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ON SUCCESSION IN A SAXICOLOUS LICHEN COMMUNITY

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Abstract: The lichen flora was sampled at each of the five sites on a near-vertical gneiss rock face. The sites were ranked according to the degree of weathering of the rock surface and were taken to represent different stages in a succession. The succession shows an increase in species richness and diversity over time, although the proportion of the rock face unoccupied by lichens increases at the oldest site. The succession will be driven by allogenic processes, physical weathering of the rock, facilitation, especially the effects of lichens on surface erosion, and by inhibition, through competition for space. At the oldest site mortality of lichen thalli becomes important, continually opening up new areas for recolonization and maintaining community diversity. The succession may be described by four phases: (1) colonization, (2) growth, (3) competition and (4) senescence.

Introduction

Succession has been defined (Connell & Slatyer 1977) as ‘ changes observed in an ecological community following perturbation that opens up a relatively large space ’. Succession in lichen communities is a slow process. Since lichens are both slow-growing, with radial growth rates typically in the range 1–5 mm y^{-1}, and long-lived, individual thalli may survive for decades, and possibly centuries (Hale 1974). As a result lichen succession will occur over tens or hundreds of years and is best studied by comparing lichen communities of different ages, assuming that these communities differ only in age, and therefore that they represent different stages of a succession (Daubermire 1968).

Previous studies of succession in lichen communities have concentrated on their role as the pioneers of soil formation, for example Winterringer & Vestal (1956) and Shure & Ragsdale (1977). This study examines primary succession in a saxicolous lichen community inhabiting a near-vertical gneiss rock face. In this case the formation and/or accumulation of soil is minimal and the succession does not, apparently, progress beyond a stage dominated by crustose and foliose lichens.

As well as a description of succession trends, it is possible to make inferences about successional mechanisms. Successional mechanisms have been discussed in general by a number of authors, for example Horn (1976), Connell & Slatyer (1977) and van Hulst (1979). In particular, we shall discuss the roles of allogenic processes, facilitation, and inhibition with emphasis on the role of competition in the succession.

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Materials and Methods

The study area was located at Snake Island, Lake Opinicon in south-eastern Ontario, at 44°34′N, 76°26′W and approximately 120 m elevation. Observations were made in 1980 and 1983. Five sites were selected along the southern shore of Snake Island. Each site was an area of near-vertical gneiss rock extending up to 5 m above water level. The five sites, designated I to V, differed markedly in the degree of erosion of the rock surface, site I showing the least weathering, and site V the most. The ranking procedure used was similar to the sixpartite scale of rock face relief employed by Creveld (1981). Site I corresponded to class 1 on this scale (smooth surface) and Site V corresponded to class 6 (many ridges and/or crevices up to 3 cm). The degree of erosion was assumed to be a function of the time elapsed since the rock face was initially exposed, as a rock slab fell away from the cliff. Since the five faces are composed of the same rock and have the same aspect this assumption is reasonable. The time for which the surfaces have been exposed is estimated to be of the order of a decade for site I and of at least several hundred years for site V.

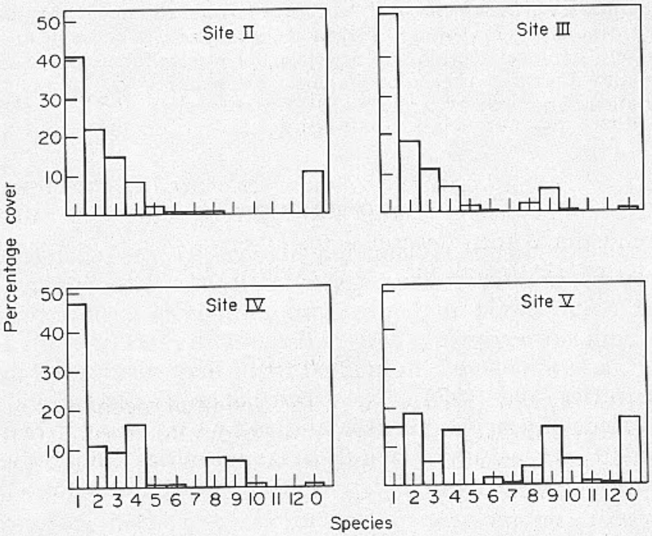

FIG. 1. Species abundance histograms, sites II–V. 0, Bare rock; 1, *Aspicilia verrucigera* Hue; 2, *Parmelia plittii* Gyelnik; 3, *Aspicilia cinerea* (L.) Körber; 4, *Rhizoplaca chrysoleuca* (Sm.) Zopf; 5, *Acarospora fuscata* (Schrader) Arnold; 6, *Physcia subtilis* Degel.; 7, *Rhizoplaca opiniconensis* Brodo *ined.*; 8, *Lepraria* spp.; 9, *Parmelia taractica* Krempelh.; 10, *Rhizocarpon grande* (Flörke ex Flotow) Arnold; 11, *Parmelia baltimorensis* Gyelnik & Fóriss; 12, *Cladonia* sp. Site I had the following composition: *Parmelia plittii* 0·2% cover, *Physcia subtilis* 0·2%; bare rock 99·6%.

A list of the species found at each site is included in Fig. 1. The abundance of each species at each site was measured as percentage cover, as has been done elsewhere, for example Karenlampi (1966) and Lawrey (1981). To measure percentage cover a 10 × 10 cm clear plexiglass grid, divided into 100 1-cm squares, was applied to the rock surface. Within the grid the percentage cover of each lichen species and also the percentage of bare rock, was estimated to the nearest 0·25%. Fifteen non-overlapping samples were taken at each site. The samples were taken at random between 1 and 2 m above water level (above the splash zone), although occasional obviously non-homogeneous areas such as major crevices, overhangs and areas of water run-off from the top of the cliff were avoided.

Results

The mean percentage cover ascribed to each species at sites II to V is shown in Fig. 1. Data from site I are given in the caption; only two species were present at low abundances. Since the sites are assumed to differ only in age we can infer that they represent different stages in a succession. Site I represents the youngest community and site V the oldest. There are few obvious trends in species abundances. *Aspicilia verrucigera* and *A. cinerea* peaked early in the succession, whereas *Lepraria* sp., *Parmelia taractica* and *Rhizocarpon grande* were more abundant at the older sites. The variation in the proportion of crustose and foliose lichens is recorded in Table 1. Although there is no consistent trend there were more foliose lichens at the oldest site. A relative increase in the abundance of foliose lichens is a commonly observed pattern in lichen succession (Hale 1967, Topham 1977). The succession involves changes in species relative abundance rather than in species composition. Six of the 12 species found occur at each of sites II to V.

The percentage of bare rock shows an interesting pattern of variation (Table 1). There is a decrease from sites I to IV, but an increase at site V so that 17% of the rock surface is devoid of lichens. This observation is discussed below.

Species richness and species diversity (measured as the Shannon Wiener function) show increasing trends from younger to older sites (Table 1). Similar trends have been described for other primary plant successions, for example Odum (1960) and Bazzaz (1975) for old field communities and Monk (1967) for forest succession.

Discussion

There have been many discussions of the potential mechanisms which shape the course of the successional process, for example Horn (1976), Connell & Slatyer (1977) and van Hulst (1979). In lichen communities, just as the successional process must be inferred, so must successional mechanisms. This discussion will examine observed features of the lichen succession at Snake Island in the light of potential mechanisms, bearing in mind that we are unable to demonstrate that site V represents a climax community.

For the succession described here there are changes in the physical environment which correlate with the age of the community. This is axiomatic given

TABLE 1. *Community characteristics at each of five study sites*

	Site				
	I	II	III	IV	V
Total cover of lichens (%)	0·4	89·3	99·1	99·2	82·5
Ratio crustose:foliose	—	2·99	3·10	4·37	1·28
Species richness	2	8	9	11	11
Species diversity ($H = -\sum_i p_i \log_2 p_i$)	1·00	1·94	2·07	2·30	2·81

that the age of a site was determined by the degree of weathering of the rock face. The physical changes include changes in substrate texture, the degree of moisture retention (increased by the presence of fine cracks and fissures), the fine scale patterns of light and shade, and potentially the availability of minerals that might be leached from the rock surface. Lichen establishment and growth is affected by these features (Hale 1967, Shure & Ragsdale 1977) and changes in them will result in changes in the composition of the lichen community.

Weathering will occur whether or not lichens are present. The succession is therefore partly allogenic, i.e. it is driven by forces independent of the community itself (*sensu* Daubermire 1968). However, the presence of lichens may also affect the weathering process. The subject is a controversial one; Cooper & Rudolph (1953) suggest that lichens contribute little to the breakup of rock surfaces, whereas Syers & Iskandar (1974) conclude that, 'lichens can be important agents in the biogeophysical and biogeochemical weathering of minerals and rocks'. If we accept the latter conclusion then there is also an autogenic component to the succession (Daubermire 1968).

Connell & Slatyer (1977) propose three models of succession: facilitation, tolerance and inhibition. Facilitation occurs when earlier species 'prepare the ground'; only after this can later species colonize. The same concept is termed 'obligatory succession' by Horn (1976). If lichens contribute to surface weathering then facilitation will occur. *Lepraria* sp., for instance, is most commonly found in crevices and consequently is more abundant on older rock surfaces. This would be an example of facilitation. However, the majority of species (7 out of 11) found at the oldest site are also found at site II. Facilitation, as defined, cannot be important for these species, although it may be more important where litter accumulation and soil formation can occur.

Tolerance occurs when later species can tolerate a lower level of some resource than earlier ones. This mechanism might occur in lichen communities where, for example, mineral availability is reduced over time, as has been discussed by Creveld (1981).

The inhibition model stresses the importance of competition in successional processes. Horn (1976) makes this explicit by referring to a 'competitive hierarchy' underlying the succession. Topham (1977) invokes this idea in ascribing the crustose-foliose successional sequence to the superior competitive abilities of foliose species. Of the physical and physiological requirements of lichens only space has been considered a resource for which competition is likely to occur (Pentecost 1980, Armstrong 1982), although Lawrey (1981) has suggested that competitive abilities may vary according to light intensity. Space is clearly a limiting resource given that overgrowth of thalli is minimal. Visual inspection of individual thalli shows that there is little overgrowth and that where it occurs one or both thalli appear discoloured and unhealthy. If competition for space is important among lichens then a number of changes in community structure over time are predicted. First, there will be an increase in the total percentage cover of lichens up to 100%. At this point competition for space becomes important and competitive exclusion may occur, causing a decline in the diversity of the community. Ultimately, if space is the only limiting resource, competition theory predicts that only a single species will persist (Armstrong & McGehee 1980). Yodzis (1978), in a more specific account of competition for space, also predicts that species richness will fall off once 100% cover is reached, though not necessarily to a single species.

The data presented here do not agree with these simple predictions. Although the percentage of bare rock falls as low as 1% at site IV, at site V it has risen again to 17%. And there is no evidence of a decline in species richness once 100% total cover is approached (Table 1). Nor is there any decline in species diversity. Such a decline would indicate the increasing dominance of one or a few species independently of any change in the number of species, suggesting incomplete exclusion. Some studies, for example Loucks (1970) and Auclair & Goff (1971), do show the predicted fall off in species diversity in the later stages of succession. But in this study competitive exclusion does not appear to be a major factor affecting community composition.

Hutchinson (1958) proposes several explanations for the absence of competitive exclusion:

(1) the environment shows short term fluctuations;
(2) the species are separated by microhabitat preferences;
(3) the community is not in equilibrium.

(1) and (2) may well apply here but we have little or no information on environmental changes or on lichen microhabitat preferences. Condition (3), however, has received considerable attention. Previous authors, for example Pickett (1980), have emphasized that non-equilibrium conditions can allow coexistence in plant communities. With reference to lichens Armesto & Contreras (1981) have concluded that equilibrium conditions, in terms of island biogeography theory, do not apply to a saxicolous lichen community, albeit one of indeterminate age. Pentecost (1980) suggests that the senescence of thalli, as well as physical erosion, will continually open up new areas for recolonization. Wirth (1972) goes as far as suggesting that physical erosion on vertical rockfaces may be so severe that a stable community will never be attained. In our study neither senescence nor erosion of the rock face was apparent at sites I or II but both occurred at the older sites, especially site V. Hale (1967) suggests that recolonization can cause cyclic changes in ‘ climax ’ community composition. The consensus, therefore, is that diversity at older sites is maintained by continual lichen mortality and recolonization. The above discussion implicates a number of processes as affecting lichen community dynamics and composition: growth rates, colonization rates, competitive interactions and mortality rates, due to senescence and/or physical damage. This list, though not necessarily complete, is similar to that suggested by Pentecost (1980). In this study community composition at site I is largely a product of colonization rates, growth rates become important as well at site II, competition (for space) is presumably most important at sites III and IV, and senescence is of most importance at site V, where recolonization rates will also be significant. The observed lichen succession will be orchestrated by this sequence of processes.

In conclusion, it is probable that allogenic processes, facilitation and inhibition all play a role in lichen succession. The effect of competition for space (the most likely mechanism for inhibition) is mitigated by mortality at older sites, which continually opens up new areas for colonization, similar to the 'chronic, patchy disturbance' of Horn (1976). As a result older sites retain a high diversity and an appreciable fraction of the rock face remains uncovered.

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