampling. This technique has been shown to be an effective method of determining species distribution (Yarranton, 1972; John, 1992; John & Dale, 1995). To this end the following hypotheses were tested:

(i).   Both *P. caperata* and *P. reddenda* are predicted to grow on boles in equal abundance within the sampling height (between 1.0 – 2.0 m) since field observations prior to the experiment suggested both of these large foliose species were abundant on boles of beech.

(ii).   The abundance of these species should be related to aspect (N, S, E and W) since this has been shown to affect thallus growth rate.

(iii). Competition between *P. caperata* and *P. reddenda* are predicted to be symmetrical (competitively equivalent). This assumption is based on the results obtained in Chapter Two where the thallus areas and the number of thallus overlaps made between two large foliose species of *Parmelia* were found to be similar (Table 7).

(iv). The morphological similarity between thalli of *P. caperata* and *P. reddenda* may be reflected by similarities in thallus dry mass.

(v). The thallus morphologies of *P. caperata* and *P. reddenda* should allow them to overlap smaller and more adpressed neighbouring thalli with ease. Therefore it is predicted that similar numbers of overlaps will be made on thalli of other lichen species by both *P. caperata* and *P. reddenda*.

4.2 Materials and methods

Sampling

Twenty mature beech trees with a bole circumference greater than 50 cm at a height of 1.0 m from the ground were randomly selected using the random number function on a scientific calculator (Sharp EL-9600) from a grid superimposed onto a map of Lower Park at Lanhydrock Estate. This allowed grid squares to be selected at random. Trees nearest the selected grid squares were then sampled. Trees that had suffered lightening damage were not sampled.

The selected trees were point sampled at intervals of 10 cm along circumferential line transects positioned 25 cm apart from 1.0 to 2.0 m. At each point lichens were identified to species and recorded together with aspect (± 20 degrees). The lowest transect was positioned 1.0 m from ground level in order to minimise animal disturbance, animal-induced eutrophication (Pirintsos *et al.*, 1993) and vegetation around the base affecting lichen distribution.

Species that contacted either *P. caperata* or *P. reddenda* were noted along with the thallus being overlapped.

Analysis of competitive interactions

Intra- and interspecific competition was evident when neighbouring thalli overlapped each other. The number of thallus overlaps made by *P. caperata* and *P. reddenda* at 10 cm intervals along five circumferential transects were counted at each of four aspects (N, S, E and W). Only thalli that touched a sampling point were counted.

To compensate for the fact that more thalli of *P. caperata* were present than *P. reddenda* the raw data were scaled for some G-analyses. This was achieved by summing the total number of overlaps made at

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a particular aspect and then dividing by the total number of individuals of *P. caperata* or *P. reddenda* present at that aspect (Figures 16, 17, 19, 20 and 21). In this way it was possible to make representative comparisons between these species and reduce the effect of sample size in determining a significant relationship (John & Dale, 1995).

Statistical analysis

A three-way split-plot analysis of variance (ANOVA) (Zar, 1996) was used to determine the effect of height (factor one with five levels), aspect (factor two with four levels) and lichen species (factor three with two levels) on the abundance of *P. caperata* and *P. reddenda* on boles between 1.0 and 2.0 m (Table 12). Tukey (HSD) multiple means test (Zar, 1996) was used to determine which means differed significantly.

Factor	Levels				
Height:	1 (1.00 m);	2 (1.25 m)	3 (1.50 m)	4 (1.75 m)	5 (2.00 m)
Aspect:	1 (North);	2 (South);	3 (East);	4 (West)	
Species:	1 (*P. caperata*);	2 (*P. reddenda*)			

Table 12. Three-way split-plot ANOVA layout for the effect of height, aspect and species on thallus abundance.

G-analyses were used to determine significant differences between the ratios of intra- and interspecific pair-wise combinations of *P. caperata* and *P. reddenda*. For these analyses G was tested against the ratio of overlapped thalli to non-overlapped thalli (Figures 16, 17, 19, 20 and 21).

Where *P. caperata* and *P. reddenda* competed with neighbouring thalli of other species significant differences between the number of thallus overlaps made were tested against a 1:1 ratio (Figure 18) since it was proposed that *P. caperata* and *P. reddenda* would compete similarly with other lichen species. The Yates correction was used since DF = 1 throughout.

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Finally, two-way ANOVA was used to determine the effect of aspect and lichen species on the dry masses of 1.5 cm diameter thallus discs. Tukey (HSD) multiple means test was used to determine which means differed significantly. All calculations were performed using Statistica™ 5.5 (Statsoft Inc., Tulsa, USA).

The effect of height, aspect and lichen species on the abundance of P. caperata and P. reddenda

Height and aspect had no effect on the abundance of *P. caperata* or *P. reddenda*. However, there was a significant difference between the relative abundance of these two species (Table 13). There was no interaction between height, aspect or lichen species.

Tukey (HSD) analysis indicated that there were significantly more thalli of *P. caperata* than thalli of *P. reddenda* ($P < 0.001$).

Effect	DF	MS	F	P
(1) Site:	4	2.72	1.74	0.139
(2) Aspect:	3	2.08	1.33	0.264
(3) Sp. Comb.:	1	105.85	67.67	<0.001
Interaction 12:	12	0.55	0.35	0.978
Interaction 12:	4	2.07	1.32	0.259
Interaction 23:	3	0.63	0.40	0.750
Interaction 123:	12	1.23	0.78	0.665
Error:	760	1.56		

Table 13. Three-way ANOVA for the effect of height (factor one), aspect (factor two) and species (factor three) on the abundance of *P. caperata* and *P. reddenda* on boles of 20 beech trees between 1.0 and 2.0 m.

Intraspecific competition

The number of overlaps made by *P. caperata* and *P. reddenda* on their own thalli was found to be similar on north, east and west facing aspects (Figure 16). Although on south facing aspects *P. reddenda* overlapped its own thalli significantly more often than *P. caperata* overlapped its own thalli (1 DF, G = 8.35; *P* < 0.01) (Figure 16), the total number of intraspecific overlaps made by these two species was similar (1 DF, G = 3.54; *P* = 0.06). All data for this analysis were scaled to reduce the effect of sample size.

Figure 16. The number of intraspecific overlaps for *P. caperata* (Pc) (shaded) and *P. reddenda* (Pr) (unshaded) represented as a % of the total overlaps made at each aspect by Pc and Pr taken from five circumferential transects on 20 beech trees. Data not sharing a common letter within an aspect differ significantly (*P* = 0.05). NS = not significant. The number of intraspecific overlaps made at each aspect are shown next to the total number of overlaps made at each aspect in parentheses: north: Pc; n = 37 (219), Pr; n = 6 (35); south: Pc; n = 10 (89), Pr; n = 23 (80); east: Pc; n = 24 (105), Pr; n = 10 (39); west: Pc; n = 22 (144), Pr; n = 6 (43).

P. caperata competing with P. reddenda

The abundance of *P. caperata* and *P. reddenda* between 1.0 and 2.0 m resulted in many interthalline contacts being made between these two species. G-analysis using scaled data indicated that overall, regardless of aspect, thalli of *P. reddenda* significantly overlapped more thalli of *P. caperata* than *P. caperata* did of *P. reddenda* (1 DF, G = 4.37; *P* = 0.04). This was particularly evident on north (1 DF, G = 11.03; *P* < 0.01) and south (1 DF, G = 3.69; *P* = 0.05) facing aspects (Figure 17).
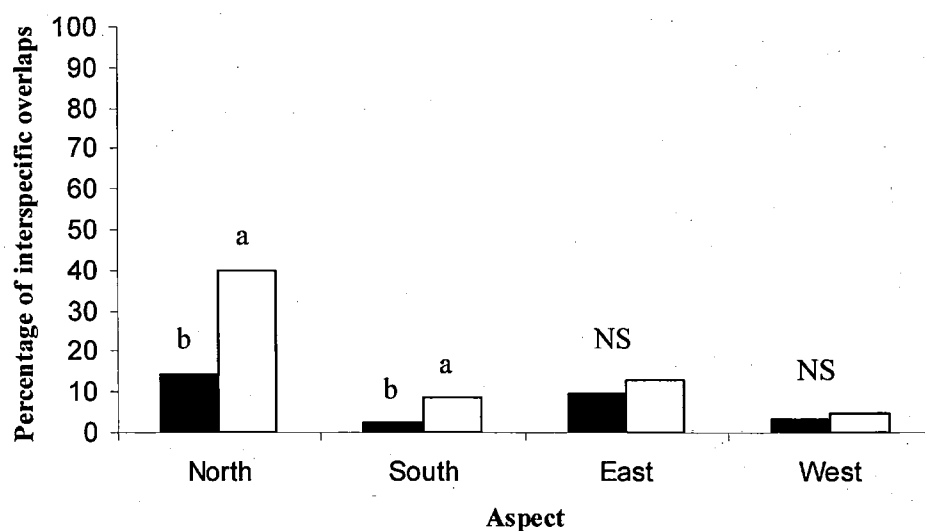
Figure 17. The number of interspecific overlaps for *P. caperata* (Pc) (shaded) and *P. reddenda* (Pr) (unshaded) represented as a % of the total overlaps made at each aspect by Pc and Pr taken from five circumferential transects on 20 beech trees. Data not sharing a common letter within an aspect differ significantly (*P* = 0.05). NS = not significant. The number of interspecific overlaps made at each aspect are shown next to the total number of overlaps made at each aspect in parentheses: north: Pc; n = 32 (219), Pr; n = 14 (35); south: Pc; n = 2 (89), Pr; n = 7 (80); east: Pc; n = 10 (105), Pr; n = 5 (39); west: Pc; n = 5 (144), Pr; n = 2 (43).

Both *P. caperata* and *P. reddenda* competed with a variety of lichen species on boles between 1.0 and 2.0 m (Table 14). However, *P. caperata* overlapped certain species that *P. reddenda* did not and *vice versa*.

Taking only those lichen species overlapped by both *P. caperata* and *P. reddenda* G-analysis (assuming a 1:1 ratio) indicated that regardless of aspect, *P. caperata* made significantly more overlaps on neighbouring thalli of other species than *P. reddenda* did (1 DF, G = 92.32; $P < 0.01$). This was particularly evident on north (1 DF, G = 80.25; $P < 0.01$), east (1 DF, G = 16.15; $P < 0.01$) and west (1 DF, G = 29.95; $P < 0.01$) facing aspects (Figure 18).
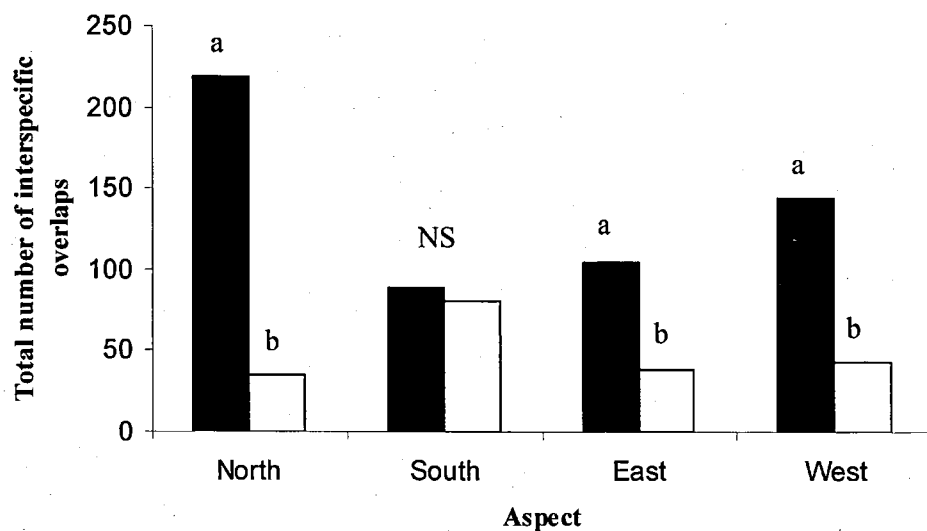
Figure 18. The total number of interspecific thallus overlaps made on 14 lichen species by *P. caperata* (Pc) (shaded) and *P. reddenda* (Pr) (unshaded) at each aspect. Data not sharing a common letter within an aspect differ significantly ($P = 0.05$). NS = not significant. North: Pc; n = 219, Pr; n = 35; south: Pc; n = 89, Pr; n = 80; east: Pc; n = 105, Pr; n = 39; west: Pc; n = 144, Pr; n = 43.

Species	P. caperata				P. reddenda			
	N	S	E	W	N	S	E	W
Anisomeridium biforme	0	1	0	0	-	-	-	-
Arthonia radiata	3	2	6	0	-	-	-	-
Cladonia coniocraea	9	2	0	4	-	-	-	-
Enterographa crassa	29	20	6	14	1	7	0	0
Evernia prunastri	3	0	0	0	-	-	-	-
Graphis scripta	9	0	0	0	0	1	2	0
Lecania cyrtella	5	0	0	4	-	-	-	-
Lecanora chlarotera	0	2	0	0	0	3	0	0
L. conizaeoides	24	7	14	17	0	7	0	0
L. jamesii	0	3	0	0	0	2	0	0
Lepraria incana	-	-	-	-	0	0	1	0
Opegrapha atra	0	6	10	0	0	0	2	0
Parmelia caperata	37	10	24	22	14	7	5	2
P. perlata	33	7	14	35	2	3	2	10
P. reddenda	32	2	10	5	6	23	10	6
P. saxatilis	5	0	0	2	-	-	-	-
P. subaurifera	-	-	-	-	0	2	8	0
P. subrudecta	-	-	-	-	0	2	0	0
Pertusaria amara	17	0	0	6	-	-	-	-
P. pertusa	10	2	3	14	0	2	2	0
Phaeographis dendritica	7	0	0	3	0	2	0	0
Phlyctis argena	5	2	1	4	0	5	4	5
Pyrenula macrospora	18	4	12	9	11	18	12	20
Pyrrhospora quernea	-	-	-	-	0	0	3	0
Usnea subfloridana	15	24	11	21	1	0	0	0
Total:	256	99	129	166	41	103	49	49
(-P. caperata):	219	89	105	144 = [557]	-	-	-	-
(-P. reddenda):	-	-	-	-	35	80	39	43 = [197]

Table 14. Number of overlaps made by *P. caperata* and *P. reddenda* on neighbouring thalli of other lichen species across five circumferential transects on the boles of beech trees (*Fagus sylvatica*) related to aspect. The notation "-" indicates no overlaps were observed.

Parmelia perlata was the only other large foliose species present that was observed to compete with *P. caperata* and *P. reddenda*. Scaling the data to reduce the effect of sample size indicated that regardless of aspect, *P. caperata* overlapped *P. perlata* significantly more often than *P. reddenda* did (1 DF, $G = 7.10$; $P < 0.01$). However, there were no significant differences between the number of overlaps made by this species on thalli of *P. perlata* at any individual aspect.

Overall, regardless of aspect, *P. perlata* made significantly more overlaps on thalli of *P. caperata* than it did on *P. reddenda* (1 DF, $G = 17.27$; $P < 0.01$). This was particularly evident on north facing aspects (1 DF, $G = 28.18$; $P < 0.01$). However, on south facing aspects the opposite was observed to occur (1 DF, $G = 3.99$; $P = 0.05$) (Figure 19).
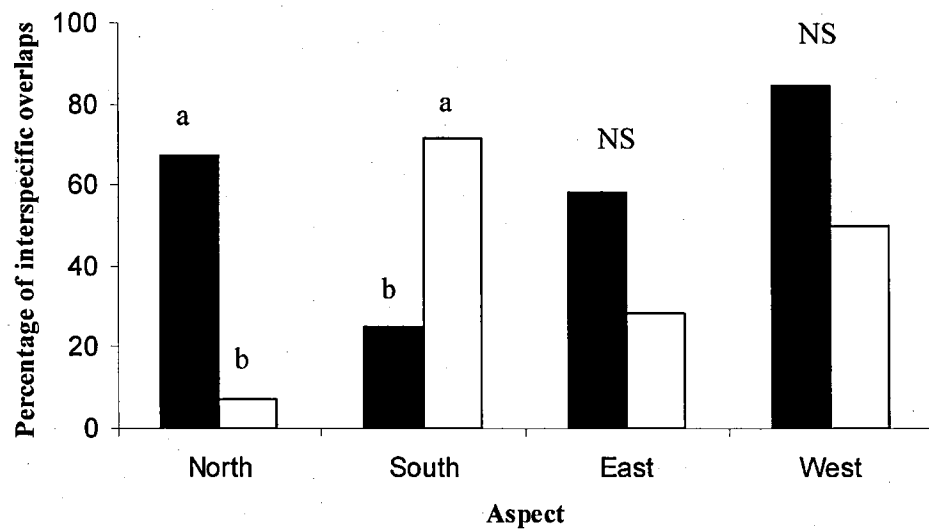
Figure 19. The number of interspecific overlaps for *P. perlata* (Pp) on thalli of *P. caperata* (Pc) (shaded) and *P. reddenda* (Pr) (unshaded) represented as a % of the total overlaps made at each aspect by Pp on Pc (north = 46; south = 12; east = 12 and west = 13. Total = 83) and Pp on Pr (north = 27; south = 7; east = 14 and west = 10. Total = 58). Data not sharing a common letter within an aspect differ significantly ($P = 0.05$). (Pp→Pc: north = 9; south = 2; east = 4 and west = 3. Pp→Pr: north = 1; south = 3; east = 3 and west = 2). Overlap data for *P. perlata* on *P. caperata* and *P. reddenda* given in Appendix-Table 6.

Pyrenula macrospora was overgrown significantly more often by *Parmelia reddenda* than by *P. caperata* (1 DF, G = 58.31; *P* < 0.01) on north (1 DF, G = 12.41; *P* < 0.01), south (1 DF, G = 12.77; *P* < 0.01), east (1 DF, G = 6.99; *P* < 0.01) and west (1 DF, G = 34.62; *P* < 0.01) facing aspects (Figure 20). Data were scaled for this analysis to reduce the effect of sample size.
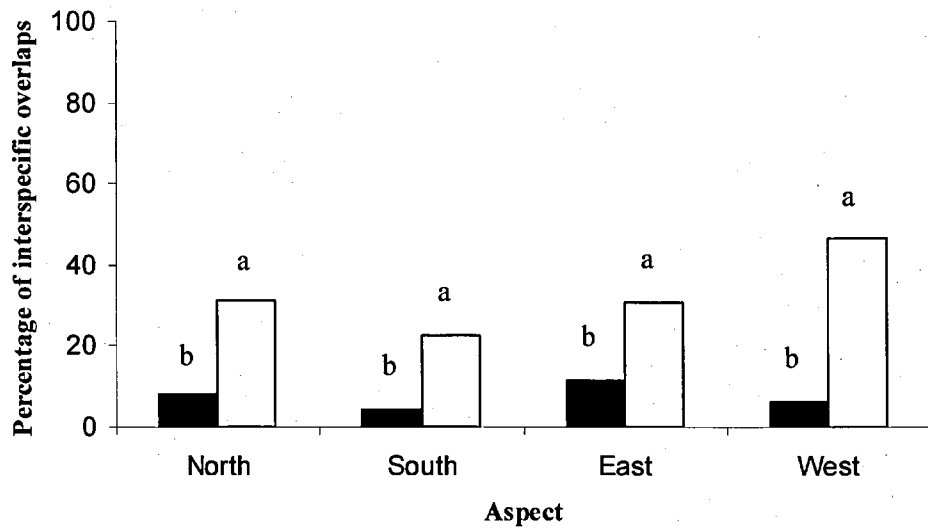
Figure 20. The number of interspecific overlaps for *P. caperata* (Pc) (shaded) and *P. reddenda* (Pr) (unshaded) on *Pyrenula macrospora* (Pm) represented as a % of the total overlaps made at each aspect by Pc on Pm (north = 219; south = 89; east = 105 and west = 144. Total = 557) and Pr on Pm (north = 35; south = 80; east = 39 and west = 43. Total = 197). Data not sharing a common letter within an aspect differ significantly (*P* = 0.05). (Pc→Pm: north = 5; south = 2; east = 2 and west = 3. Pr→Pm: north = 2; south = 5; east = 3 and west = 4).

Thalli of *Phlyctis argena* were overlapped significantly more by *Parmelia reddenda* than by *P. caperata* (1 DF, G = 9.33; *P* < 0.01), with significantly larger number of thalli being overlapped on east (1 DF, G = 6.33; *P* = 0.01) and west (1 DF, G = 4.70; *P* = 0.03) facing aspects (Figure 21). Data were scaled for this analysis to reduce the effect of sample size.
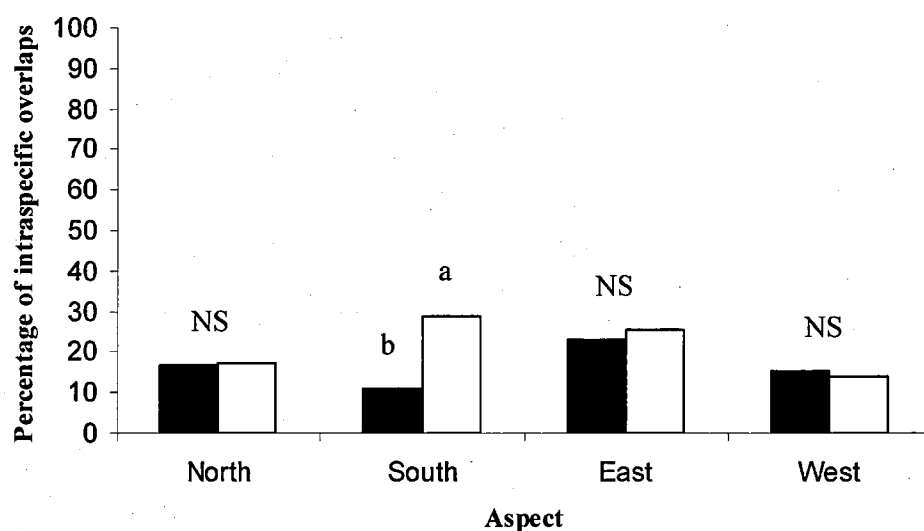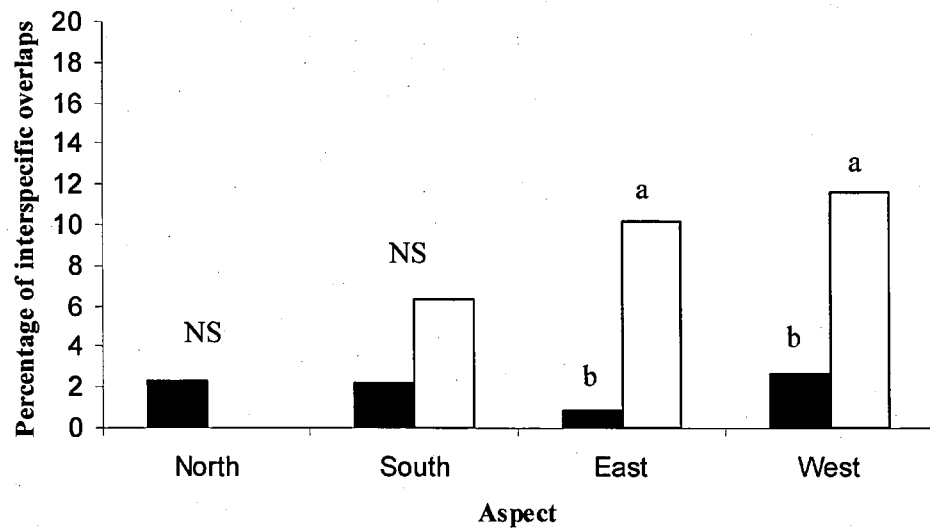

Figure 21. The number of interspecific overlaps for *P. caperata* (Pc) (shaded) and *P. reddenda* (Pr) (unshaded) on *Phlyctis argena* (Pa) represented as a % of the total overlaps made at each aspect by Pc on Pa (north = 219; south = 89; east = 105 and west = 144. Total = 557) and Pr on Pa (north = 35; south = 80; east = 39 and west = 43. Total = 197). Data not sharing a common letter within an aspect differ significantly (*P*=0.05). NS = not significant. (Pc→Pa: north n=2; south n=1; east n=1 and west n=1. Pr→Pa: north n=0; south n=2; east n=2 and west n=1).

Thallus morphology has been shown to affect the competitive ability of a species and where a thallus is notably heavier a competitive advantage may be realised (Appendix-Table 7). However, two-way ANOVA indicated that there was no significant difference between the thallus dry masses of *P. caperata* and *P. reddenda* and that dry mass was unrelated to aspect. There was no interaction between the two factors (Table 15).

Effect	DF	MS	F	P
(1) Aspect:	3	0.0001	0.57	0.64
(2) Species:	1	0.0001	0.46	0.50
Interaction:	3	0.0001	0.36	0.78
Error:	24	0.0002		

Table 15. Two-way ANOVA for the effect of aspect and lichen species on thallus dry masses of 32 x 1.5 cm discs (four per aspect) for *P. caperata* and *P. reddenda* taken from the boles of 20 beech trees (*Fagus sylvatica*) n = 16.

Do thalli of P. caperata and P. reddenda grow on boles in equal abundance within the sampling height? Furthermore, is abundance related to aspect?

The vertical zonation of some epiphytic lichen species has been well documented (Hale, 1952; Harris, 1970; St. Clair *et al.*, 1986; John, 1992) and abundant species like *P. caperata* and *P. reddenda* show some vertical zonation patterns. There is evidence to suggest that *P. caperata* and *P. reddenda* have different patterns of zonation on trees with the former having an optimum cover approximately one third of the way up the tree while the latter occurs mainly in the middle regions of the trunk (Harris, 1970). Such patterns may be explained in terms of the individual thallus morphology of the species and water availability (Harris, 1970) which varies according to the microtopography of the bark. Substrata with a high microtopography have a rougher surface than those with a lower microtopography and consequently remain damp for longer periods of time.

Despite the limited vertical distance (between 1.0 and 2.0 m) of the circumferential sampling, *P. caperata* was significantly more abundant than *P. reddenda* (Table 13). Microenvironmental factors such as substrate pH, moisture levels and the microtopography of the substrate would not be expected to change significantly over such a short vertical distance unless the boles were influenced by shading from other vegetation or subject to sudden changes in directional growth resulting in a convoluted bole. All boles surveyed had vertical directional growth and were free from shading by neighbouring vegetation. Therefore, the significantly greater abundance of *P. caperata* on north, east and west facing aspects than *P. reddenda* (Table 13) may imply that *P. caperata* is zoned towards the lower third of the trunk as suggested by Harris (1970).

Alternatively, *P. caperata* may simply be able to overlap other species due to its thalli being large and less adpressed compared with the thalli of its competitors, or it may just be a better disperser to trees and over time there may be larger numbers of *P. reddenda*.

It has been claimed that *P. caperata* shows an optimum cover on oak trees aged 30 to 35 years. The decrease in cover after this time is said to reflect unfavourable growing conditions, thallus senescence

(Harris, 1970) or possibly succession. This was not evident on the 20 boles surveyed which contained significantly more thalli of *P. caperata* than *P. reddenda* (Table 13). However, since the ages of the 20 boles surveyed ranged between 75 and 90 years it is possible that *P. caperata* was previously more abundant than is evident today. Unfortunately there have been few lichen surveys conducted on the Lanhydrock Estate and none, to my knowledge, have recorded species abundance.

The abundance of *P. caperata* and *P. reddenda* on boles between 1.0 and 2.0 m appeared not to be effected by aspect ($F = 1.33$; $P = 0.264$) (Table 13).

Competitive interactions

Is competition between P. caperata and P. reddenda symmetrical (competitively equivalent)?

Intraspecific competition

At some positions on the trunk *P. caperata* and *P. reddenda* overlapped their own thalli. G-analysis indicated that significantly more intraspecific overlaps were made by *P. reddenda* than by *P. caperata* on south facing aspects only (1 DF, $G = 8.35$; $P < 0.01$) (Figure 16). This may be a consequence of differences in thallus morphology between these two species. The lobes of *P. caperata* and *P. reddenda* rise conspicuously above the substrate (personal observation) which facilitates competition, whether intra- or interspecific. Due to both abiotic and biotic interference some lobes will be either more or less adpressed than their conspecific neighbours which may cause a reduced or enhanced ability to overlap their own thalli. However, this is only speculative and overall, regardless of aspect, both species made similar numbers of intraspecific overlaps (1 DF, $G = 3.54$; $P = 0.06$).

Are morphological similarities between thalli of P. caperata and P. reddenda reflected by similarities in thallus dry mass? Do the thallus morphologies of P. caperata and P. reddenda allow them to overlap smaller and more adpressed neighbouring thalli with ease on a similar number of occasions?

Interspecific competition

Thalli of *P. caperata* and *P. reddenda* were abundant on boles between 1.0 and 2.0 m and inevitably came into contact. When such competition occurred thalli of *P. caperata* were overlapped significantly more often by *P. reddenda* particularly on north and south facing aspects (Figure 17). This may suggest that *P. reddenda* has some competitive advantage over *P. caperata*.

Microenvironmental factors, resistance to herbivorous grazing by microarthropods and aspect all affect the competitive success of a species, but clearly morphological differences between thalli are also important, with heavier thalli having a competitive advantage when overlapping species with lighter thalli. Since both *P. caperata* and *P. reddenda* have thalli of similar dry masses (Table 15) it is reasonable to suggest that the competitive advantage of *P. reddenda* over *P. caperata* was not established through differences in thallus mass.

Both species have large foliose thalli with prominently raised thalline margins. Perhaps the thalline margins of *P. reddenda* are more inflexible and less susceptible to mechanical deformation during competition with other foliose thalli. Alternatively there may be some allelopathic effect which confers a competitive advantage over other thalli. Initially, the secondary compounds produced by these two species were thought to be similar (Culberson, 1969) so this is perhaps unlikely to be the case.

However, *P. caperata* synthesises the *para*-depside atranorin ($C_{19}H_{18}O_8$) under certain conditions but *P. reddenda* synthesises and stores it permanently (White & James, 1985). This may dictate a competitive advantage in *P. reddenda* by facilitating growth rates since it has been shown that the fluorescence maximum of atranorin corresponds almost exactly to that of chlorophyll (Rao & LeBlanc, 1965) thereby promoting photosynthesis. However, the precise mechanism by which any realistic competitive advantage could be achieved remains uncertain.

The only other large foliose species present was *Parmelia perlata*. G-analysis of the number of overlaps made on this species indicated that overall, regardless of aspect, *P. perlata* was overlapped

significantly more often by *P. caperata* than by *P. reddenda* (1 DF, G = 7.10; *P* < 0.01). Aspect did not affect the number of overlaps made on thalli of *P. perlata* by *P. caperata* or *P. reddenda*. This could suggest that *P. caperata* has a more competitively efficient thallus than *P. perlata*. However, since *P. perlata* overlapped *P. caperata* significantly more than it overlapped *P. reddenda* (1 DF, G = 17.27; *P* < 0.01), it seems reasonable to assume that both *P. caperata* and *P. perlata* are competitively equivalent.

However, *P. caperata* only overlapped thalli of *P. perlata* 89 times out of a total of 557 overlaps (16%) (Table 14) while *P. perlata* overlapped *P. caperata* 52 times out of a total of 83 (63%). *P. reddenda* overlapped thalli of *P. perlata* 17 times out of a total of 197 overlaps (8.6%) while *P. perlata* overlapped thalli of *P. reddenda* 16 times out of a total of 58 (28%).

Therefore, since *P. perlata* overlapped thalli of *P. caperata* more than it did *P. reddenda* in a competitive hierarchical pyramid, *P. reddenda* would be at the top due to it having overlapped *P. caperata* significantly more often than the reciprocal (Figure 22).
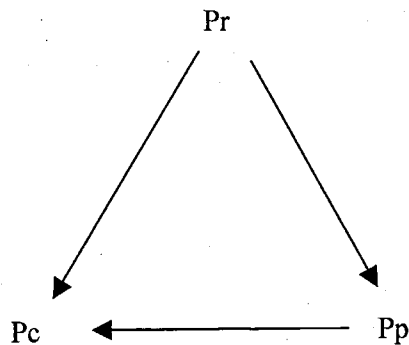
Figure 22. A proposed competitive hierarchical pyramid for *P. caperata* (Pc), *P. perlata* (Pp) and *P. reddenda* (Pr) based on the number of thallus overlaps made by each species.

This suggests that perhaps *P. reddenda* may have a more competitively efficient thallus morphology than the other two species.

A variety of other lichen species were also identified on the boles between 1.0 and 2.0 m that were in competition with *P. caperata* and *P. reddenda*. Seven species were overlapped exclusively by *P. caperata* while four were overlapped exclusively by *P. reddenda* (Table 14).

G-analysis testing against a 1:1 ratio of thallus overlaps made on neighbouring thalli by *P. caperata* and *P. reddenda* indicated that 14 species were overlapped significantly more often by *P. caperata* than by *P. reddenda* (1 DF, G = 92.32; *P* < 0.01), particularly on north, east and west facing aspects (Figure 18). This is simply a function of the larger abundance of *P. caperata* on the boles than *P. reddenda* which allow proportionally larger numbers of overlaps to be made on neighbouring thalli of other species.

However, thalli of *Pyrenula macrospora* were overlapped significantly more often by *P. reddenda* than by *P. caperata* (1 DF, G = 58.31; *P* < 0.01) at all aspects (Figure 20). This may be explained by the presence of more thalli of *P. reddenda* being adjacent to thalli of *Pyrenula macrospora*. Similarly, *Phlyctis argena* was overlapped by *Parmelia reddenda* significantly more often than by *P. caperata* (1 DF, G = 9.33; *P* < 0.01) at east and west facing aspects (Figure 21). This may be a consequence of reduced competition from adpressed crustose species facilitating the colonisation and growth of *P. reddenda* at these locations on the boles. This could suggest that *P. caperata* and *P. reddenda* do not occupy the same niches on the boles of beech between 1.0 and 2.0 m.

If *P. reddenda* shares a niche with crustose species which offer less interspecific competition than foliose species this may suggest an escape strategy (Skellam, 1951) since it appears to be avoiding competition with large foliose species like *P. caperata*. Alternatively, *P. reddenda* may be a more efficient disperser to corticolous substrata than *P. caperata* or *P. perlata* and, over time, it could exclude these and other foliose species from locations on boles where there is predominantly crustose lichen cover.

Chapter Five

The effect of nutrient treatments on the growth and competitive abilities of *Parmelia caperata* and *P. reddenda* on beech trees (*Fagus sylvatica*).

5.1 Introduction

As farming practices become ever more intensive lichen species are increasingly exposed to elevated nutrient levels. There is evidence to suggest that anthropogenic N deposition far exceeds the N critical load, resulting in many European ecosystems suffering eutrophication (Emmett *et al.*, 1995; Eugster *et al.*, 1998) with further deposition leading to hypertrophication, where nutrient levels are greatly increased above those found naturally.

Further evidence suggests that such conditions cause changes in species composition within higher plant populations (Jornsgard *et al.*, 1996; Kuylenstierna *et al.*, 1998; Boyer & Zedler, 1999). For instance, in Dutch forests it has been observed that species composition has changed from a lichen-dominated to grass-dominated vegetation as a direct result of hypertrophic conditions (Van Der Eerden *et al.*, 1998).

Other effects associated with excess N deposition include defoliation and deterioration of foliage in forest ecosystems which may result in the removal of suitable habitats for epiphytic lichen species (Van Der Eerden *et al.*, 1998). Furthermore, the increased algal growth that is observed under eutrophic and hypertrophic conditions (O'Dare, 1990; Wootton, 1991) covers the thallus and restricts light to the photobiont. This may ultimately lead to the complete loss of certain species from trees (Gilbert & Purvis, 1996).

Elevated nutrient levels have also been seen to cause changes in species composition of lichen communities (Vagts & Kinder, 1999) by increasing the radial growth rate of nitrophilous species (Armstrong, 1984; Crittenden *et al.*, 1994; Sanchez-Hoyos & Manrique, 1995; Miller & Brown, 1999), in some instances by as much as 15 – 32% per year (Lewis Smith, 1995), while inhibiting growth in nitrophobous (acidophytic) species (Armstrong, 1984; Vagts & Kinder, 1999). In such situations it has

been proposed that competitive exclusion of some lichen species might occur (Lawrey, 1981; Vagts & Kinder, 1999) therefore leading to a reduction in species diversity.

It is unclear what impact nutrient addition will have on the growth and competitive abilities of individual lichen species. Furthermore, the use of lichen transplants to maintain species richness and diversity in storm damaged areas (Kew Gardens and Lanhydrock Estate) requires careful monitoring since it is uncertain how transplants will respond to new environments where nutrient levels may be different from the species previous environment.

The aim of this chapter is to determine the effect of elevated nutrient levels on the growth rates of *P. caperata* and *P. reddenda* using a reciprocal transplant experiment conducted on the boles of beech trees (*Fagus sylvatica*) within the Lanhydrock Estate. The growth of *P. caperata* and *P. reddenda* under four nutrient applications and four species combinations will be assessed. The effect of aspect on growth and competitive ability will not be assessed since it was previously found not to significantly affect the abundance of *P. caperata* or *P. reddenda* on the boles of beech trees (Chapter Four).

In this experiment thalli of *P. caperata* (Pc) were transplanted into neighbouring colonies of itself (Pc→Pc) and *P. reddenda* (Pc→Pr). Similar transplants were established for *P. reddenda* (Pr) (Pr→Pr and Pr→Pc). Here the transplanted thalli were in direct contact with neighbouring thalli resulting in the possibility of immediate competition.

In addition, thalli of *P. caperata* were transplanted into cleared areas within neighbouring colonies of itself (Pc→Cl.Pc) and *P. reddenda* (Pc→Cl.Pr). Again, similar transplants were established for *P. reddenda* (Pr→Cl.Pr and Pr→Cl.Pc). The purpose of the cleared area was to allow the transplants to become acclimatised to their new environmental conditions prior to any competitive interactions taking place and furthermore, to reduce the effect of physiological stress arising from fragmentation and transplantation (Seaward – personal communication).

How *P. caperata* and *P. reddenda* competed intra- and interspecifically under different levels of nutrient application and species combination was further assessed by counting the frequency of overlaps made by each species. The transplantation of one species into a conspecific or heterospecific colony should result in the beginning of a competitive interaction over time. The use of a reciprocal experimental design should provide some insight into whether competition between *P. caperata* and *P. reddenda* is asymmetrical or symmetrical under conditions of anthropogenic nutrient addition. This should provide

some insight into whether a dominance hierarchy exists between them. To this end the following hypotheses were tested:

(i).   It is proposed that nutrient addition will increase lichen growth rates, as measured by changes in thallus diameter, up to an optimum frequency of nutrient application compared with control applications of distilled water (no nutrients).

(ii).   Thallus growth rates should be larger when transplants are placed into cleared areas of their own or other neighbouring thalli (Pc→Cl.Pc, Pc→Cl.Pr and Pr→Cl.Pr, Pr→Cl.Pc). This is based on the assumption that unimpeded thalli grow faster than impeded thalli. This can be measured by comparing with the appropriate species combinations that did not have cleared areas (Pc→Pc, Pc→Pr and Pr→Pr, Pr→Pc).

(iii).   If nutrient addition increases thallus growth rates compared with control nutrient applications, the time taken for neighbouring thalli to make contact should be reduced. This should increase the amount of competition between *P. caperata* and *P. reddenda* as measured by the frequency of thallus overlaps.

(iv).   Although it is assumed that intraspecific competition is more intense than interspecific competition (Keddy, 2001) it is predicted that conspecific species combinations will show a lower frequency of overlaps than heterospecific combinations since differences in thallus morphology dictate the competitive success of a species.

(v).   *P. reddenda* should out compete *P. caperata* since it appears at the top of a competitive hierarchical pyramid (Chapter Four) under conditions of no experimentally elevated nutrient conditions. This will be tested by observing the frequency of overlaps made between these two species at each species combination.

5.2 Materials and Methods

Substrata

Beech (*Fagus sylvatica*) is common throughout the British Isles and is a native species on both chalk and limestone soils (Perkins, 1984).

Transplants, confined to beech substrata, were established in Lower Park at the Lanhydrock Estate which offers a landscape feature comprising mainly ancient trees in a parkland setting. However, this area has only been managed as a wood pasture since the early eighteenth century and consequently the lichen flora present may be expected to reflect changes in management over this period (O'Dare, 1990).

Sixteen beech trees with a bole girth greater than 50 cm at a height of 1.0 m were randomly selected within Lower Park (Figure 23). Beech has a relatively low microtopography compared with other species due to its smooth bark. This helped reduce the influence of microtopography on growth and competitive ability and in addition aided the removal and re-establishment of thallus transplants.
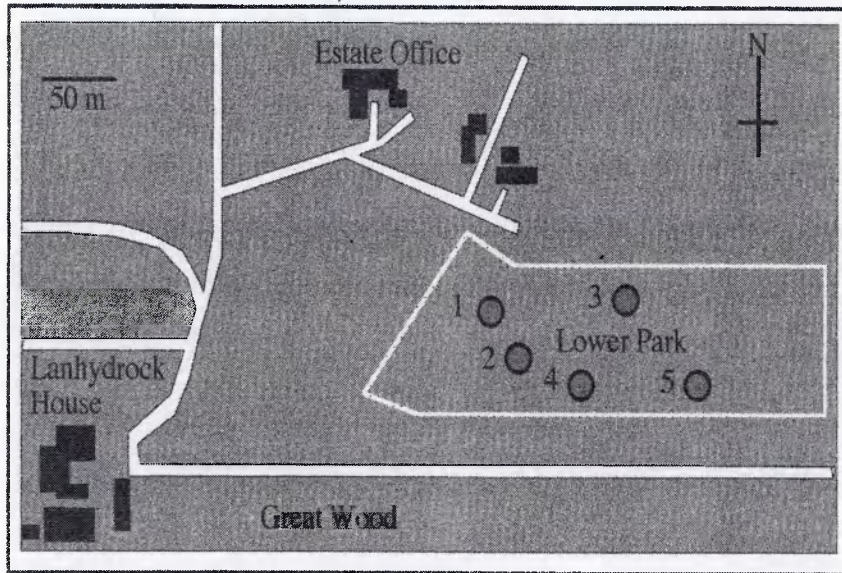
Figure 23. Map of the Lanhydrock Estate showing location of Lower Park, surrounding parkland and estate buildings. The reciprocal transplants were established on boles within stands 1 – 5. Scale: 1 cm : 50 m.

Lichen material

A 1.5 cm diameter cork borer was used to cut out circular thallus discs (transplants) along with a small plug of bark. Transplants were only removed from established colonies of *P. caperata* and *P. reddenda* with thallus material taken from regions as near to the lobe edges as possible since these are the locations where most growth occurs (Armstrong & Smith, 1998). The bark plugs were glued in place using Bostik™ No. 1 all purpose adhesive which has been shown not to affect the growth rates of some lichen species (Armstrong, 1981).

Four transplants were established for each species (Table 16) on each of sixteen boles positioned between 1.0 and 2.0 m from ground level. The spatial position of each transplant was determined by the location of established colonies of suitable size. Within these colonies only thalli having a diameter greater than four centimeters were selected since these are shown to have a more constant growth rate (Hale, 1967; Armstrong, 1973).

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Intraspecific competition was assessed by transplanting thallus discs of *P. caperata* (Pc) and *P. reddenda* (Pr) into established neighbouring colonies of themselves (Pc→Pc and Pr→Pr). Prior to placing the transplant a 1.5 cm thallus disc had to be removed from the recipient colony. The removed disc was used later in another transplant on the same bole. Transplants were also placed into colonies where a 2.0 cm diameter cleared area had been made. This provided a gap between neighbouring thalli of 0.25 cm and prevented thalli from touching immediately (Pc→Cl.Pc and Pr→Cl.Pr).

Interspecific competition was assessed by transplanting thallus discs of *P. caperata* and *P. reddenda* into established neighbouring colonies of the other species (Pc→Pr and Pr→Pc). Transplantation into 2.0 cm cleared areas was also set up (Pc→Cl.Pr and Pr→Cl.Pc).

The use of such reciprocal transplantation may provide an insight into whether a dominance hierarchy exists between *P. caperata* and *P. reddenda* or alternatively whether there is some degree of niche separation between them.

Analysis of growth rates

A digital vernier gauge was used to measure the largest diameter of the thalli prior to nutrient application. Measurements were recorded in July 1997, and at six monthly intervals thereafter until August 1999 which provided an indication of thallus growth for *P. caperata* and *P. reddenda* under different frequencies of nutrient application and species combination.

However, interpretation of the results was based exclusively on thallus diameters after two years growth at the end of the experimental period (August 1999). These were subtracted from the initial thallus diameter (1.5 cm) in order to determine the mean change in thallus diameter for each species.

Competition within and between species was evident when thalli overgrew each other. This required one thallus to overlap another at a point where they met. The frequency of overlaps for *P. caperata* and *P. reddenda* were counted at the end of the experimental period and expressed as a percentage of the total number of overlaps that could theoretically have been made under each application frequency and species combination.

Experimental design

Thallus plugs of 1.5 cm diameter were placed into conspecific and heterospecific species combinations (Table 16). Two factors were tested in this experiment, a nutrient addition factor (Hoagland's Solution) with four levels (x0; x2; x4 and x16 frequencies of application) and a species combination factor with eight levels (four conspecific and four heterospecific – Table 16).

Nutrient treatments were randomly assigned to each of the 16 boles which provided four replicates for each of the four nutrient levels. Each bole contained one complete set of eight reciprocal thallus transplants positioned between 1.0 and 2.0 m from ground level.

All transplants had been completed by February 1997. A period of one month was allowed prior to initial treatment with Hoagland's Solution so that the species could acclimatise to their new environmental conditions and to reduce physiological stress (increased respiration) arising from transplantation and fragmentation (Seaward – personal communication).

Conspecific species combinations

Pc→Pc   *P. caperata* transplanted into itself

Pc→Cl.Pc   *P. caperata* transplanted into a 2.0 cm cleared area of itself

Pr→Pr   *P. reddenda* transplanted into itself

Pr→Cl.Pr   *P. reddenda* transplanted into a 2.0 cm cleared area of itself

Heterospecific species combinations

Pc→Pr   *P. caperata* transplanted into *P. reddenda*

Pc→Cl.Pr   *P. caperata* transplanted into a 2.0 cm cleared area of *P. reddenda*

Pr→Pc   *P. reddenda* transplanted into *P. caperata*

Pr→Cl.Pc   *P. reddenda* transplanted into a 2.0 cm cleared area of *P. caperata*

Table 16. Reciprocal species combination transplants for *P. caperata* and *P. reddenda* used on the boles of 16 beech trees in Lower Park at the Lanhydrock Estate.

Nutrient treatment

Freshly prepared Hoagland's Solution of pH 6.5 (Appendix - Table 4) diluted to 10% original strength was used to saturate the transplanted thalli. This dilution was thought to be representative of N concentrations found naturally within soil-based environments (British Society of Soil Science, 1999) and provided a N concentration of 9.80 g dm^{-3} (Appendix - Table 5).

Applications were randomly assigned to each tree (one application treatment per tree) at the following application frequencies:

(i).   x0 (applied 0 times with 16 applications of distilled water in 16 days)

(ii).   x2 (applied twice with 14 applications of distilled water in 16 days)

(iii).   x4 (applied four times with 12 applications of distilled water in 16 days)

(iv).   x16 (applied 16 times with 0 applications of distilled water in 16 days)

Distilled water was applied for the remainder of the 16 days to ensure consistent thallus wetting. This prevents variations in thallus water content from affecting growth rate acting through changes in NCAR.

Nutrient treatments were applied only during dry weather conditions to reduce dilution. Small paint brushes were used to apply the solutions in order to prevent runoff problems encountered when applying solutions to thalli attached to vertical substrata. Epiphytic lichens dry out quickly and it has been estimated that $1 - 2$ ml of water per gram of thallus is required to cause rehydration (Pike, 1978). Therefore, application continued until saturation was visibly noted (a consistent darker colouration of previously drier thalli or drips forming on the leading edges of already moist thalli).

Statistical analysis

Growth rate

Two-way ANOVA was used to determine which variable (application frequency or species combination) affected thallus growth rate. Tukey (HSD) multiple means test (Zar, 1996) was used to indicate which means differed significantly.

Competition

Whether or not the ratio of intra- and interspecific overlaps to the total number of overlaps made was independent of application frequency and/or species combination was determined by G-analysis testing against a 1:1 ratio. Although competition between *P. reddenda* and *P. caperata* was predicted to be asymmetrical the use of a 1:1 ratio is acceptable since both species are in equal abundance at the beginning of the experiment. Yates correction was used throughout since DF = 1. All calculations were performed using Statistica™ 5.5 (Statsoft Inc., Tulsa, USA).

Missing thalli

Student's t-test (Zar, 1996) was used to determine whether lichen thalli lost from each application frequency, regardless of species combination, was significantly different from losses experienced by control applications (x0 – no nutrients).

Growth rates

Two-way ANOVA indicated that both application frequency and species combination had a significant effect on thallus growth rate. In addition the effect of factor one was modified by the effect of factor two (Table 17).

Effect	DF	MS	F	P
(1) App. Freq.:	3	1.02	112.17	<0.001
(2) Sp. Comb.:	7	0.07	8.31	<0.001
Interaction:	21	0.09	9.86	<0.001
Error:	50	0.01		

Table 17. Two-way ANOVA for the effect of application frequency (App. Freq.) (factor one) and lichen species combination (Sp. Comb.) (factor two) on the thallus diameters of *P. caperata* and *P. reddenda*.

Application frequency

Tukey (HSD) analysis indicated nutrient addition at x2 ($P < 0.01$) and x4 ($P < 0.01$) frequencies of application produced significantly larger thallus diameters than controls. The higher application at x16 significantly reduced thallus growth compared with x2 ($P < 0.01$), x4 ($P < 0.01$) and controls ($P < 0.01$) (Figure 24).
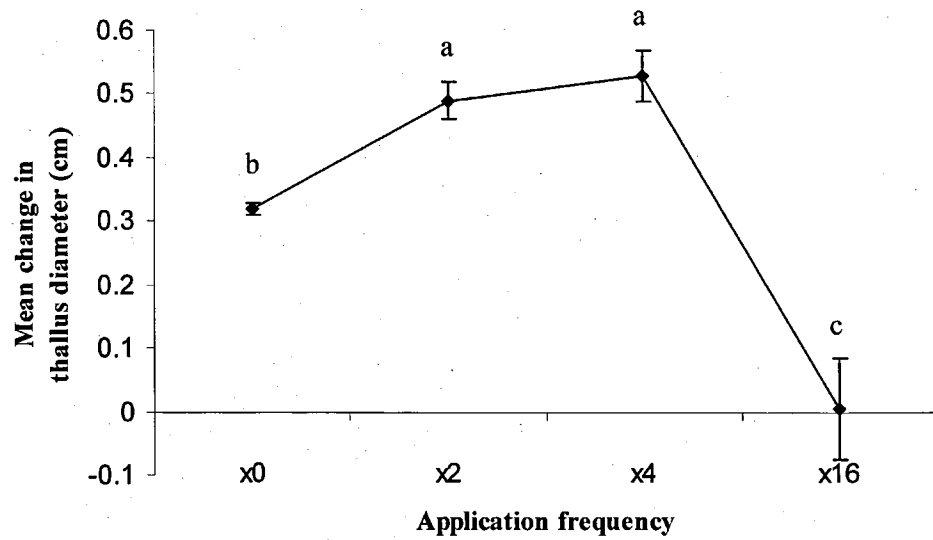
Figure 24. The effect of application frequency on thallus diameters of *P. caperata* and *P. reddenda* at all species combinations. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$). Bars are SEM (x0 n = 24; x2 n = 21; x4 n = 21 and x16 n = 16).

Species combination

Thallus growth of *P. caperata* and *P. reddenda* was similar under most pair-wise combinations. However, when *P. caperata* was transplanted into a cleared area of *P. reddenda* (Pc→Cl.Pr) growth was significantly less than in other species combinations (Figure 25).
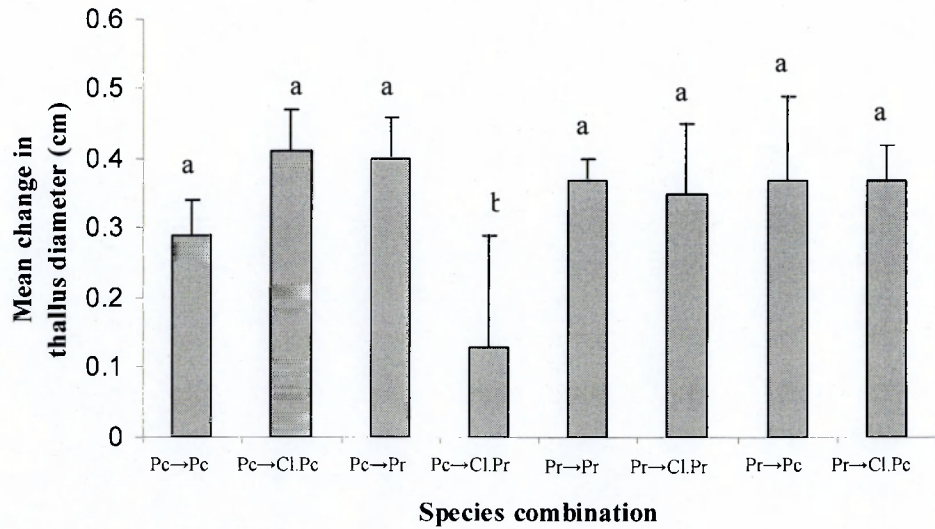
Figure 25. The effect of species combination on the summed thallus diameters of *P. caperata* (Pc) and *P. reddenda* (Pr) under each frequency of nutrient application. Data not sharing a common letter differ significantly (Tukey HSD test $P = 0.05$). Bars are SEM (Pc→Pc n = 13; Pc→Cl.Pc n = 10; Pc→Pr n = 8; Pc→Cl.Pr n = 10; Pr→Pr n = 13; Pr→Cl.Pr n = 10; Pr→Pc n = 9; Pr→Cl.Pc n = 9).

5.4 Results – thallus competition

Application frequency

G-analysis testing against a 1:1 ratio indicated that *P. caperata* and *P. reddenda* made similar numbers of thallus overlaps at each application frequency. However, both species made significantly fewer overlaps at x16 than x0 (1 DF, G = 7.76; $P < 0.01$), x2 (1 DF, G = 5.58; $P = 0.02$) and x4 (1 DF, G = 4.56; $P = 0.03$).

Individual scaled G-test results for all pair-wise and non-pair-wise intra- and interspecific competitive interactions between thalli of *P. caperata* and *P. reddenda* are shown in Table 18. There were no significant differences between any species combinations.

Pc→Pc versus:	G	P		Pc→Cl.Pr versus:	G	P
Pc→Cl.Pc	0.65	0.42		Pr→Pr	1.82	0.18
Pc→Pr	0.65	0.42		Pr→Cl.Pr	0.04	0.85
Pc→Cl.Pr	1.46	0.23		Pr→Pc	0.04	0.85
Pr→Pr	0.02	0.89		Pr→Cl.Pc	0.04	0.85
Pr→Cl.Pr	1.00	0.32				
Pr→Pc	1.00	0.32				
Pr→Cl.Pc	1.00	0.32		Pr→Pr versus:	G	P
				Pr→Cl.Pr	1.30	0.25
Pc→Cl.Pc versus:	G	P		Pr→Pc	1.30	0.25
Pc→Pr	0.00	1.00		Pr→Cl.Pc	1.30	0.25
Pc→Cl.Pr	0.16	0.69				
Pr→Pr	0.90	0.34				
Pr→Cl.Pr	0.04	0.85		Pr→Cl.Pr versus:	G	P
Pr→Pc	0.04	0.85		Pr→Pc	0.00	1.00
Pr→Cl.Pc	0.04	0.85		Pr→Cl.Pc	0.00	1.00

Pc→Pr versus:	G	P		Pr→.Pc versus:	G	P
Pc→Cl.Pr	0.16	0.69		Pr→Cl.Pc	0.00	1.00
Pr→Pr	0.90	0.34				
Pr→Cl.Pr	0.04	0.85				
Pr→Pc	0.04	0.85				
Pr→Cl.Pc	0.04	0.85				

Table 18. G-analysis summary table showing the frequency of thallus overlaps made by all species combinations of *P. caperata* and *P. reddenda* in pair-wise competition. $P = 0.05$, DF = 1 throughout.

During the course of the experiment some transplanted thalli were lost (Table 19). Student's paired samples t-test indicated that significantly larger numbers of thalli were lost from application frequency x16 than x0 (t_{14} = 2.366, P = 0.03). Similar numbers of thalli were lost from the remaining application frequencies.

Transplant	Lost transplants at each application frequency			
Pc→Pc	1	1	0	1
Pr→Pr	1	0	1	1
Pc→Cl.Pc	1	1	2	2
Pr→Cl.Pr	2	3	0	1
Pc→Pr	1	2	3	2
Pr→Pc	2	1	1	3
Pc→Cl.Pr	0	1	2	3
Pr→Cl.Pc	0	2	2	3
Total:	8	11	11	16

Table 19. Number of transplants lost for each application frequency of nutrient solution at the end of the experimental period.

5.5 Discussion

Does nutrient addition increase lichen growth rates, as measured by changes in thallus diameter, up to an optimum frequency of nutrient application compared with control applications of distilled water (no nutrients)? Are thallus growth rates larger when transplants are placed into cleared areas of their own or other neighbouring thalli?

The effect of anthropogenic nutrient addition on lichen growth rates is of great importance since the rate of thallus growth determines the rate at which neighbouring thalli make contact and this affects intra- and interspecific competition.

P. caperata and *P. reddenda* responded to nutrient addition in similar ways at all frequencies of application. The findings of this chapter suggest that nutrient addition at x2 and x4 application frequencies significantly increases thallus growth rates compared with controls (x0) and x16 (Figure 24). Further nutrient addition (x16) resulted in significantly reduced growth rates compared with controls and other application frequencies (Figure 24), perhaps as a direct result of nutrient toxicity or a breakdown in the lichen symbiosis (Nash, 1996). These results are similar to those observed in Chapter Three (Figure 9).

Thallus growth of *P. caperata* and *P. reddenda* was found to be similar under most species combinations and all application frequencies. Only when thallus growth in all species combinations were individually compared with growth observed when *P. caperata* was transplanted into a cleared area of *P. reddenda* (Pc→Cl.Pr) were significant differences apparent. This could be attributed to only two replicates out of four remaining at the end of the experimental period combined with poor thallus growth under x16 frequency of nutrient application for this species combination.

This suggests that *P. caperata* and *P. reddenda* have similar rates of thallus growth in both conspecific and heterospecific pair-wise combinations.

Does nutrient addition increase the amount of competition between P. caperata and P. reddenda as measured by the frequency of thallus overlaps? Do conspecific species combinations show a lower frequency of overlaps than heterospecific combinations? Do thalli of P. reddenda compete asymmetrically with P. caperata?

Growth of the lichen thallus is increased at x2 and x4 frequencies of nutrient application compared with controls (x0) and x16 (Figure 24). Therefore the time taken for thalli to make contact under applications x2 and x4 should be reduced compared with control (x0) and x16 application frequencies. This rationale appears to be partially true since both species made similar numbers of overlaps at each application frequency. However, significantly more overlaps were made by both species at x0, x2 and x4 application frequencies than at x16.

This confirms higher nutrient applications (x16) reduce thallus growth which in turn decreases the number of competitive interactions between neighbouring thalli. This is in broad agreement with the results of Chapter Three.

The similar numbers of overlaps at application frequencies x0, x2 and x4 may be a consequence of interference competition whereby the production of allelochemicals may inhibit a less adpressed thallus from overlapping a more adpressed one. Armstrong (1985) suggested that *Parmelia conspersa* may be an allelopathic species since it produces usnic acid. Interestingly, *P. caperata* produces usnic acid while *P. reddenda* does not. Under conditions of nutrient enrichment the synthesis of usnic acid might aid the competitive ability of *P. caperata* when competing with *P. reddenda*. This may allow it to establish competitive equivalence with *P. reddenda* but only under conditions of nutrient enrichment (Figure 26) since it was found that *P. reddenda* was at the top of a competitive hierarchical pyramid when competing with *P. caperata* and *P. perlata* where no nutrient solution had been added (Chapter Four).

Although the production of allelopathic secondary compounds can reduce thallus growth and therefore compromise competitive success, both species synthesise the *para*-depside atranorin which may increase growth rate by promoting photosynthesis since it has a fluorescence maximum corresponding almost exactly to that of chlorophyll (Rao & LeBlanc, 1965). Atranorin synthesis may become more pronounced under conditions of elevated nutrient status. Whether growth is increased uniformly in *P. caperata* and *P. reddenda* is uncertain.

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Pr
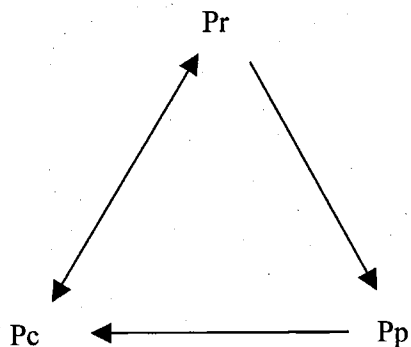
Pc ← Pp

Figure 26. A proposed competitive hierarchical pyramid for *P. caperata* (Pc), *P. perlata* (Pp) and *P. reddenda* (Pr) under conditions of nutrient enrichment based on the number of thallus overlaps made by each species. Note that no overlap data were collected for Pp and its asymmetrical competition with Pc and Pr is based on data from Chapter Four.

It is feasible that the supply of additional nutrients may allow usnic acid synthesis to occur without the trade off in thallus growth due to increased atranorin production. In addition, the presence of usnic acid in *P. caperata* may reduce thallus grazing by microarthropods which has been shown to cause substantial damage to thalli (Hilmo, 1994; Glenn *et al.*, 1995). Although the use of allelochemicals is an appealing explanation it is only speculative since no measurements of secondary compounds were made.

Another possible explanation for the similarity in competition at x0, x2 and x4 frequencies of nutrient application is that a 'truce' develops between neighbouring thalli and radial growth of both thalli stops at the point where the thalli make contact. This is most likely a consequence of the ability of one thallus to overlap another which depends upon the morphology of the leading edge of individual thalli (Pentecost, 1980). During intraspecific competition the leading edges of conspecific thalli would have similar degrees of adpression and should produce similar numbers of thallus overlaps between species. This was shown by *P. caperata* and *P. reddenda* when competing intraspecifically (Pc→Pc and Pr→Pr) (1 DF, $G = 0.02$; $P = 0.89$) (Table 18).

During interspecific competition the leading edges of foliose thalli may simply push against each other causing their lobes to be raised further from the substrate. This was observed on numerous occasions

during the course of this field experiment and may partially account for the similarity in competitive ability between *P. caperata* and *P. reddenda* (Pc→Pr and Pr→Pc) (1 DF, G = 0.03; P = 0.86) (Table 18) under conditions of nutrient treatment.

It would appear that competition between *P. caperata* and *P. reddenda* is symmetrical under conditions of nutrient enhancement since both species make similar numbers of thallus overlaps regardless of application frequency and species combination. However, there is compelling evidence from the species survey carried out in Chapter Four that under conditions of no experimentally added nutrients competition between *P. caperata* and *P. reddenda* is asymmetrical (Figures 17 and 22). This would tend to suggest that these species might occupy different niches on the boles of beech and that their degree of niche separation may less important under conditions of anthropogenic nutrient addition since *P. caperata* is able to compete symmetrically with thalli of *P. reddenda* in areas where nutrient enrichment occurs.

Chapter Six

Discussion

There are many abiotic and biotic factors which may act independently or indeed together to determine the growth and community structure of higher plant communities. The same factors may also be responsible for determining the growth rate of a lichen thallus. Among the abiotic factors it appears that compounds of sulphur (SO_x) and nitrogen (NO_y) are important since they contribute significantly towards environmental acidification, particularly at locally polluted sites where concentrations of these compounds are high. The National Expert Group on Transboundary Air Pollution have recently suggested that although the potential acidity due to S deposition has been reduced in the UK between 1989-1999, the relative contribution by N, particularly NO_3^- and NH_4^+, has increased (NEGTAP, 2001).

The importance of nutrient supplementation for increasing plant growth in environments where nutrients are limiting has long been recognised, as demonstrated by the Park Grass Experiments established in 1856 at Rothamsted by Lawes and Gilbert which are still in progress today (Tilman, 1982; 1987). Nutrient addition experiments have indicated almost all plants are nutrient limited in nature since their growth rate increases with supplementary fertilisation. However, these experiments also reveal that increased fertilisation causes a significant reduction in species diversity (Tilman, 1982). Such changes in community composition are easily recognised when experimenting with larger plant species like grasses. However, smaller plants demonstrate similar effects under conditions of increased fertilisation but their changes in community composition may be easily overlooked. This is almost certainly the case with lichens despite growing on a wide variety of substrata and covering a broad range of ecological amplitudes.

Although there have been several attempts to reduce the rate of N deposition the total deposition in the UK is estimated to be 380 kt-N which approximates a mean deposition of 17 kg N ha^{-1} (NEGTAP, 2001). However, in certain areas of the UK this mean value is exceeded. This is particularly the case in the south west of England where N deposition is estimated to lie within the range 17-25 kg N ha^{-1}. Therefore a better understanding of how such eutrophic conditions may determine growth, competition and community structure is essential.

To this end the nutrient addition experiments carried out in Chapter Three and Chapter Five suggested nutrient supplementation increased thallus growth up to an optimum application frequency. Application above the optimum resulted in a decline in growth rate presumably as a result of nutrient toxicity. These results were in broad agreement with the nutrient addition experiments of Austin and Austin (1980) using grass grown in monoculture and in different species combinations across a nutrient gradient. The result that plants grew bigger when provided with supplementary nutrients is not in itself surprising. However, the grasses occupied different habitats in the field and therefore their response to nutrient supplementation was noteworthy (Keddy, 2001).

The species used in this thesis, *Parmelia caperata*, *P. reddenda* and *P. saxatilis*, occupy the same, or similar, substrata in the field but *Xanthoria parietina* is often abundant at eutrophic locations. In both transplant experiments (Chapters Three and Five) all four species demonstrated maximum thallus growth at nutrient application x4 and a reduction in growth at x16.

That all four species have similar rates of growth under conditions of nutrient supplementation is surprising since it was initially proposed that nitrophilous species like *X. parietina* would exhibit larger thallus diameters. Clearly *X. parietina* thrives in areas where nutrient enrichment occurs and this may simply indicate a mechanism for tolerating conditions of nutrient toxicity which, above certain concentrations, are deleterious to other lichen species. This would allow it to colonise areas where lichen competition is perhaps less abundant. The idea that weak competitors might escape from superior competitors and therefore survive was proposed by Skellam (1951) and may be a factor worth considering with nitrophilous species like *X. parietina*. Escape strategies have been noted in higher plants that colonise salt marshes. Here *Salicornia europa* colonises the high salinity areas of salt marshes in order to escape competition from *Spartina patens* (Keddy, 2001).

There have been many attempts to define the term competition (Milne, 1961) and correct its often misuse (Grime – personal communication) where many authors have used it to represent the Darwinian struggle for existence (Grime, 2001). Confusion over a precise and accurate definition has led some authors to propose abandoning the term altogether (Harper, 1961). Grime (2001) claims the term competition is too important and far too useful to be allowed to suffer such a fate and proposes an extremely precise definition which considers competition as the tendency of "neighbouring plants to utilise the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space" (Grime, 1979; 2001).

However, this thesis considers competition in a less rigorous and mechanistic manner and therefore views it as the negative affects that one organism has upon another by consuming, or controlling access to a resource that is limited in availability (Keddy, 2001). The negative effect that one organism has upon another relates much more precisely to the negative effects arising from one lichen thallus overlapping another. In this case dominant thalli would directly control access to the resources of the subordinate thalli. This invariably occurs when lichen species possessing a less adpressed thalline margin overgrow their more adpressed neighbours as they compete for space and light on the substrate.

However, conspecific thalli have a similar morphology and intraspecific competition may result in a 'truce' with radial growth of both thalli being terminated at the points of thallus contact (Pentecost, 1980). This is frequently observed in crustose species where the thalline margins are closely adpressed to the substrate. In foliose species the margins are not constrained by the substrate and are free to overgrow conspecific neighbours. Conspecific foliose thalli in dense populations make many intrathalline overlaps which suggest a competitive advantage must have been gained over neighbouring thalli. This may have been achieved through abiotic factors (wind and rain can flatten a raised thalline margin) and/or biotic factors (grazing by microarthropods, presence of allelopathic compounds and small variations in genotype). In fact there is evidence to suggest that a diversity of growth forms might evolve in conspecific populations. Such evidence arises from the identification of different mycobionts within the same lobe, or different parts of the lobe, of two species of *Parmelia* resulting in intrathalline differences (Armstrong & Smith, 1992). Furthermore, the concentration of secondary compounds within the thallus differs significantly between lobes of *Parmelia conspersa* (Nash, 1996) which could result in lobes that contain less secondary compounds being preferentially grazed.

The species surveys carried out in Chapter Two and Chapter Four suggested that conspecific thalli of *P. caperata*, *P. reddenda*, *P. saxatilis* and *X. parietina* all made similar numbers of intraspecific overlaps. Since the competitive effects of conspecific neighbours are relatively equal it is likely that diffuse competition is partially responsible for determining conspecific community structure.

Where conspecific thalli overlap interference competition prevents the overgrown thallus from gaining further access to space and light. This usually results in the overgrown thalli initially becoming paler in colour (personal observation) as secondary compounds and thallus components are broken down arising from increased respiration in the overgrown portion. Prolonged overgrowth usually results in death

of the subordinate thallus in the region of overlap. However, there is evidence to suggest that marginal overlapping in some lichen species may be less detrimental since photosynthesis remains active for longer periods in the thicker centres of *Lasallia pustulata* thalli than the thinner margins during periods of thallus dehydration (Hestmark *et al.*, 1997). Although this may be true for umbilicate lichens it is almost certainly not the case for species of *Parmelia* and *Xanthoria* which would exhibit signs of deterioration due to their compressed habit and the fact that they grow primarily from the thallus margins (Hestmark – personal communication).

At the other end of the competition continuum monopolistic competition occurs where one of the neighbouring species is the primary contributor to competition intensity with other species having a relatively minor effect. This may occur through increased fertilisation which tends to result in a shift away from diffuse competition towards monopolistic competition within a community (Keddy, 2001). However, this was not demonstrated by either *P. caperata*, *P. saxatilis* or *X. parietina*. Thalli of *P. caperata* however, competed asymmetrically with thalli of *X. parietina*. This produced a dominance hierarchy with *P. caperata* at the top of the hierarchical pyramid (Figure 27).

Where experimental nutrient supplementation occurs (Chapter Three) symmetrical competition is still evident between *P. caperata* and *P. saxatilis* and between *P. saxatilis* and *X. parietina*. However, *P. caperata* and *X. parietina* now also demonstrate symmetrical competition (Figure 27).

Figure 27. A proposed competitive hierarchical pyramid for thalli of *P. caperata* (Pc), *P. saxatilis* (Ps) and *X. parietina* (Xp) under conditions of (a) no experimentally added nutrients and (b) nutrient supplementation. The nutrient-driven change from asymmetrical (a) to symmetrical (b) is indicated using wider arrows.

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It would appear that nutrient supplementation has stimulated a change from transitive competition (Krebs, 1994) where a linear hierarchy existed between *P. caperata* and *X. parietina* to intransitive competition where neither species is seen to exert a dominant effect over the other.

Changes in pH as a result of adding Hoagland's Solution (pH 6.5) should not directly affect *P. caperata* since it is a neutrophytic species. Therefore it may be assumed that any compromise in competitive ability shown by *P. caperata* under conditions of experimental nutrient supplementation may have arisen from either nutrient toxicity which can stimulate excessive algal growth over the thallus (Scott, 1960; O'Dare, 1990) thereby reducing photosynthetic ability, or by a breakdown in the symbiosis (Scott, 1960; Nash, 1996). It is also feasible than an osmotic effect could have been responsible but this would have been almost impossible to determine accurately during the course of the experiment.

Since thalli of *P. caperata* are considerably less adpressed than those of *X. parietina* it can potentially make larger numbers of overlaps on this species than the reciprocal. Given that *X. parietina* can tolerate eutrophic and even hypertrophic conditions, as witnessed by its abundance near livestock farms and bird perching sites, this may be one strategy by which it may escape continuous competition pressure from *P. caperata* and other large foliose species. In these eutrophic locations, although foliose species with prominently raised margins are not particularly common (personal observation), there is usually an abundance of crustose species which may explain why *X. parietina* is able to establish so successfully. This is primarily due to the fact that adpressed thalli will always lose when competing with thalli that have a superior ability to overlap neighbouring thalli (Hestmark – personal communication). This may indicate that some degree of niche separation exists between *P. caperata* and *X. parietina*.

Dominant species are usually recognised by their numerical abundance (Krebs, 1994) and the species survey conducted on the boles of beech suggested that *P. caperata* was the dominant foliose lichen species (F = 67.67; $P < 0.001$) (Chapter Four). However, *P. reddenda* made significantly more overlaps on thalli of *P. caperata* on both north (1 DF, G = 11.03; $P < 0.01$) and south (1 DF, G = 3.69; $P = 0.05$) facing aspects than *P. caperata* made on *P. reddenda* (Figure 17). This may suggest that *P. reddenda* has a more competitively efficient thallus morphology than *P. caperata* and competes asymmetrically with it. On east and west facing aspects competition between these two species was symmetrical. This may have resulted from thalli pushing against each other without actually recording an overlap (personal observation).

Under conditions of experimental nutrient supplementation (Chapter Five) competition between *P. reddenda* and *P. caperata* became symmetrical rather than tending towards further monopolistic (asymmetrical) competition by *P. reddenda* which would further exclude other species by increasing its competitive effects upon neighbours (Keddy, 2001) (Figure 28).
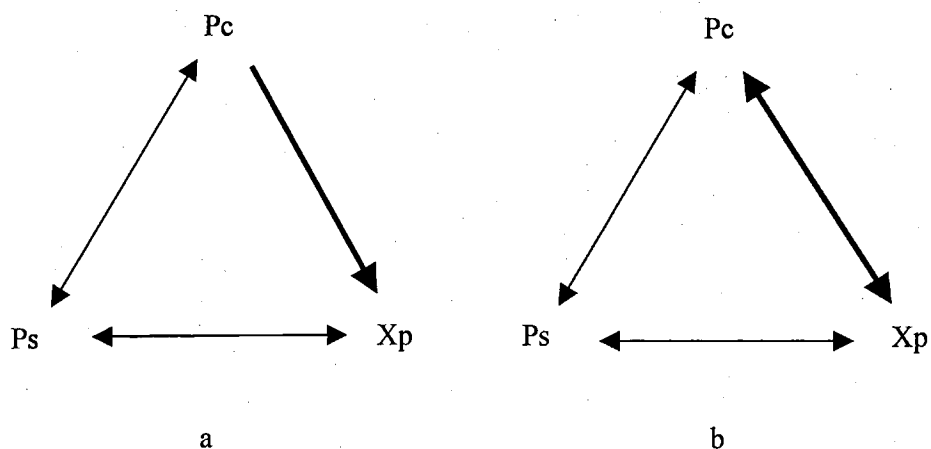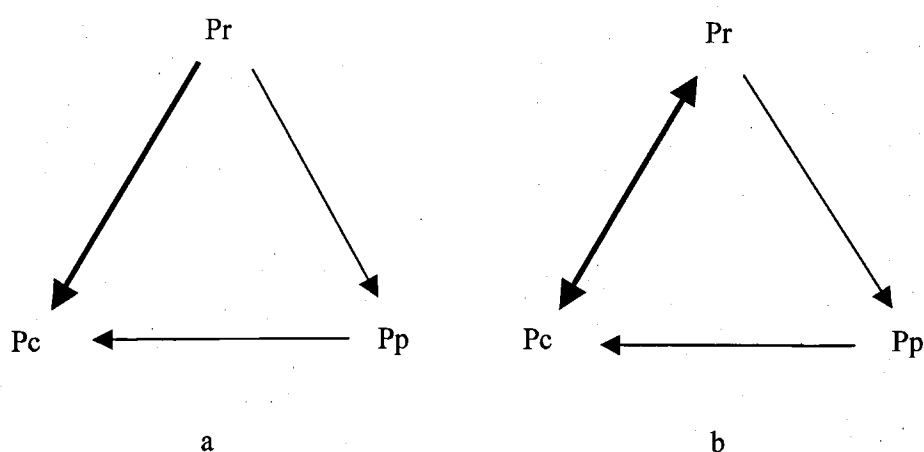

Figure 28. A proposed competitive hierarchical pyramid for thalli of *P. caperata* (Pc), *P. reddenda* (Pr) and *P. perlata* (Pp) under conditions of (a) no experimentally added nutrients and (b) nutrient supplementation. The nutrient-driven change from asymmetrical (a) to symmetrical competition (b) is indicated using wider arrows. Note that in (b) no overlap data were collected for Pp and its asymmetrical competition with Pc and Pr is assumed to remain unchanged.

Symmetrical competition between thalli of *P. caperata* and *P. reddenda* may be a consequence of additional nutrients facilitating the production of secondary compounds like usnic acid in *P. caperata* and not in *P. reddenda*. In this way thalli of *P. caperata* may achieve symmetrical competition with those of *P. reddenda* through mechanisms of interference competition. This allelopathic effect has been observed in thalli of *Parmelia conspersa* which also produce usnic acid (Armstrong, 1986).

Alternatively the leading edges of competing thalli of *P. caperata* and *P. reddenda* may push against each other causing their margins to be raised further from the substrate without actually overlapping each other. This was observed on numerous occasions during competitive encounters between these two species during the course of the species survey (Chapter Four) and reciprocal transplant experiment (Chapter Five).

Under conditions of no experimental nutrient supplementation asymmetrical competition between *P. reddenda* and *P. caperata* will tend to eventually exclude *P. caperata* from niches occupied by *P. reddenda* and lead to the formation of a dominance hierarchy (Keddy, 2001) with *P. reddenda* at the top. Symmetrical competition between *P. reddenda* and *P. caperata* allows both species to coexist.

That *P. reddenda* and *P. caperata* demonstrate symmetrical competition in the presence of nutrient supplementation runs contrary to the predictions of an equilibrium model of resource competition. The model predicts that addition of nutrients which are limiting the growth of some species, and the subsequent competition for these nutrients, should result in changes to community structure whereupon decreases in species richness and evenness are observed (Tilman, 1982; Rajaniemi, 2002).

The apparent dominance of *P. caperata* may be the result of large numbers of this species in the environment and may not be the result of competition with *P. reddenda* or any other lichen species. The abundance of *P. caperata* may be a consequence of it having better dispersal and colonisation mechanisms than *P. reddenda*. Since coexistence requires a trade-off in competitive ability versus dispersal ability (Tilman & Kareiva, 1997) this may partially explain why *P. caperata* is more abundant yet *P. reddenda* is the better competitor. The use of trade-offs in establishing coexistence has been demonstrated in two species of fungi. *Aspergillus* is competitively dominant over *Penicillium*. However, *Penicillium* is capable of producing a greater number of daughter colonies and is a better coloniser of new sites than *Aspergillus*. This allows both species to coexist within the same local environment (Armstrong, 1976b).

Alternatively *P. caperata* and *P. reddenda* may be in the process of establishing a dominance hierarchy which may change over time through succession and ultimately favour *P. reddenda* as the dominant species in terms of greater abundance. That species take different periods of time to respond and do not react instantaneously, as assumed by the Lotka-Volterra model, is an important consideration when looking at changes in community structure.

Multispecies coexistence occurs because the species at the top of a competitive hierarchical pyramid cannot occupy all sites simultaneously. The empty sites not occupied by the dominant species provide 'homes' for less efficient competitors if they are sufficiently good dispersers. Coexistence therefore occurs because local displacement by the best competitor is never permanent. When the best competitor dies its site may become free for colonisation by the less efficient competitor (Tilman & Kareiva, 1997).

This may go some way to describing the competitive interactions that occur between *P. caperata* and *P. reddenda* when no additional nutrient supplementation is provided.

Competition for nutrients is the major factor determining the species composition of natural plant communities (Tilman, 1982). The mechanisms by which changes to community structure occur are certainly complex and there is evidence to suggest that species interactions along gradients of resource availability may additionally depend on abiotic factors (Pugnaire & Luque, 2001). Interestingly maximal plant diversity can occur on soils of intermediate fertility with low and high fertility soils supporting a much lower species richness (Grime, 1973). In fact two of the most species-rich plant communities in the world occur on very nutrient poor soils located in the Fynbos of South Africa and the heath scrublands of Australia. Nearby communities on more nutrient rich soils are reported to have a much lower plant species richness (Tilman, 1982). Therefore, only the addition of one or more nutrients which are limiting the growth of some species should result in changes to community structure. Where soil is sufficiently nutrient rich further fertilisation will result in a reduction in species diversity (Tilman, 1982).

Chapters Three and Five indicate that experimental nutrient supplementation results in a swing from asymmetrical competition towards symmetrical competition. Therefore this would not result in a reduction in species diversity. That *P. reddenda* competes asymmetrically with *P. caperata* under conditions of no experimental nutrient supplementation (Chapter Four) may indicate that these two species have some degree of niche separation in order to coexist. This is further supported by *P. reddenda* making significantly more overlaps on *Pyrenula macrospora* (1 DF, $G = 58.31$; $P < 0.01$) at all aspects (Figure 20) and *Phlyctis argena* on east (1 DF, $G = 6.33$; $P = 0.01$) and west (1 DF,
$G = 4.70$; $P = 0.03$) facing aspects (Figure 21) than *P. caperata* made on these crustose species (Chapter Four). This is simply a function of more thalli of *P. reddenda* situated next to crustose species therefore reinforcing the idea that *P. reddenda* and *P. caperata* occupy separate niches in order to coexist on the boles of beech.

The reciprocal transplant experiment (Chapter Five) indicated that experimental nutrient supplementation allowed *P. reddenda* and *P. caperata* to compete symmetrically (Figure 28). Therefore, if some degree of niche separation does exist between *P. reddenda* and *P. caperata* it clearly becomes less important under conditions of nutrient supplementation.

Understandably the use of anthropogenic nutrient addition to promote plant growth and improve crop yields is a sensitive environmental issue. From 1939 to 1981 the amount of inorganic fertiliser used in the U.K increased by 550% (Hayward, 1992). It has recently been reported that addition of liquid manure on farm land may be restricted to applications during October only. This is planned to take effect from 2003 in an attempt by the Government to reduce soil nitrate levels which cause contamination and also to reduce the numerous complaints relating to noxious smells during the tourist season. It has been suggested that three times the quantity will be spread during October on an estimated 15, 000 farms across Britain. This represents approximately 15% of the countryside. It is thought the increased slurry spread will be absorbed by plants during cultivation (Elliott, 2002).

Such large amounts of N based slurry deposited onto the land over such a short time period has the potential to create eutrophic or even hypertrophic conditions resulting in changes to higher plant community structure which in turn will effect the local lichen community structure. Any reduction in species diversity of lichen communities or change in their competitive interactions may alter the interspecific competitive abilities of higher plants (Newsham et al., 1995) and affect the interception of rainfall and the deposition of water and nutrients in woodlands (Knops et al., 1996). Therefore any change in lichen community structure resulting from anthropogenic nutrient addition may have ramifications within higher plant communities. This in itself is a strong argument for not overlooking the effect nutrient application has on lower plant communities.

Although there is compelling evidence for increased fertilisation causing significant reductions in species diversity (Tilman, 1982; Wilson & Tilman, 1991; Wootton, 1991; Marschner, 1995; Schellberg et al., 1999) it would appear that this may not always be the case with lichen species. That competition between P. caperata and X. parietina and between P. reddenda and P. caperata becomes symmetrical under conditions of increased fertilisation suggests that although the competitive interactions between species have changed there is not necessarily a reduction in species diversity. Clearly it could be argued that since these species are now competing with one another symmetrically there will be increased competition pressures on other neighbouring thalli which could result in some species being excluded.

This is an area open to further research but such a swing towards monopolistic competition in both higher plant and lichen communities is a prediction of the competitive hierarchy model which assumes that all species have the best performance in terms of size and growth rate at the same end of the resource

gradient. This is the commonest situation for plants – and also perhaps for some lichens – which all share a requirement for a few basic resources (light, water and mineral nutrients). A second assumption is that the species vary in competitive ability in a predictable manner as a result of resource acquisition or ability to interfere with neighbours. This is clearly demonstrated in some lichen communities with interference mechanisms such as prominently raised thalline margins and the production of secondary allelopathic compounds.

Therefore the competitive hierarchy model is predictive and may be used to determine the order in which species will be distributed along a resource gradient. Whether this model can satisfactorily predict the position of foliose lichen species like *P. caperata, P. reddenda, P. saxatilis* and *X. parietina* in terms of their competitive hierarchy is disputable since it predicts monopolistic competition arising through competitive asymmetry which may not always be true (Chapters Three and Five).

The model further assumes that competitive abilities are negatively correlated with fundamental niche width (a function of a species ability to efficiently disperse and colonise new sites) perhaps due to a trade off between ability for interference competition and ability to tolerate low resource levels. In a competitive hierarchy the dominant species occupies the preferred end of the gradient and the subordinates are displaced down the gradient at a distance determined by their position in the hierarchy. This is almost certainly the case with *P. caperata* which appears above *X. parietina* in a dominance hierarchy (Chapter Two) and *P. reddenda* which appears above *P. caperata* (Chapter Four).

Although during the course of these experiments some transplants were subject to animal interference (Chapter Three) and some thalli were lost resulting in a smaller number of replicates than anticipated (Chapter Five) there is nevertheless sufficient evidence to suggest that nutrient addition increases radial growth rate in lichens up to an optimum application and therefore reduces the time taken for neighbouring thalli to make contact. Furthermore there is evidence to suggest that under conditions of nutrient supplementation the direction of competition (symmetrical or asymmetrical) between two lichen species can change and such a change may not necessarily result in a monopolistic situation arising where one of the species becomes dominant. Therefore there is a possibility that when asymmetrical competition changes to symmetrical competition under conditions of nutrient supplementation a reduction in species diversity may not necessarily follow. This could partly explain why there is a lack of compelling evidence

to support competitive exclusion among lichens. In fact the replacement of some species by others is thought to be simply a process of succession (Lawrey, 1991).

The use of fertilisation to increase crop yields therefore needs to be viewed in a much broader context that encompasses the impact elevated nutrient levels have on lower plant communities. Such considerations would certainly be worthwhile if deleterious changes to lichen community structure, and in turn higher plant community structure, are to be avoided in the future.

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Appendix-Tables

Image Analyser	Counting
288	281
193	183
473	466
258	252
353	349
634	625
617	609
490	483
229	226
548	541
121	119
325	319
760	753
442	436
406	396
109	104
123	119
512	505
206	201
117	113
811	799
367	358
181	177
203	200
178	177

Appendix-Table 1. Thallus areas taken from 50 photographs calculated using an image analyser and by counting whole squares and part squares on 2 x 2 mm^2 graph paper. Paired samples t-test indicated that the two data sets were not significantly different (t_{48} = 0.106; $P = 0.916$).

Treatment (App. Freq.)	Number of thalli present	Number of thalli lost	% thalli lost
0	840	166	19.76
1	504	122	24.20
2	504	114	22.62
4	504	125	24.80
8	504	104	20.63
16	504	103	20.44

Appendix-Table 2. Lichen thalli lost from all slates for each treatment between July 1994 and May 1995.

Treatment (App. Freq.)	% thalli lost for each species		
	P. caperata	P. saxatilis	X. parietina
0	9	49	41
1	11	35	53
2	7	36	56
4	7	46	46
8	13	38	48
16	20	47	32

Appendix-Table 3. Percentage of thalli lost from all slates for each treatment between July 1994 and May 1995.

Solution	Reagent	Concentration		Use at
		(g dm^{-3})	(ml dm^{-3})	(mM)
1	KNO_3	60.66	600	10.11
2	$NH_4H_2PO_4$	11.5	100	11.50
3	$MgSO_4.7H_2O$	49.29	200	24.64
4	$CaCl_2.2H_2O$	73.51	500	14.70
5	H_3BO_3	0.57	9.25	6.16
	$MnCl_2.4H_2O$	0.36	1.83	19.67
	$ZnSO_4.7H_2O$	0.045	0.153	29.41
	$CuSO_4.5H_2O$	0.016	0.064	25.00
	$(NH_4)_6Mo_7O_{24}.4H_2O$	0.087	0.07	124.29
6	FeNaEDTA	21.79	56.6	38.50

Appendix-Table 4. The composition of Hoagland's Solution used in each treatment.

	Concentration			
	Nitrogen		Nitrate or ammonium	
Reagent	%	(g dm^{-3})	(%)	(g dm^{-3})
KNO_3	13.86	8.40	61.35	37.20
$NH_4H_2PO_4$	12.18	1.40	14.79	1.70
$(NH_4)_6Mo_7O_{24}.4H_2O$	10.03	0.009	12.90	0.01

Appendix-Table 5. The amount of nitrogen, nitrate and ammonium as a percentage and in grams per litre (g dm^{-3}) present in Hoagland's Solution

	P. perlata → P. caperata	P. perlata → P. reddenda
North:	31 (46)	2 (27)
South:	3 (12)	5 (7)
East:	7 (12)	4 (14)
West:	11 (13)	5 (10)

Appendix-Table 6. The frequency of thallus overlaps made by *P. perlata* on thalli *of P. caperata* and *P. reddenda* at each of four aspects. Number of thalli of *P. perlata* at each aspect are show in parentheses.

	Thallus dry mass (g)	
	Parmelia caperata	*Parmelia reddenda*
North:	0.035 (0.0065)	0.035 (0.0065)
South:	0.020 (0.0041)	0.033 (0.0095)
East:	0.028 (0.0085)	0.025 (0.0050)
West:	0.028 (0.0103)	0.033 (0.0095)

Appendix-Table 7. The mean dry masses of 1.5 cm diameter thallus discs of *Parmelia caperata* (n=16) and *P. saxatilis* (n=16) at each of four aspects with standard error in parentheses.

|	U	V	W	X	Y	Z
A	0	16	4	4	2	1
B	1	0	8	2	8	16
C	8	1	2	1	0	0
D	16	4	4	0	2	16
E	8	0	1	8	8	0
F	16	0	4	2	2	1
G	0	0	4	16		

Appendix-Figure 1. Random assignment of the six treatments as arranged at sites 1 and 2. The numbers represent the frequency of each application of Hoagland's Solution per 16 days. The letters allow the coordinates of each slate to be established for treatment at the correct frequency of application.
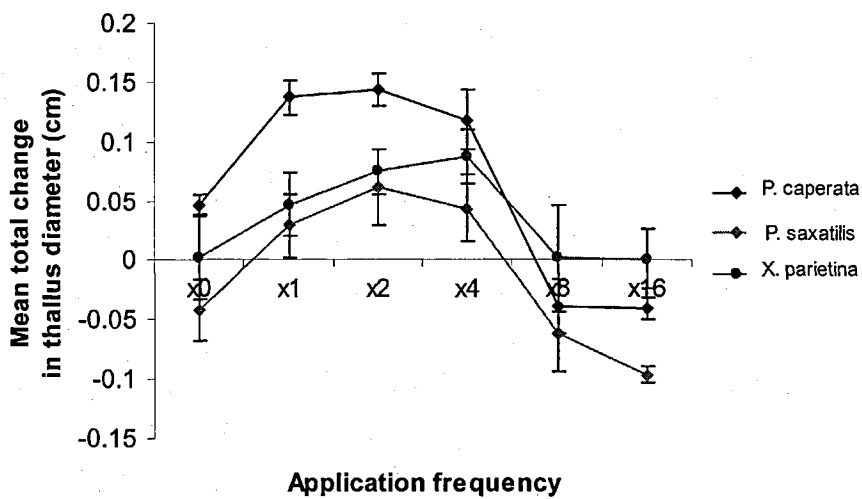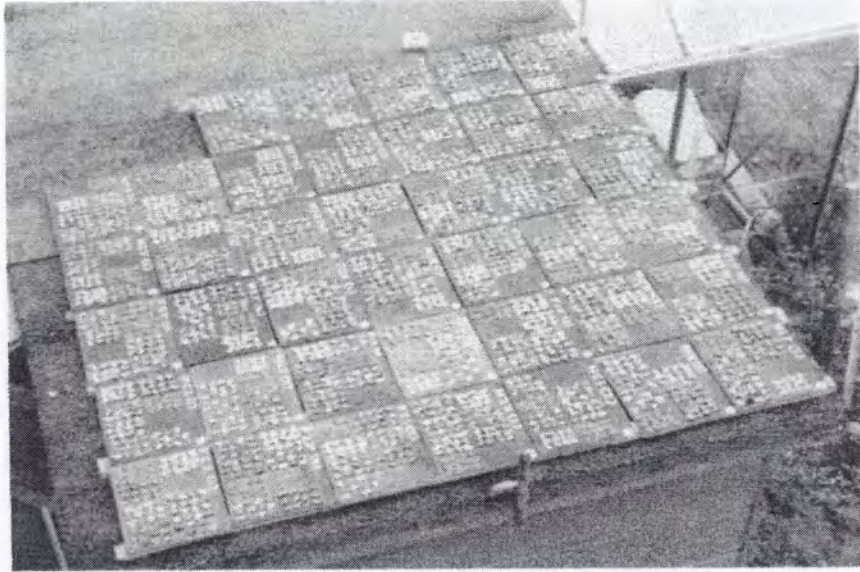

Appendix-Figure 2. Individual species responses of *P. caperata*, *P. saxatilis* and *X. parietina* to application of Hoagland's Solution. Bars are SEM.
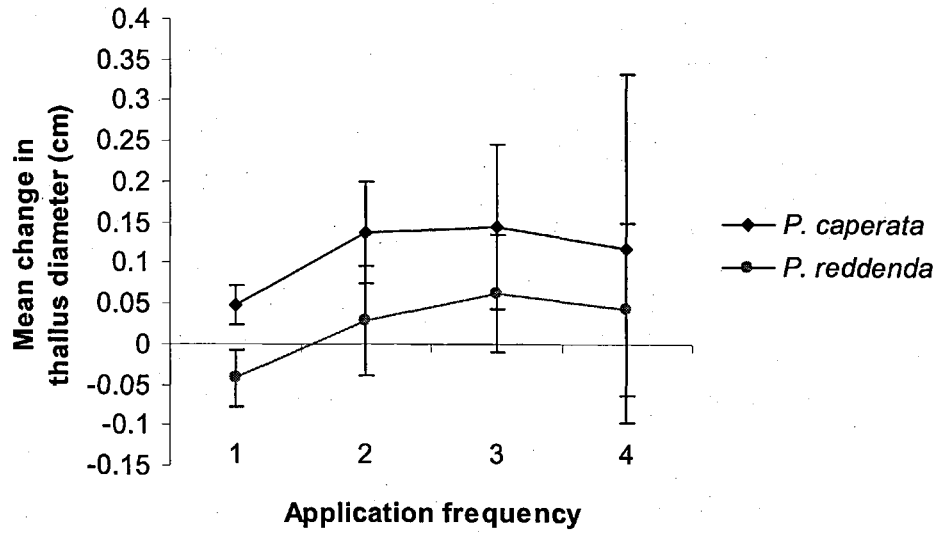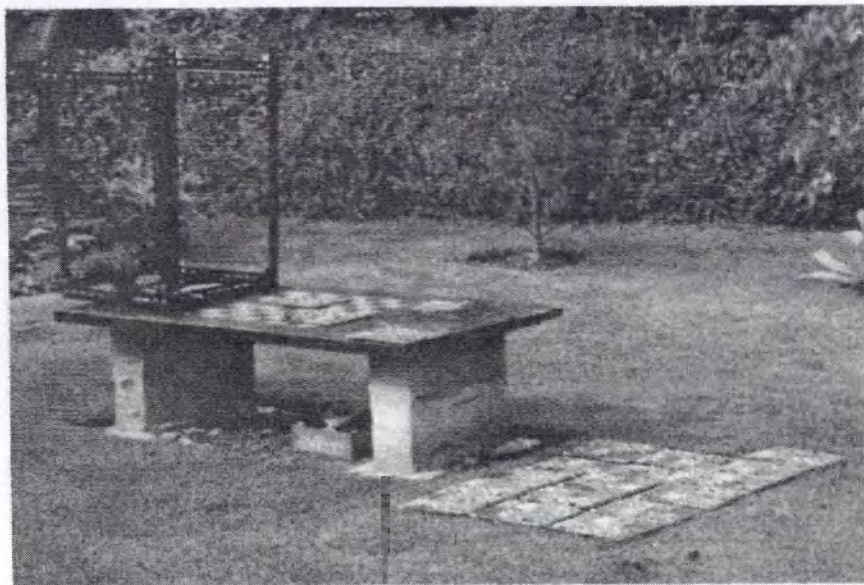
Appendix-Figure 3. Individual species responses of *P. caperata* and *P. reddenda* to application of Hoagland's Solution. Bars are SEM.

Appendix-Plate 1. The 40 slates used in the transplant experiment in Chapter Three randomly positioned on the flat roof of a garden shed. The green netting used to reduce animal disturbance is just visible.

Appendix-Plate 2. The camera stand used to photograph individual slates for the transplant experiment in Chapter Three.

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