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Chapter 7

Epiphytes and Epiliths

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7.1 INTRODUCTION

Epilithic or saxicolous bryophytes may be defined as those growing directly on the surface of rock, and in this chapter do not include aquatic species; epiphytic or corticolous species are those growing on the bark of living trees and shrubs. In the literature, authors dealing with epiphytes usually adhere strictly to the above definition, probably because of the well-defined nature of the habitat, although a few (e.g. Barkman, 1958) include species on dead tree stumps and logs. On the other hand, and this makes the interpretation of some data difficult, the term saxicolous is often taken (e.g. Yarranton, 1967a) to include plants growing on soil or detritus overlying rock as well as those occurring directly on rock surfaces. In the account of epiliths in this chapter the strict definition is followed as far as possible. There has been considerably more work done on epiphytes, especially of a phytosociological nature, than on epiliths. There are probably several reasons for this - the epiphytic habitat is much more discrete and the number of species involved is usually much fewer (see, for example, Table 7.1).

With both epiphytes and epiliths there are obligate and facultative species. Obligate epiphytes are usually restricted to bark and very rarely occur on other substrates. Similarly, obligate epiliths are usually only found on rock. Facultative species are regularly found on more than one substrate type.

7.2 SEXUALITY AND HABITAT

Before dealing with the two groups there are data on the reproductive behaviour of epiphytes and epiliths in Britain that are worth considering. From Table 7.1 it may be seen that the proportions of monoecious obligate

epiliths and epiphytes are greater than might be expected when compared with mosses in general. This suggests that the tendency toward homozygosity that may result from monoecism may be of selective advantage in species that are adapted to specific habitats. Conversely, the proportions of dioecious species among facultative epiliths and epiphytes is higher than might be expected suggesting that the heterozygosity resulting from dioecism is advantageous in species that are catholic in their choice of habitat.

It is also of interest to note that twelve of the thirteen dioecious obligate epiphytes have vegetative propagules, usually in the form of multicellular gemmae. These include *Dicranum flagellare*, *D. montanum*, *Orthotrichum jvelli* and *Habrodon perpusillus*; the exceptional species being *Leptodon smithii*.

Table 7.1 Numbers of monoecious and dioecious British mosses.

	Monoecious	Dioecious
All species	287 (41.5%)	494 (58.5%)
Obligate epiliths	68 (53.1%)	60 (46.9%)
Facultative epiliths	19 (23.7%)	61 (71.3%)
Obligate epiphytes	20 (60.6%)	13 (39.4%)
Facultative epiphytes	15 (34.1%)	29 (65.9%)

A further curious feature of the reproductive behaviour of some corticolous mosses is that the peristome of the capsule opens when it is moist so that spore dispersal will occur during or shortly after rain or heavy dew. This phenomenon has been observed in corticolous species of the Leucodontaceae and Cryphaeaceae and in such genera as *Forsstroemia*, *Pyliasia* and *Neckera* (Patterson, 1953). This behaviour has been noted only in epiphytic species although many epiphytes exhibit the more usual opening of the peristome on drying. It is difficult to see the selective advantage of spore dispersal during wet periods unless this is associated in some way with spore germination in which case it might be expected to occur in epiliths as well.

### 7.3 EPIPHYTES

During the past thirty years there has been intensive work on epiphytic bryophytes in Japan by Horkawa, Hosokawa, Iwasuki, Nakanishi and their co-workers but, elsewhere, the studies have been less systematic. The most detailed account of cryptogamic epiphytes is Barkman's (1958) *Phytosociology and Ecology of Cryptogamic Epiphytes*. Jones (1959) says of this work 'Every conceivable aspect of everything relating to epiphytes is

considered in turn with great thoroughness. . . . Over the past twenty years there has also been much done on the effect of atmospheric pollution on epiphytic bryophytes (see Chapter 12). Most of the work on epiphytes is of a descriptive nature and, except in Japan, there has been little experimentation.

Epiphytic bryophytes may be obligate or facultative epiphytes. In Britain there are some 33 obligate epiphytes and about 44 facultative epiphytes (see Table 7.1). Twenty-four facultative and twelve obligate epiphytes have been reported from the Adirondak Mountains, New York State (Slack, 1975). Examples of British obligate epiphytes include *Tortula laevipila*, *T. papillosa*, *Zygodon conoides*, *Orthotrichum* and *Uloa* spp., *Leskea polycarpa*, *Cryphaea heteromalla* and *Pyliasia polyantha*. Such species are only very rarely found on other substrates. Facultative epiphytes include *Bryum capillare*, *Dicranum* spp., *Isotrichum myosuroides*, *Cirriphyllum crassinervium*, *Hypnum cupressiforme* s.l., *Metzgeria* spp., *Plagiochila* spp., and *Frullania* spp. Some species that are epiphytes in one geographical area are not so in another. Thus, the following species occur on the bark of softwood and hardwood trees up to a height of two metres in the United States: *Campyllum chrysophyllum*, *Fissidens cristatus*, *Thuidium delicatulum*, *Rhodobryum roseum*, *Hylacomium brevirostre*, *Ctenidium molluscum*, *Lepidozia sylvatica*, *Blepharostoma trichophyllum*, *Hypnum imponens*, *Nowellia curvifolia* and *Barranania pomiformis* (Billings and Drew, 1938). These species only exceptionally occur on tree trunks in Europe. On the other hand, such species as *Uloa crispata* and *Ptilidium pulcherrimum* are epiphytic throughout their range. The majority of pioneer species on trees are obligate epiphytes, whilst most later colonizers and succession climax species are facultative epiphytes (Herzog, Koskinen, cited in Barkman, 1958).

#### 7.3.1 The tree as a habitat

Whilst the majority of workers have confined themselves usually to the lowest two metres of trees (e.g. Richards, 1938; Hale, 1952; Pike *et al.*, 1977 and many Japanese workers) have studied the epiphytes of whole trees. There are usually three or four well-marked regions recognized: the tree base (mostly to one metre above soil level); the trunk and the crown with the latter being divided into two parts, large branches, and small branches and twigs. Study of the whole tree presents obvious difficulties which may be overcome either by the examination of fallen trees (e.g. Hale, 1952) or by using climbing techniques (e.g. Pike *et al.*, 1977). The tree base is colonized mostly by facultative epiphytes including species from the surrounding ground; the trunk and larger branch species may be facultative or obligate epiphytes whilst those of the smaller branches and twigs are usually pioneer obligate epiphytes.

Trees present a wide variety of habitat types for bryophytes, these depending upon light intensity, relative humidity and atmospheric pollution, which in turn are influenced by geographical location and the proximity of other trees, and upon the physical and chemical nature of the bark of the host tree or phorophyte.

### 7.3.2 Epiphytic communities

The most comprehensive accounts of epiphytic communities are by Barkman (1958), Iwatsuki (1960) and Iwatsuki and Hattori in a series of nineteen papers, the most recent being 1970. Other papers on the topic published since Barkman (1958) are Beals (1965), Engle (1960), Gough (1975), Hoffman (1971), Hoffman and Boe (1977), Hoffman and Kazmier-ski (1969), LeBlanc (1963), Nakanishi (1966), Pike *et al.* (1975), Rasmussen (1975), Slack (1976, 1977) and Sjøgren (1961).

#### (a) Classification of communities

Barkman (1958) used an hierarchical system of nomenclature to describe cryptogamic epiphytic communities in the Netherlands and adjacent regions. The basic unit is the association and associations are grouped into alliances and these into orders and there is a system of rules governing nomenclature akin to the *International Code of Botanical Nomenclature*. In the area concerned Barkman recognized 40 associations grouped into 10 alliances and four orders. The taxa are usually defined on the basis of faithful species and ecology. Iwatsuki (1960), using a similar system of community classification, recognized 33 associations and 10 alliances from the five major forest types in Japan.

Whether it is possible to produce a really satisfactory unit of classification for epiphytic bryophytes is open to question. The hierarchical system of the Zürich-Montpellier school as utilized by Barkman (1958) and Iwatsuki (1960) is unsatisfactory as it is to some degree subjective and attempts to categorize variation in community composition in an artificial taxonomic manner and is too inflexible, particularly where governed by nomenclatural rules. Further, it is the life-forms of the species making up the communities, not their taxonomic identity, that is important ecologically. A greater understanding of the ecology of epiphytic communities might be gained if these were analysed in terms of life-forms as well as species composition.

Phillips (1951) pointed out that 'The fact that many species appear in associations other than the ones they dominate and are even characteristic constituents of those other associations, shows that the dividing line between associations is not sharp but that many of them intergrade'. Further, Hale (1952) says that 'When variation in abundance with height is analysed

quantitatively the delimitation of associations becomes a questionable procedure'.

Nevertheless, within a limited geographical area, it is useful to have associations based on the degree of constancy and cover of each species as this allows for comparisons both within and between different areas. It should be borne in mind, however, that although the name of an association is based upon that of one or more species, those species are not necessarily dominant or even present. The significance of this is indicated by a comment of Hoffman and Kazmier-ski (1969) who point out that species associations, because of different effects of competition, may be better indicators of microclimatic conditions than presence or absence of particular species which may be widely distributed. There is also an observation, relevant in this context, by Rasmussen and Hertig (1977) that 'It is often mistakenly assumed from "normal" association analyses that species under certain ecological circumstances are closely associated with each other. In many cases, the truth is that they are only associated with the ecological conditions in a given habitat, but otherwise show high interspecific competition....'

If the species composition of an association is the result of competition then, clearly, life-forms are highly important. Japanese authors have made a point of indicating the life-forms of epiphytic bryophytes (pp. 199-201). If other authors had done the same it would be possible to make more meaningful comparisons, both between different host species and between different geographical areas.

#### (b) Examples of epiphytic communities

As might be expected there is vertical zonation in epiphytic bryophyte communities and the following examples will suffice to illustrate this. Life-forms, where known, are based on those of Gimmingham and Birse (1957), Horkawa and Nakanishi (1954) and Mägdefrau (see Chapter 2).

In the Killarney oakwoods, south-west Ireland, there are three associations (or climax associates) (Richards, 1938). The first association occurs on tree bases up to 1-2 m and is dominated by *Hylacomium brevirostre*, *Thuidium tamariscinum* (both wetfs), *Isoetecium myosuroides*\* and *I. myurum* (both rough mats) and the upward limit is determined by humidity. Trunks and larger branches have an association dominated by *Isoetecium myosuroides* (rough mat) with other species such as *Plagiochila spinulosa*, *P. punctata* (tall turfs) and *Hymenophyllum wilsonii*; this association is intolerant of high winds and bright illumination. The climax association of twigs and small branches is dominated by *Uloia crispata* (small cushions) and *Frullania tamarisci*

\* Although the individual shoots of *Isoetecium myosuroides* are denoid the overall effect is that of a rough mat.

(smooth mat). This latter association is also found on the branches of the shrub *Vaccinium myrtillus* and on trees of *Ilex aquifolium* the latter two associations occur though they are not very well defined.

On *Fraxinus excelsior* and *Fagus sylvatica* in northern Jutland, Denmark (Rasmussen, 1975) on the first 2.5 m of the trunks there are three inter-related associations, discernable using random sampling and statistical techniques. Nearest the ground is an association composed of *Homalia trichomanoides* (fan), *Lophocolea heterophylla* (rough mat), *Brachythecium ruabulum*, *Plagiommium undulatum* (wets) and *Isoetecium myosuroides* (rough mat). Higher up the trunk is an association, the most important constituents of which are *Metzgeria furcata* (smooth mat or thread-like), *Homalothecium sericum*, *Leucodon scirvoldes* (rough mats), *Neckera pumila* (fan), *Frullania dilatata* (smooth mat), *Orithotrichum lyellii* and *Zygodon viridissimus* (small cushions); in intermediate situations is an association composed of *Porella platyphylla*, *Raddula complanata*, *Pylaisia polyantha* (smooth mats), *Antitrichia curtipendula* (wet), *Isoetecium myosuroides*, *Pterogonium gracile* (rough mats), *Neckera complanata* (fan) and *Bryum capillare* (cushion). *Hypnum cupressiforme* (smooth mat) occurs in all three associations. The species of the intermediate association and of the other two associations are not mutually exclusive. If an analysis using only the five most common species is carried out (Rasmussen and Hertig, 1977) there is a distinction into two communities, one near the tree bases consisting of *Hypnum cupressiforme*, *Isoetecium myosuroides* and *Neckera complanata* and one at the upper levels composed of *Homalia trichomanoides*, *Hypnum cupressiforme*, *Neckera complanata* and *Metzgeria furcata*. Clearly, the inter-relationships of species within communities even in a small area of relatively uniform environmental conditions are highly complex.

The only systematic studies on the physiological ecology of epiphytic bryophytes have been carried in Japan (see Hosokawa *et al.*, 1964) in the *Fagus crenata* forest of Mt. Hiko, Kyushu, south-west Japan and it is useful to know something of the communities involved. The epiphytic vegetation is described by Omura *et al.* (1955). They recognized five associations, which they referred to as epilitha, on *Fagus crenata*. At or near the tree bases where light intensity is low and relative humidity high the predominant species are *Thuidium cymbifolium*, *Hylacomium cavifolium*, *Bryhnia novea-angliae* (all wets), *Homaliodendron scalpellifolium* (feather) and *Thamnobryum sandei* (dendroid). On the trunks, and occasionally the bases of main branches, are *Pterobryum arbuscula*, *Anomodon giraldii*, *Neckera yezoana*, *Dolichomitria cavifolia* (all dendroid), *Macrosporiella scabrisseta* (tall turf) and *Metzgeria conjugata* (thalloid mat). The third association, which occurs mainly on the undersides of the primary branches, is composed of lichens. On the upper parts of trunks and on

branches the species that occur are *Boulaya mitemii*, *Macromirium prolongatum*, *Okamuraea hakoniensis* (all rough mats), *Frullania montilata* (smooth mat), *Dicranum fragilitiforme*, *Dicranodontium dendudatum* (both short turfs) and five lichen species. On the ultimate branches the small cushion-forming *Uloa crispa* is the only bryophyte and is associated with several lichen species.

Two examples illustrate variation within an association and in the distribution of associations under different climatic conditions. Omura and Hosokawa (1959), studying the *Thuidium cymbifolium*-*Homaliodendron scarpellifolium* association at the base of *Fagus crenata* trees on Mt. Hiko, south-west Japan; found that there was variation in species composition and cover within and between individual associations with location of the tree, height from the ground and aspect and considered that these were probably related to humidity and light intensity.

In a study of bryophyte-macrolichen communities of *Pseudotsuga menziesii* at eight sites in an area approximately 100 × 100 km on the Olympic Peninsula, Washington, USA (Hoffman and Kazmierski, 1969) it was found that community structure was related to climatic factors. Six associations occur and their vertical distribution depends on climate and aspect. Taking the north-east side of trunks as an example, under mesic conditions a community dominated by *Hypnum circinale*, *Dicranum fuscens* and *Scapania bolanderi* extends well above 4 m. As conditions become drier this community extends less far up the trunks and gives way, at first above and then right to the tree bases, to a community composed of *Hypnum circinale*, *Dicranum fuscens* and the lichen *Lepraria membranacea*. As conditions become more xeric this community in turn gives way to one of *Hypnum circinale* and the lichens *Lepraria membranacea* and *Sphaerophorus globosus*. Under the most xeric conditions the communities are composed entirely of lichens.

On a wider geographical basis there may be similarities between associations in different regions particularly if the associations are not treated as rigid inflexible units. For example, some of the associations of epiphytes in Michigan, USA (Phillips, 1951) resemble those in Virginia, USA, southern Norway, Switzerland and northern Italy, Poland and the Rhône Valley. The *Neckera pennata* association has parallels in Tennessee, USA and various parts of Europe. The *Ptilidium californicae* association and certain associations of the *Dicrano-Bazzanion* in Japan are somewhat similar to those of boreal Europe and North America (Iwatsuki, 1960). Similarly, associations of the Japanese *Uloton asiaticae* may have affinities with associations of the *Uloton crispae* of Barkman (1958) and *Uloa crispa* communities in North America.

On the other hand, although statistically delimited associations on *Fraxinus excelsior* and *Fagus sylvatica* in northern Jutland, Denmark

(Rasmussen, 1975) do bear resemblance to Barkman's (1958) *Ulotium bruchii*, *Neckera*-*Isoetium myosuroides* associations and *Homalium* sub-alliance (categories of the Zürich-Montpellier school), there are too many differences to relate the type of communities arrived at using different methods of definition.

A possibly more realistic approach is, rather than making comparisons on the basis of species composition, to make them on the basis of life-form composition since it is the life-form spectra of the communities that is ecologically important, not their taxonomic constitution.

### 7.3.3 Succession

To study colonization and succession it would be necessary to place permanent quadrats on young trees and observe these over a period of very many years. The alternative is the study of communities on trees of differing ages within a more or less uniform environment. This was done in Michigan, USA (Phillips, 1951). On young trees pioneer associations are *Frullania* spp., sometimes *Ptilium pulcherrimum* or *Radula complanata* (which may follow *Frullania*), *Orthorhynchium sordidum* and *Uloia crispata*, the latter two requiring protection, such as knot holes, for establishment. These are followed by pleurocarpous moss associations. Depending on environmental factors the association may be, from xerophytic to less xerophytic, *Homomallium adnatum*, *Pylaisia selwynii*, *Leucodon sciuroides*, *Porella platyphylloides*, *Neckera pennata* or *Anomodon minor*.

Whilst the pioneer species vary from place to place, primary colonizers are usually algae or crustose lichens, followed by foliaceous lichens or mosses and the latter by fruticose mosses (Barkman, 1958). In Europe, pioneer bryophytes include *Orthorhynchium*, *Uloia* and *Zygodon* spp. (usually requiring protection for establishment), *Hypnum cupressiforme*, *Neckera pumila*, *Frullania* spp. and *Metzgeria furcata* (Barkman, 1958; Grubb *et al.*, 1969; Rasmussen, 1975). Martin (1938) reports *Pylaisia polyantha* as a pioneer in western Scotland but this is probably an error for *Hypnum cupressiforme* var. *resupinatum*. Which particular species arrives first and how succession proceeds varies with the situation of the tree species and the microclimate. Thus, Grubb *et al.* (1969) report that *Uloia crispata* is a primary colonizer in Britain that is suppressed by later species, especially *Hypnum cupressiforme* which in turn is succeeded by *Dicranum scoparium*. At Fontainebleau, France, succession follows a different pattern (Doignon, cited in Barkman, 1958). On oaks, after 15–20 years, foliaceous lichens appear, after 20–25 years, *Frullania dilatata*, then *Orthorhynchium affine* and *O. schimperii*, then *Hypnum cupressiforme* and *Orthorhynchium lyelli*; *Uloia crispata* appears after 25 years, *Anomodon viuculosus*, *Porella platyphylla* and *Neckera* after 35 years, *Leucodon sciuroides* and *Zygodon* after 40 years. On beech twigs at Fontainebleau

(Doignon, cited in Barkman, 1958) the first bryophytes to appear are *Uloia bruchii* and *Hypnum cupressiforme* succeeded by *Frullania dilatata* and the lichen *Parmelia asperata*. In woods in Amsterdam (Rynders, cited in Barkman, 1958), the first bryophytes to establish on *Salix alba* and *Sambucus nigra* after 16–17 years are *Frullania dilatata* followed two years later by *Uloia bruchii*. In the Killarney oakwoods, south-west Ireland (Richards, 1938), the tree base pioneer is *Isoetium myosuroides* which may be invaded but not replaced by woodland floor species. On trunks and larger branches *Isoetium* is again a pioneer, possibly preceded by lichens. It may invade the *Uloia*-*Frullania* association of larger branches but not of smaller branches or twigs where the *Uloia*-*Frullania* association is the climax. In that habitat the pioneers are usually *Uloia crispata* and *Frullania germana* and later species that come in include *Frullania tamarisci*, *Plagiochila spinulosa* and *P. punctata*.

Except perhaps in the tropics and subtropics it would seem that the bryophyte communities on mature tree trunks are climax communities. Barkman (1958) points out that in the tropics and subtropics the cryptogamic epiphytic communities are merely a stage in a succession that will culminate in a phanerogamic epiphyte community but that this climax is never reached in temperate climates as the trees do not live long enough for sufficient accumulation of 'soil' to allow the establishment of higher plants to any extent. The implication is, therefore, that in such regions the cryptogams do not form climax communities. This seems a rather extreme approach especially as, except in very moist areas, there is no indication that any further stage in the succession is likely to occur even on very old trees. This is supported by the observations of Hosokawa and Omura (1959) on *Fagus crenata* trees on Mt. Hiko, Kyushu, Japan. Analysis of data gathered from quadrats at various heights on the trees over a period of five years indicated the presence of a climax community.

### 7.3.4 Life-forms

It is only in Japan that large-scale studies have been carried out on the distribution of epiphytic bryophyte life-forms. The life-forms used are based on the categories of Gimmingham and Robertson (1950) and added to by Horikawa and Nakanishi (1954) and Iwatsuki and Hattori (1956). The detailed phytosociological accounts of such authors as Hattori, Hosokawa, Iwatsuki, Nakanishi and their co-workers contain tables in which the life-forms of the various species are indicated.

Iwatsuki (1960) discusses the life-forms from the five main Japanese forest types. Table 7.2 shows the vertical distribution of life-forms in the forest alliances *Vaccinium*, *Pinetum punitae* (alpine forest), *Abieton maresii* (sub-alpine coniferous forest), *Fagion crenatae* (montane deciduous hardwood forest), *Tsugion sieboldii* (montane coniferous



structure of epiphytic communities rather than bark pH and moisture content. Bearing in mind that it is not possible to consider any one environmental factor in isolation, they can be dealt with under two main headings, the nature of the bark of the host tree and microclimate.

(a) *The bark*

(i) *Host specificity.* Whilst most authors consider that the species of the host tree is of major importance in determining the nature of the epiphytic community there is one claim to the contrary. Phillips (1951) points out that similar associations in different geographical areas occur on quite different tree species indicating that the tree species is not an important factor. He considers that it is microclimatic conditions that are significant and that optimum moisture conditions will enable an epiphyte to colonize more or less any tree as moisture will compensate for such inimicable features as low pH, smooth bark, youth of the tree and exposure. He considers restriction to particular tree species as being characteristic of drier areas. However, it is probably only in tropical montane cloud forest that such optimum climatic conditions prevail (see Chapter 3, pp. 97–8), so that the argument is not relevant. Further, it may well be that different tree species in different geographical areas which have similar epiphytic communities have similar bark types or that the combination of one bark type under one set of climatic conditions produces an environment as compatible to a particular epiphytic association as the combination of a somewhat different pair of variables in another geographical area. From the fact that different associations occur on different tree species it can only be concluded that the nature of the bark and, therefore, the identity of the host species is of great importance in determining the composition and structure of epiphytic communities and this thesis is supported by numerous observations (e.g. Beals, 1965; Culberson, 1955; Hale, 1955; Iwatsuki, 1960; Martin, 1938; Rasmussen, 1975; Slack, 1976). A few examples will demonstrate this.

In Argyll, western Scotland (Martin, 1938) the number of bryophytes recorded from different tree species varies. Nineteen taxa were recorded from *Quercus robur*, 19 from *Fraxinus excelsior*, 11 from *Betula pendula*, 8 from *Acer pseudoplatanus*, 9 from *Fagus sylvatica* and 9 from conifers. The frequency of species on different trees also varies. In Argyll, *Dicranum scoparium* is most common on *Quercus* and *Betula* and is absent from *Fraxinus* and *Acer*; *Homalothecium sericeum* is most common on *Fraxinus* and absent from *Quercus* and *Betula*.

In northern Wisconsin, at breast height, *Anomodon miror* is most common on *Acer saccharum*, and *Tilia americana*, *Dicranum montanum* on *Pinus strobus*, *Tsuga canadensis* and *Betula lutea*, *Orchrorrhynchium* spp. on

*Populus* spp., *Ptilidium pulcherrimum* on *Pinus strobus* and *Uloia crispa* on *Betula lutea* and *Populus* spp. (Culberson, 1955).

Slack (1976) found in the Adirondack Mountain Preserve, New York State that there was a considerable degree of phorophyte specificity. *Neckera pennata*, *Porella platyphloidea*, *Anomeodon rugelii*, *Pylaisia imbricata*, *Pseudolekeella nervosa*, *Raula complanata* and *Leucodon brachypus* are restricted to *Acer saccharum*; *Frullania asagrayana*, *Dicranum montanum*, *Ptilidium pulcherrimum*, *Hypnum pallescens* and *Dicranum viride* are restricted to *Betula alleghaniensis*; only *Frullania eboracensis* and *Platygyrium repens* are common to both tree species.

In the coniferous forest of Mt. Honokawa, Shikoku, Japan (Iwatsuki and Hattori, 1966) *Leucodon okamurae* is common on *Tsuga sieboldii* trunks but rare on those of *Abies firma*. *Brotherella yokohamae*, *Clasobryella kusatsienseis*, *Dicranum hamulosum*, *Hypnum triso-viride*, *Bazzania fauriana*, *Chandonanthus hirtellus* and *Odonotichisma grosserrucosum* are more abundant on *Tsuga* whilst *Haplohynum longinerve*, *Hypnum plumaeforme*, *Macromitrium gymnosorum*, *Maecivaria ulophylla*, *Okamuraea plicata*, *Ptilorhizopsis dentata* and *Trocholejeunea saudovicensis* are more abundant on *Abies*. Similar differences were found between the epiphytic communities of the two conifer species in another part of Japan, Wariwa, Nichinan, Honshu (Iwatsuki and Hattori, 1956).

If a trunk is inclined this has an effect on the distribution of epiphytes. Barkman (1958) suggests that with inclined trunks, rain water will trickle to the lower side so that epiphytes will grow all round the trunk. When there is an epiphyte cover on the upper side this will absorb rain, depriving the lower side of water. In England, Pitkin (1975) found that trickling of rainwater to the under side does not appear to occur and epiphytes rarely if ever colonize the underside of inclined trunks. On inclined trunks of *Fraxinus excelsior* and *Fagus sylvatica* (Rasmussen, 1975) species diversity is higher when the angle of inclination is 5°–15° but at greater angles of inclination the number of species drops, with *Hypnum cupressiforme* and *Homalothecium sericeum* becoming dominant on the upper side. Probably, these two species have a greater competitive ability on an inclined than on a vertical trunk.

(ii) *Physical nature of the bark.* The only attempt to determine the hardness of bark, a feature said by many authors to be important, was by Culberson (1955) who investigated hardwood and softwood trees in northern Wisconsin. He found no direct correlation between epiphyte communities and hardness of bark although softwood and hardwood trees differed with respect to this feature and in their epiphyte communities.

Data on the microtopography of bark is conflicting. Olsen (1917) says

that small acrocarpous mosses such as *Orhorrhichum* and *Uloa* spp. are typical of smooth bark although other authors (e.g. Barkman, 1958) say they occur on rough bark and in knot holes and leaf scars. According to Barkman (1958) *Neckera pumila*, *Perigynandrium* and *Leskea* occur on smooth bark. The stability of the bark is obviously important and Gough (1975) considers that exfoliation of the bark is the most important factor determining the distribution of epiphytes communities in Boulder County, Colorado, USA.

In Japan (Iwatsuki, 1960), associations characteristic of smooth bark, for example the *Ulo-Frullaniemum* associations extend down the trunks of smooth barked trees such as *Betula grossa*, but on other kinds of trees are usually restricted to the crowns. It also appears that xerophytic associations in Japan tend to occur on smooth bark and hygrophilous ones on soft-barked trees.

(iii) *Moisture and pH*. Estimates of bark water content vary, depending upon the methods of estimation and of expressing the results. Reports of bark pH are also variable although differences may be due to the degree of atmospheric pollution and amount of rainfall. Staxang (1969) relates differences in bark pH of deciduous trees in Sweden to atmospheric pollution. The pH of bark of *Quercus robur* and *Q. petraea* in North Wales and Devonshire, areas of high rainfall and low pollution, varies from 4.9 to 5.2 whilst from sites in the vicinity of Oxford, where rainfall is lower and pollution higher, the range is 3.4 to 4.0 (Pitkin, 1973b). Factors affecting bark pH are discussed in Chapter 11 (p. 412).

An example of the importance of bark moisture capacity and pH is provided by studies on the moisture content of the bark of *Liriodendron tulipifera*, *Fagus grandifolia*, *Fraxinus americana* and *Tsuga canadensis* in an area of eastern Tennessee (Billings and Drew, 1938). These showed that the field moisture content of the bark of the three angiosperms was higher by a factor of two to seven than that of *Tsuga*. In all four species, moisture content was greater at a height of one metre than at 1.5 m and that in turn was greater than at 2 m. The moisture content on the south side, the direction from which the rain came, was higher than on the north side. The *Tsuga* had a bark pH of 4.28 to 4.96, the other species a pH of 5-6. There is a marked difference in the bryophyte associations of the angiosperms and the gymnosperm. Every specimen of the former studied had communities of *Neckera pumila*, *Anomodon attenuatus* and *A. rostratus* and many had *Campyllum chrysophyllum*, *Brachythecium oxycladum* and *Fissidens cristatus*, none of which was found on *Tsuga*. Conversely, communities of *Uloa crispata*, *Dicranum fulvum*, *Bazzania denudata*, *B. trilobata*, *Hypnum reptile* and *Mnium hornum* were exclusive to the bark of *Tsuga*. These differences were interpreted in terms of differences in the moisture content

and pH of the various barks as other environmental conditions were similar. Vertical zonation on the trunks is explicable in terms of the upward decrease in moisture content. This latter is also remarked on by Rasmussen (1975). On *Fraxinus excelsior* in Denmark there is a decrease in the number of species upwards, whilst on *Fagus sylvatica* there is no distinct trend. This correlates with the data (Rasmussen, 1975 citing Sjogren) that *Fraxinus* trunks are moister near the base than above, whereas the moisture content of *Fagus* bark is more uniform.

The effect of pH on corticolous bryophytes in culture is shown in Table 7.3. These data agree with field observations (Pitkin, 1973a, b) and may account at least in part for the distribution patterns of bryophytes in Britain where low pH may be related to high atmospheric pollution.

Table 7.3 Growth of epiphytes on agar cultures at various pH's over a period of twelve weeks (Pitkin, 1973b).

pH	<i>Hypnum cupressiforme</i>	<i>Cryphaea heteromalla</i>	<i>Isoetecium myosuroides</i>
3	Many shoots dead.	Dead.	Many shoots dead.
4	Dark green, shoots spindly.	Some shoots dead, others dark green.	Growth largely prostrate, plants dark green.
5	Robust, shoots dark green.	Vigorous shoot growth, shoots dark green.	Robust, shoots dark green.
6	Very robust, shoots dark green.	Robust, shoots dark green.	Robust, shoots dark green.
7	Robust, shoots pale.	Shoot growth, shoots pale.	Robust, shoots dark green.
8	Poor growth, shoots yellow/green.	Poor growth, shoots pale yellow.	Poor growth, shoots yellow/green.

An example where the occurrence of epiphytes is related to bark pH and air pollution comes from the observations in a region of high atmospheric pollution in the Aalborg-Norrendly area of north Denmark (Johnsen and Soehning, 1976). The species, *Tortula lanifolia*, *T. subulata*, *Leskea polycarpa*, *Orthorrhichum diaphanum*, *Tortula vitreces* and *Zygodon viridis-sinus* only occur near to a cement plant which releases calcareous dust, those species with the narrowest range being listed first. The dust raises the bark pH and clearly this allows the establishment of species that would otherwise be susceptible to the degree of atmospheric pollution in the area concerned.

(iv) *Chemical nature of the bark*. It is often suggested that the chemical nature of the bark is important in determining the composition of epiphytic communities (e.g. Martin, 1938; Iwatsuki, 1960), although little evidence has been given until recently in support of this. Barkman (1958) divides

trees into three groups on the basis of bark electrolyte content. Those with eutrophic bark, including *Acer* spp., *Sambucus nigra*, and *Prunus avium*, those with mesotrophic bark, including *Quercus* spp., *Fagus sylvatica*, *Fraxinus excelsior* and *Salix alba*, and those with oligotrophic bark such as *Betula*, *Picea* and *Abies*. Several associations are restricted to eutrophic and mesotrophic barks. Facultative epiphytes that occur on eutrophic bark, if also facultative epiliths, occur on basic rocks whilst similar bryophytes of oligotrophic bark occur on siliceous rocks.

Table 7.4 shows the results of culture experiments with corticolous mosses using bark extracts. These agree well with field observations, especially the growth of *Lophocolea heterophylla* on *Picea abies* as it is often the only bryophyte on spruce in Britain (Pitkin, 1973b). This suggests that the chemical nature of the bark is indeed a factor affecting growth of epiphytic bryophytes.

Table 7.4 Growth on water extracts of different barks after 13 weeks (g organic carbon per plant) (from Pitkin, 1973b).

Height above ground	<i>Fraxinus excelsior</i>		<i>Quercus</i> sp.		<i>Sambucus nigra</i>		<i>Picea abies</i>	
	60 cm	120 cm	60 cm	120 cm				
<i>Cryphaea heteromalla</i>	2.25	1.13	0.43	0.37	2.31		0.28	
<i>Hypnum cupressiforme</i>	3.10	1.06	1.88	1.27	2.12		0.72	
<i>Lophocolea heterophylla</i>	3.14	0.92	2.37	1.15	1.86		2.40	

In experiments with gemmae of *Uloa phyllantha* (Pitkin, 1973a, b) it was shown that these would not germinate on bark discs taken from 10 m up a *Quercus petraea* trunk but grew readily on discs from beneath the epiphyte cover at the foot of the tree. The gemmae germinated on discs from 10 m up the tree after these had been washed in running water for one month suggesting the presence of a leachable inhibitor or inhibitors in the bark. If such leachable substances occur in bark this could explain in part the epiphyte cover extending further up a tree in wetter areas and supporting Phillip's (1951) argument that ample moisture will negate the effect of deleterious aspects of the environment.

(b) *Microclimate: light intensity and atmospheric humidity*

Light intensity and relative humidity are inversely correlated, the former being at its maximum at the tree crown and the latter at the tree base. This had been suggested by numerous authors (e.g. Olsen, 1917; Richards, 1938) and has been confirmed by Omura *et al.* (1955). The effect of humidity, which is related to rainfall, is marked. This is indicated by growth rates of *Hypnum cupressiforme* and *Isoetecium myosuroides*

described on p. 210. In another instance, in mesic areas of the Olympic Peninsula, Washington, with annual rainfall in the region of 3000 cm, up to 17 epiphytic bryophytes occur on the trunks of *Pseudotsuga menziesii*; at the other extreme, with an annual rainfall of about 60 cm the number of bryophyte species is three (Hoffman and Kazmierski, 1969). Further, as mentioned on p. 197 vertical zonation is also markedly affected by rainfall and consequent relative humidity. In Argyll, Scotland, in exposed areas, bryophyte cover is less dense, zoning less marked and vertical extent reduced as compared with protected areas with higher relative humidity (Martin, 1938).

An illustration of the effect of height on cover by particular species is given by Slack (1976) from the Adirondack Mountain Preserve. Over a height range from 0 to 2 m, the mean percentage cover of *Neckera pennata* rises from 0% at 0 m to 27% at 1 m dropping to 6% cover at 2 m; *Anomodon rugelii* rises from 0% cover at 0 m to 8% at 0.5 m and drops to 0 at 1 m; *Parrygyrium repens* rises from 0% cover at 1 m to 20% at 2 m; *Platyasia irritata* shows a similar pattern to *Parrygyrium*.

Whilst there are no quantitative data available it is amply evident from field observations that there is a close correlation between rainfall and the luxuriance of epiphyte cover. There is, however, one observation that suggests that another source of moisture may be important. In the Transvaal, South Africa (Jacobsen, 1978), over a three year period, the growth of epiphytic mosses at Bloemfontein and at Woodbush was 45 and 47 gm respectively per 10 × 10 m plot although the rainfall was 2.5 times greater at the latter site than the former. Although no meteorological data were available it was considered that mist was an important contributory factor to this phenomenon at Bloemfontein.

There is a relationship between vertical distribution, rate of evaporation and desiccation resistance. Generally, species in the crown are more resistant to desiccation than those at the tree base (Hosokawa and Kubota, 1957; Hosokawa *et al.*, 1964). For example, *Uloa crispula* and *Boulaya mitlenii* which occur in crowns are more drought-resistant than tree base species such as *Homaliodendron scalpellifolium*, *Hylacomium cavifolium* and *Thuidium cymbifolium*. The resistance of crown species to desiccation is greater in the winter than in summer. This may be due partly to increased humidity when the photophyte (*Fagus crenata*) is in leaf and to the greater physiological activity in the summer. This correlates with observations of Tagawa (1959) who found that the evaporation potential in tree crowns is greater in winter than in summer.

There is also a relationship between compensation point and vertical distribution. This was shown experimentally by Hosokawa and Odani (1957) as is indicated in Table 7.5. Clearly, the light requirements of species affects their vertical distribution. Light saturation curves (Miyata

**Table 7.5** Vertical zonation of species related to minimum light intensity necessary to reach compensation point. (Modified from Hosokawa and Odani, 1957).

Habitat	Species	Minimum light intensity (lux)	Optimum light intensity (lux)
Uppermost branches	<i>Uloa crispula</i>	6000	± 20,000
Boughs	<i>Bouleya mitreii</i>	1200	10,000–20,000
Trunk	<i>Anomodon giraldii</i>		
	<i>Pterobryum arbuscula</i>		
Tree base	<i>Thuidium cymbifolium</i>	400	± 10,000
	<i>Hylocomium curvifolium</i>		
	<i>Thuidium sandei</i>		
	<i>Homalodendron scalpellifolium</i>		

and Hosokawa, 1961) suggest that plants on the lower parts of trunks are shade species and those on the crowns light-demanding species.

In a recent study of the physiology of four epiphytic mosses growing on *Acer saccharum* in the Adirondack Mountains, USA, Tobiesen *et al.* (1978) found that *Plagiomnium cuspidatum*, a facultative epiphyte, required a higher water content for optimum photosynthesis but had a more rapid assimilation rate than did the three obligate epiphytes, *Anomodon rugelii*, *Neckera pennata* and *Uloa crispula*. The *Uloa* was found to be more tolerant of desiccation than the *Neckera* with which its vertical range overlaps.

### 7.3.6 Nutrition

Species on twigs and outer branches probably obtain their nutrients from bark, rain, dust and perhaps small quantities of leaf leachate. Those species on the lower parts of the trunk probably obtain nutrients from leaf leachates and leachates from bryophytes higher up. Species of the upper trunk and lower branches are in an intermediate position (Grubb *et al.*, 1969). After comparative measurements of nutrients in *Hypnum cupressiforme*, the bark of the host species (*Fraxinus excelsior* and *Fagus sylvatica*) and bulk precipitation in north Denmark (Rasmussen and Johnsen, 1976), it would appear that the moss accumulates nutrients mainly from atmospheric precipitation and possibly also from stem-flow.

Evidence that epiphytes are, to some extent, dependent upon stem-flow for nutrients is provided by Pitkin (1973b). He showed that growth of *Hypnum cupressiforme*, *Cryphaca heteromalla* and *Lophocolea heterophylla* was generally greater on an extract of bark made from stem-flow

water than on a bark extract made with pure water. The topic is dealt with further in Chapter 11, pp. 404–14.

It would appear that species, such as *Uloa crispula*, on ultimate branches are able to grow with a lower internal content of certain nutrients such as nitrogen, potassium and sodium than species of larger branches and trunks (e.g. *Hypnum cupressiforme* and *Dicranum scoparium*) which have nutrient contents similar to those of terrestrial bryophytes (Grubb *et al.*, 1969). It is not known if the low supply of nutrients to the species of outer branches is a limiting factor. Material of *Uloa crispula* from the Lake District and North Wales has a higher nutrient content than specimens from north-west Scotland but this is possibly due to growth restriction by atmospheric pollutants (Grubb *et al.*, 1969).

In considering the nutrient content of epiphytes it is necessary that lichens are also taken into account. Pike *et al.* (1972) estimated the total nitrogen content of the epiphytes of an old growth *Pseudotsugamenziesii* forest, in which there are about 10 trees per acre, (i.e. 25 trees per hectare) about 75 km east of Eugene, Oregon, USA. They found that of the 225 gm total, bryophytes contained 82 gm and lichens 143 gm (including 127 gm held by the single species *Lobaria oregana*). They consider that this could represent a significant input into the forest ecosystem and that nitrogen may enter the soil from stem-flow leachates from the epiphytes.

### 7.3.7 Growth, productivity and biomass

Measurements of the growth rate of epiphytic mosses have only been made on pleurocarpous species which, because of their 'two-dimensional' habit, are more easily dealt with than 'three-dimensional' acrocarpous species. The only example of growth rate of an acrocarpous species is of *Uloa crispula* with an annual diameter increment of up to 2 mm (T. J. Bines in Pitkin, 1975). Growth of corticolous bryophytes is slow and depends upon environmental conditions. In studies on the effects of moss gathering by florists in the montane deciduous forests of Transvaal, South Africa, it was estimated that regeneration of bark species took seven to ten years after harvesting (Jacobsen, 1978). Table 7.6 shows the growth rate of four pleurocarpous mosses from Wychwood, Oxfordshire, England.

The position on the tree, the tree species and the geographical location affect growth rate (Pitkin, 1975). In Oxfordshire, growth of *Isoetecium myosuroides* is more rapid at a height on the trunk of 30–100 cm than at 150–200 cm and the growth of *Hypnum cupressiforme* is more rapid on the upper side than the under side of inclined trunks. These two examples suggest that the reason for the greater luxuriance of bryophytes near tree bases than higher up the trunk and on the upper side of inclined trunks is more rapid growth. *Hypnum cupressiforme* grows faster on *Fraxinus excelsior* than on *Quercus* spp. but the growth rates of both *H. cupressi-*

**Table 7.6** Annual growth in mm in 1971 of four corticolous mosses from Wychwood, Oxfordshire. (Modified from Pitkin, 1975).

<i>Hypnum cupressiforme</i>	14.5 mm
<i>Isoetium myosuroides</i>	16.0 mm
<i>Homalothecium sericeum</i>	15.9 mm
<i>Neckera pumila</i>	10.6 mm

*forme* and *Platygyrium repens* differ from tree to tree of the same species under apparently identical environmental conditions. The effect of different climatic conditions is illustrated in Table 7.7.

There does not appear to be any inherent seasonal growth pattern, at least in Britain, growth being directly related to prevailing weather conditions (Pitkin, 1975). There is a close correlation between monthly rainfall minus evapotranspiration and shoot growth rate.

The only example of productivity of corticolous bryophytes is from the montane deciduous woods in Transvaal (Jacobsen, 1978). Up to a height of 2 m (the height to which Bantu gatherers collect bryophytes for florists) on tree trunks, the annual productivity is estimated to be 4700 g ha<sup>-1</sup> (equivalent to a growth rate of 7.64%). This is not very informative as no data are provided to relate this to tree number, climate, etc.

**Table 7.7** Growth rate of two corticolous pleurocarpous mosses over a six month period (May–October, 1971) at four localities in England. From data kindly provided by Dr P. H. Pitkin.

Locality	Rainfall	Altitude	Growth rate (mm month <sup>-1</sup> )	
			<i>Hypnum cupressiforme</i>	<i>Isoetium myosuroides</i>
Wyham	224.2 mm	70 m	1.38 mm	± 0
Wychwood	301.9 mm	150 m	1.56 mm	1.36 mm
Roborough	437.0 mm	110–115 m	4.80 mm	4.99 mm
Black Tor	696.0 mm	345–420 m	5.47 mm	6.00 mm

There are two examples of biomass, one from Hungary, the other from the USA. Simon (1974) estimated the biomass of bryophytes (the predominant species being *Hypnum cupressiforme* accompanied by *Platygyrium repens*, *Bryum flaccidum*, *Brachythecium salebrosum*, *Plagiomnium cuspidatum*, *Anomodon attenuatus*, *Frullania dilatata*, *Uloa crispata* and *Neckera besseri*) from oak forest (*Quercetum petraeae-cerris*) from the

Bükk Mountains, Hungary, as 43.375 kg ha<sup>-1</sup>. Simon considers that in this type of Hungarian forest the epiphyte flora is less rich than in several other types of Hungarian forest. If one takes the annual productivity of Transvaal montane forests (Jacobsen, 1978) of 7.64% as 4700 g ha<sup>-1</sup>, then bryophyte biomass up to a height of 2 m would be in the region of 61 kg ha<sup>-1</sup>.

Pike *et al.* (1977) estimated the biomass of epiphytes on a 450-year-old *Pseudotsuga menziesii* near Eugene, Oregon and their results are given in Table 7.8. In a second example (Pike *et al.*, 1972), the weight of bryophytes on a 65 m tall tree was estimated to be 8.9 kg with 3.9 and 4.9 kg from the trunk on main branches respectively. When wet the bryophytes will be three to four times heavier and it is considered that this may be a significant factor affecting branch fall.

**Table 7.8** Biomass in kilograms of epiphytic bryophytes on a 450 year old tree of *Pseudotsuga menziesii* (1.46 m dbh, 77 m height). Modified from Pike *et al.*, 1977.

	Mosses	Liverworts
Trunk	2.49 ± 0.13	0.00
Branches	2.06 ± 1.39	0.07 ± 0.07
Branchlets	0.03 ± 0.04	0.03 ± 0.04
Total	4.57 ± 1.58	0.10 ± 0.11

### 7.3.8 Epiphytes and pollution

Generally speaking, epiphytes are more susceptible to atmospheric pollution than epiliths and the lower part of a tree provides a more sheltered habitat than does the upper part. In Britain, obligate epiphytes such as *Orthotrichum*, *Uloa* and *Zygodon* species and *Lejeunea ulicina* are usually more susceptible to pollution than are facultative epiphytes such as *Dicranoweisia cirrata*, *Hypnum cupressiforme* and *Homalothecium sericeum*. It has been shown (Syratt and Wanstall, 1968) that *Dicranoweisia cirrata* has a very high content of chlorophyll *a* and is capable of converting sulphite to sulphate with a high degree of efficiency compared with other species. This may account for its wide distribution as an epiphyte in Britain even in areas of high atmospheric pollution. Figs 7.1 and 7.2 show the distributions of *Dicranoweisia* and *Lejeunea ulicina* in Great Britain and Ireland. Whilst the former species is widespread, the latter is absent from most of lowland Britain downwind from areas producing pollutants despite the occurrence of suitable habitats.

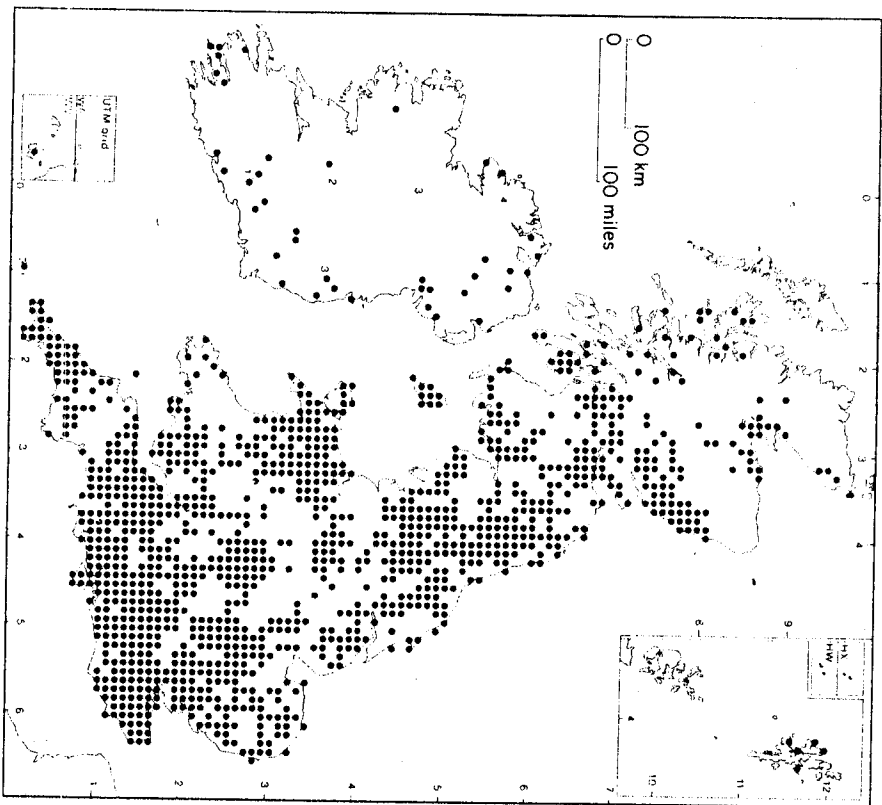


Fig. 7.1 Distribution map of *Dicranoweisia cirrata* in Britain. This species is tolerant of atmospheric pollution. Reproduced from Smith (1978).

#### 7.4 EPILITHS

Studies on epilithic bryophytes date back to the early years of this century, commencing with the work of Grebe (1911) and Schade (1912) although there had been earlier attempts at classifying bryophytes on the basis of the substrate upon which they grew (e.g. Molendo, 1865; Pfeffer, 1871). By the end of the first 30 years of this century a considerable amount of phytosociological work had been done leading to the recognition of various types of saxicolous communities or associations (Gams, 1932). There

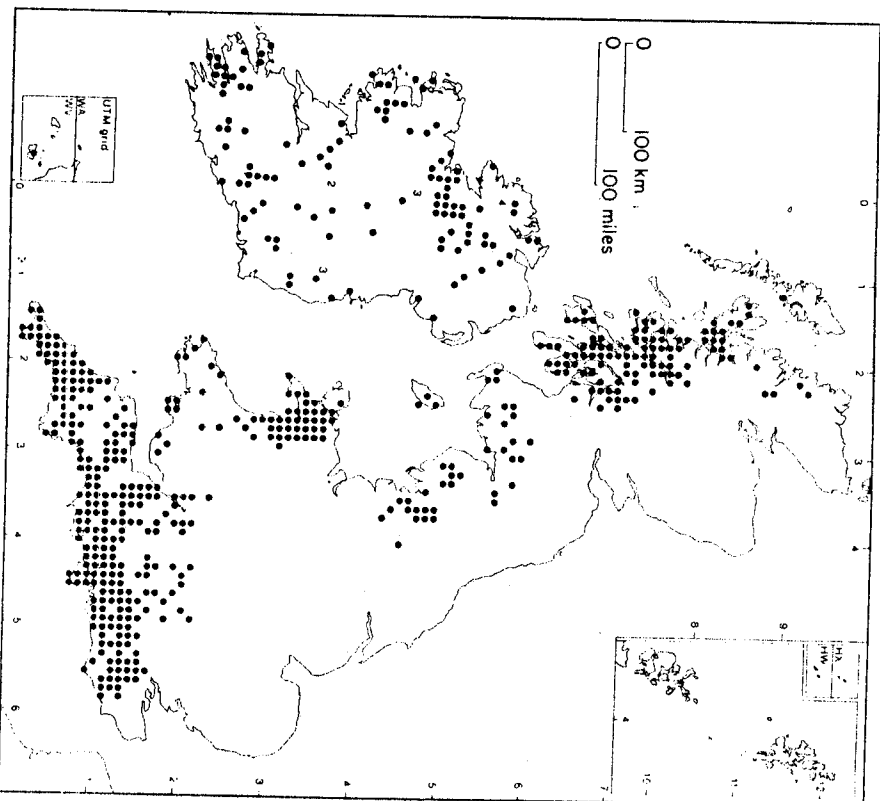


Fig. 7.2 Distribution map of *Lejeunea ulicina* in Britain. This species is intolerant of atmospheric pollution (prevailing winds are from the south-west). Reproduced from Smith (1978).

have been few studies on succession or the dynamics of epilithic communities but in recent years there have been some detailed investigations into the factors affecting the distribution and frequency of rock species, for example by Bates (1975, 1978), Nagano (1969, 1972) and Yarranton (1967a,b,c,d), although the efforts of this last author mainly centre round statistical methodology.

As pointed out by Gams (1932) species growing on rock may be obligate or facultative epiliths. Examples of the former are *Tortella* and

*Gymnosorium* spp. (including *Hymenostylium*), almost all members of the *Grimmiaceae*, *Seligeria* and *Blindia* spp., *Orthotrichum anomalum*, *O. cupulatum*, *O. rupestre*, *Uloa hutchinsiae*, *Gymnomitron crenulatum*, *Porella thuja*, *Marchesia mackaii* and *Frullania microphylla*. These species are only very rarely found on any other substrates and when this does occur may be of sufficient interest to merit note (e.g. Duncan, 1965). There are numerous examples of facultative epiliths, such as *Dicranum* spp., *Tortella tortuosa*, *Bryum capillare*, *Thamnobryum alopecurum*, *Heterocladium heteropterum*, species of *Isoetecium*, *Brachythecium*, *Eurhynchium*, and *Rhynchostegium*, *Homalothecium sericeum*, *Hypnum cupressiforme* s.l., *Conocephalum conicum*, *Metzgeria* and *Plagiochila* spp., *Diplophyllum albicans*, *Scapania nemorosa*, *S. gracilis*, *Porella platyphylla*, *Frullania* spp. and some Lejeuneaceae.

#### 7.4.1 Epilithic communities

Workers have attempted to describe and classify communities on the basis of species composition and to elucidate the importance of environmental factors in the distribution of epiliths. Rock communities have been defined on the basis of the most common or constant species. Thus, several saxicolous communities are dominated by members of the *Grimmiaceae* (Gams, 1932). European examples of these are the *Drypodontium hartmanni* (= *Grimmietum hartmannii*) of dry shady siliceous rocks in forest regions, the *Grimmietum elaiorisi* from similar but moister habitats, the *Grimmietum ovalis* (= *G. commutatae*) and *Grimmietum laevigatae* (= *G. campestris*) from dry sunny siliceous rocks, the *Schistidium apocarpum* from less dry and less acid rocks and the *Grimmietum orbicularis* from dry sunny limestone rocks. Other examples of associations are the *Diplophyllum albicans*, containing many leafy liverworts and sometimes *Hymenophyllum* in oceanic parts of Europe and the *Conocephalium* (= *Fagaelleium*).

Whilst some of these communities such as the *Grimmietum laevigatae* (e.g. from south-eastern USA), the *G. orbicularis* (e.g. from limestone outcrops in north-west Wales) and the *Diplophyllum albicans* (e.g. from western Britain and Ireland) are readily recognizable, these associations have been based on subjective assessments of species frequencies and are only applicable where there are clear-cut discontinuities between associations. On a wider geographical basis, there may be sufficient similarities between certain communities to arouse comment. Thus, apline communities dominated by *Andraea rupestris* and *Racomitrium* and *Grimmia* spp. in Japan (Horikawa *et al.*, 1961) correspond very closely with those described from montane parts of Germany (Hübschmann, 1955).

In many areas, objective assessments of species associations using

random sampling techniques and statistical analyses indicate that there are continua rather than distinct species groupings and that these can be related to environmental gradients, factors that may be overlooked in subjective studies. Also, it may be misleading to compare communities from different geographical areas, at least without details of the micro-environmental data, as species habitat requirements may vary from region to region. Two extreme examples illustrate this. *Polytrichum commune* is apparently a xeric epilith in the USA but a plant of wet peaty habitats in Europe; *Scapania undulata* occurs on dry sandstone in Illinois, USA (Stotler, 1976), but is a plant of submerged or flushed rocks in Europe.

There are a number of examples which indicate the differences in the structure of the communities and of the gradation between one association and another within communities. On different sandstone exposures in two canyons in southern Illinois (Stotler, 1976; West and Stotler, 1977) aspect and moisture are important micro-environmental factors affecting species distribution. The importance value (Greig-Smith, 1964) of *Conocephalum conicum* at the lowest levels is 17.12 and it is the most important element (i.e. the community is a *Conocephalium* to use Gams' (1932) terminology), whilst at the highest levels on the sandstone it is twenty-seventh in importance with a value of 1.44. Presumably, with increasing height the importance value of *Conocephalum* drops from 17.12 to 1.44 making difficult any attempt to define any part of the community as a *Conocephalium* unless arbitrary divisions of the habitat are used.

Other areas that provide examples of the continuum between associations or degree of frequency of species are the bryophyte-macrolichen communities on Old Red Sandstone outcrops on Cape Clear Island, southern Ireland (Bates, 1975) and on limestone outcrops in the driftless area of Wisconsin, USA (Footo, 1966). On Cape Clear Island the most maritime communities, dominated by *Schistidium maritimum* and *Uloa phyllantha*, grade into the least maritime communities where the predominant species are *Grimmia trichophylla*, *Hypnum cupressiforme* var. *resupinatum* and *Isoetecium myosuroides*. There are no clear-cut species associations.

On the limestone in Wisconsin, 103 bryophyte and macrolichen species were recorded in random quadrats (Footo, 1966), mostly infrequent, but 12, including *Schistidium apocarpum*, occurred in most habitats so that the cryptogamic vegetation could only be considered a single community. Many of the other species were limited to particular ecological niches and earlier workers in the area had recognized distinct associations. Because the frequency and cover of species varies in different stands, the naming of associations varied with each previous worker. With the continuous nature of the variation when the vegetation is analysed on a larger random scale it is not possible to delimit associations. This is in contrast with the limestone

associations delimited in Germany (Klement, 1950, 1959), Poland (Motyka, 1925) and Golland, Sweden (Du Rietz, 1925). Some of the European associations correspond with some of the stands on the Wisconsin limestone, but it seems likely that with larger scale and less subjective techniques of sampling and data analysis continuous variation or at least some degree of intergradation between associations would be found.

#### 7.4.2 Establishment and succession

There is no definite information on the mode of establishment of saxicolous species but it is evident from field observation and experiment that colonization of virgin rock may be by spores or by vegetative fragments.

The Icelandic island of Surtsey first appeared off the coast of Iceland as the result of a volcanic eruption in November 1963 and the first bryophytes, *Funaria hygrometrica* and *Bryum argenteum*, were discovered on a sand-bank in August 1967 (Fridriksson, 1975). The first saxicolous species, *Pogonatum urnigerum* and *Racomitrium canescens* were found in 1969 and by 1972 there were at least 17 species, several of them obligate epiliths, on the island. These plants could only have arrived on Surtsey as wind-blown spores. The spread of some of these, especially members of the *Grimmiaceae*, was extremely rapid. In 1971, *Schistidium stricum* was known from only one site, in 1972 it was the fifth commonest bryophyte; *Schistidium apocarpum* in 1971 was known from only two quadrats, in 1972 it inhabited 31 quadrats. Both these species fruit freely and their rapid dispersal could well be by spores.

On exposed granite rock in North Carolina, USA, *Grimmia laevigata* is very common, forming coalescing patches, but fruits very rarely. In the laboratory (Keever, 1957) shoots and portions of shoots produced protonemata which adhered firmly to both hard and soft granite fragments and gave rise to new leafy shoots. Once developed, drying enhanced the adherence of the protonemata to the rock. From experiments it was evident that most favourable conditions for establishment of fragments are under a regime of wetting every four or five days (by rain or dew) for three weeks during cool weather followed by a period of dry sunny weather. It is likely that in nature fragments of *Grimmia laevigata* may be caught in irregularities of the surface of the granite and, assuming the conditions approximate to those above, give rise to new plants. It is also possible, on the basis of laboratory observations, that *Orhoriichum anomalum* becomes established in a similar fashion (Johnsen, 1969). It is unlikely in the case of the *Grimmia* that establishment is from spores in view of the rarity of fruiting.

It is usually assumed that lichens are the first colonizers of bare rock. On Surtsey (Fridriksson, 1975) the first saxicolous mosses appeared in 1969,

the first lichens did not appear until 1970 although lichens are the first colonizers of lava flows on Iceland itself, especially at high altitudes. Even where they are the first colonizers it is unlikely that such lichens play any further part in the subsequent succession. This is partly because of the extremely slow growth of crustose lichens and partly due to their life-form. Over a period of 17 years, there was no detectable growth in crustose lichens on rock at Isle Royale, Lake Superior, USA (Cooper, 1928). In North Carolina, *Grimmia laevigata* at low altitudes and *Andreaea rothii* and *Racomitrium geterositichum* at high altitudes are thought to be the first effective colonizers (Oosting and Anderson, 1937, 1939; Keever *et al.*, 1951). The reason for this is that the early lichens accumulate negligible quantities of soil particles, unlike mosses. *Grimmia laevigata*, for example, accumulating debris to the extent that only the tips of the tufts protrude. The *Grimmia* mats are successively invaded by stages dominated by (1) *Cladonia-Selaginella*, (2) *Polyptrichum ohioense*, (3) *Andropogon* and (4) conifers (Oosting and Anderson, 1939). The *Grimmia* forms more or less circular mats (Keever *et al.*, 1951) on which later stages in the succession develop in concentric rings of the different species, successive rings being made of plants requiring more soil and moisture, with most recent invaders nearest the centre.

Although *Grimmia laevigata* is the most important pioneer species on the granite in the south-eastern United States, *Grimmia pilifera* (Keever *et al.*, 1951), *G. oheyi* and *Hedwigia ciliata* (McVaugh, 1943) may also play a role. In Texas, where the climate is hotter and drier, *Grimmia laevigata* appears to be the only moss species that is a primary colonizer (Whitehouse, 1933). At altitudes of 1100–1170 m in North Carolina (Oosting and Anderson, 1937) the first colonizers are *Andreaea nypensis* and *Racomitrium microcarpon* and these are invaded by *Cladonia-Selaginella* and other mosses, then higher plants and, when mats reach sufficient size, woody plants. By contrast with both the low and the high altitude situation in North America, on Hawaii there is no evidence of cushion formation on lava flows (Jackson, 1971), angiosperms growing in rock crevices and mosses (*Racomitrium lanuginosum* and *Campylopus densifolius*) occurring on intervening rock surfaces.

On some rock habitats, especially where the surface is steeply sloping or vertical, bryophytes may form the climax community. On superficial examination these communities appear stable but if studied over a period of time it is evident that cyclic changes take place; further the behaviour of particular species with regard to recolonization varies with environmental conditions.

On shaded sandstone rocks in Sussex, England, (Paton, 1956) a cycle may be started by the falling away of thalloid mats of *Pellia epiphylla*, the loss of moss cushions or the death of *Tetraphis pellucida*. Primary

colonizers invading the spaces so left, such as small hepatics forming compact mats, are displaced by mosses and foliose lichens. On wet rocks there appears to be a cycle from bare rock to *Isoeterygium elegans* to the filmy fern *Hymenophyllum tunbrigense* or bare rock to *Dicranella heteromalla* and *Tetrarhis pellucida* to *Pellia epiphylla*. Loss of the mats so formed will start the cycle all over again. On drier rocks, the situation is more complex and, on dry rock for example, there seem to be at least four possible cycles. These are bare rock to (1) the lichen *Crocynia* to *Tetrarhis*, (2) *Isoeterygium myosuroides*, with or without an intermediate hepatic mat, to *Hymenophyllum*, (3) hepatic mat (*Cephalozia media*, *Lepidozia reptans*, *Lophocolea heterophylla*, *Odontoschisma denudatum*) to large hepatics (e.g. *Lophozia attenuata*, *Bazzania trilobata*) and/or moss cushions (e.g. *Mnium hornum*, *Dicranum scottianum*). (4) *Scapania gracilis*. The duration of the various cycles is unknown.

Table 7.9 shows the rate of colonization of 5 × 5 cm (approximately) quadrats scraped clear of vegetation within pure stands on rocks with varying degrees of moisture. That most species have their maximum recolonization rate on a particular rock type indicates the importance of micro-environmental factors, in these cases particularly, water. The rock

**Table 7.9** Rate of recolonization of denuded 5 × 5 cm quadrats on (a) wet rocks, (b) moist rocks and (c) dry boulders. Modified from Paton (1956f).

Species	Habitat	6 months	18 months	4½ years
<i>Cephalozia media</i>	(b)	Almost closed	—	—
	(c)	Present	Less than half-closed	—
	(a)	Almost closed	Closed	—
<i>Isoeterygium elegans</i>	(a)	Present	Half-closed	Closed
	(b)	Sometimes present	Present	Half-closed
	(c)	Present	Very scattered	—
<i>Lepidozia reptans</i>	(a)	Present	Almost closed	—
	(b)	Present	Less than half-closed	—
	(c)	Present	Closed	—
<i>Pellia epiphylla</i>	(a)	Almost closed	—	—
	(b)	Present	Half-closed	Scattered
	(c)	Present	Very scattered	—
<i>Tetrarhis pellucida</i>	(a)	Present	Young plants	—
	(b)	Present	Closed	—
	(c)	Present	Closed	—

types upon which a species shows the maximum rate of recolonization is also the rock type upon which the species is most abundant.

Brief observations on succession on boulders in a Killarney oakwood in Ireland (Richards, 1938) are of interest. There are two associates, the open boulder associate and the closed boulder associate. The former is characterized by the presence of *Diplophyllum albicans*, *Heterocladium heteropterum* var. *flaccidum* and *Sematophyllum micans*, the latter by *Hylacomium brevirostre*, *Rhytidadelphus loreus*, *Thuidium tamariscinum*, *Dicranum majus*, *Plagiothecium undulatum*, *Polyptrichum formosum* and *Hymenophyllum tunbrigense*. It appears that the open boulder associate is a stage in the succession to the closed boulder associate and there is an intermediate stage where there is a high frequency of *Plagiothecium undulatum*. The species of the open boulder associate tend to be small and adhere to the rock surface by means of rhizoids, hence are adapted as primary colonizers. The species of the closed associate form coarse wets which are easily detached, so starting a new cycle of associates.

#### 7.4.3 Life-forms

There is little published information on life-forms of saxicolous bryophytes. In exposed habitats, the predominant life-forms are small cushions and smooth and rough mats, in sheltered, humid or damp habitats, short and tall turfs, small and large cushions and various mat forms are important constituents. It is suggested by Gimmingham and Robertson (1950) that the life-form spectra within any one habitat type are essentially similar. They give as an illustration communities on montane siliceous and limestone boulders. Of the 31 and 28 species respectively recorded from the two types of boulder, there are only eight in common, although the life-form compositions are more or less similar. This lends support to the argument on pp. 194 and 198 that it is the life-form that is ecologically important.

Observations on siliceous and limestone boulders in the vicinity of Bangor (see Table 7.10) (Bartholomew, 1980), from habitats with essentially similar macroclimates, show that the life-form spectra are very different. It is likely that the differences in the life-forms are explicable in terms of the water-holding capacity of the rock, the limestone holding more water than the acidic rock. Other data in Table 7.10 indicate that the life-form spectra of rocks are very much influenced by environmental factors, especially light intensity and moisture or humidity. This is in keeping with the findings of Yarranton and Beasleigh (1968) who concluded that the distribution of species in limestone grikes was determined by microclimate as affected by the microtopography of the grikes. Gimmingham and Birse (1957) found that the zonation of life-forms on a partly shaded wall could be related to humidity and light intensity.

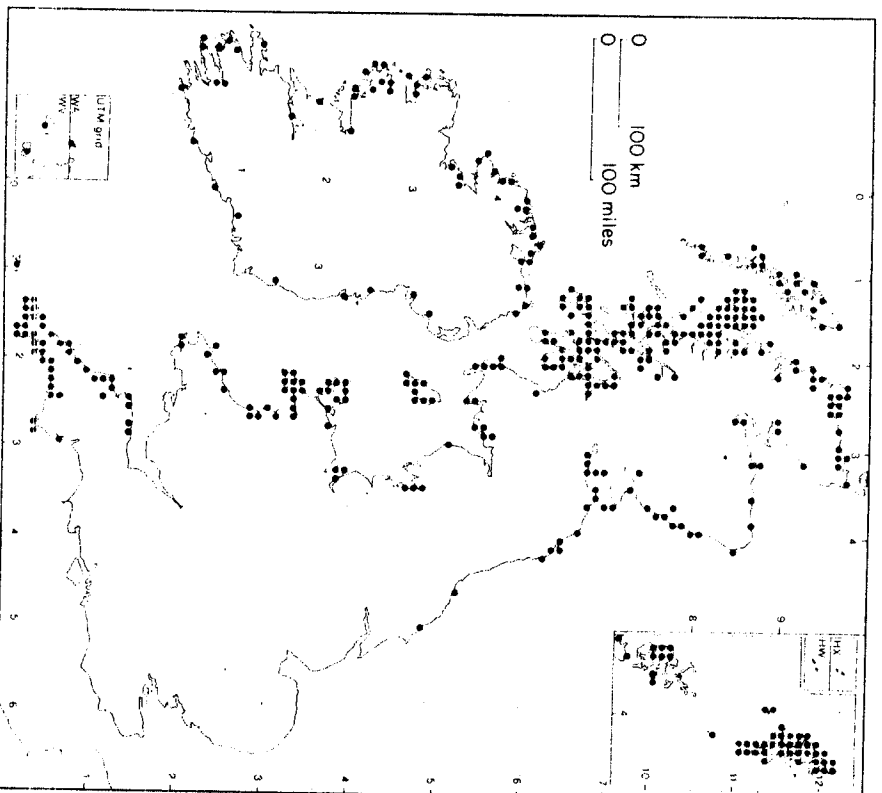
**Table 7.10** Proportions (% dry weight) of various life-forms from boulders in various types of habitat in the vicinity of Bangor, North Wales. Modified from Bartholomew (1980).

Life-form	Siliceous boulders in humid wood	Limestone boulders in humid wood	Siliceous boulders in woodland stream	Exposed, dry limestone boulders
Tall turfs	15	20	4	—
Rough mats	73	16	80	—
Smooth mats	4	—	11	46
Thread forms	2	18	—	—
Wetfs	6	—	—	—
Short turf	—	4	2	38
Dendroid	—	42	3	—
Small cushions	—	—	—	16
No. of species	16	10	12	12

#### 7.4.4 Influence of environmental factors

It is often extremely difficult to ascertain the precise effect of particular environmental factors either on the occurrence of individual species or on the structure of communities. Early attempts at determining the effects of environmental factors began with the work of Schade (1912) on saxicolous communities in German mountains but it is evident from recent work that there is no straightforward answer to problems of frequency and distribution. With some species it is evident that one ecological feature is of great significance in determining distribution, although whether it is that particular feature of the habitat that is significant or whether, in that habitat, competition is less severe for the species concerned is not clear. In the British Isles, for example, *Schistidium maritimum* is found only on acidic rocks within about 400 m of the shoreline (unless the substrate is a relic of a former shoreline); *Seligeria paucifolia*, except for one location in Northern Ireland is restricted to shaded chalk. Distribution maps of these species (Figs. 7.3 and 7.4) reflect very closely the distribution in Britain and Ireland of chalk and acidic maritime rocks.

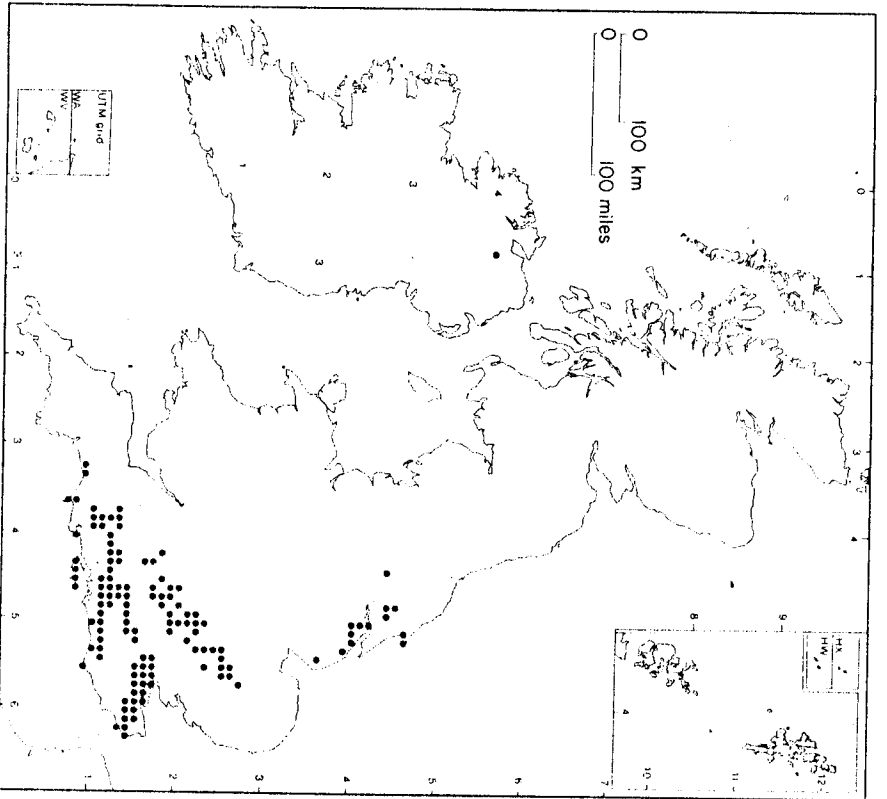
There are several examples of the complex interactions between micro-environmental and microclimatic factors from recent studies of epilithic communities. In limestone grikes (vertical fissures) near Kemble, Kettle township, Ontario, Canada, (Yarranton and Beasleigh, 1968) *Anomodon attenuatus*, *Brachythecium salebrosum*, *Schistidium apocarpum*, *Gymnosorium aeruginosum*, *Leskea nervosa*, *Thamnobryum alleghaniense*, and *Seligeria doniana* are all highly sensitive to width, depth and aspect of



**Fig. 7.3** Distribution map of *Schistidium maritimum*, a species of acidic maritime rocks in the British Isles. Reproduced from Smith (1978).

grikes. It seems, however, that microtopography does not affect the distribution of bryophytes directly, but that the chemical nature of the rock and the micrometeorology as affected by the microtopography are likely to be the controlling factors.

In the limestone bryophyte-macrolichen communities of southern Illinois, USA (Stotler, 1976; West and Stotler, 1977), about 50% of the species have restricted distributions, suggesting that micro-environmental conditions are important relative to species occurrence. On the limestone outcrops of the driftless area of Wisconsin (Foote, 1966) there is a moisture continuum; the frequency of each species of the bryophyte-macrolichen



7.4 Distribution map of *Seligeria paucifolia*, a species mainly of shaded chalk in the British Isles. Reproduced from Smith (1978).

community varies with moisture and frequencies of different species peak at different points along the moisture gradient.

On Cape Clear Island, southern Ireland, there is a continuum in the bryophyte-macrolichen community composition related to environmental conditions (Bates, 1975). The continuum is from the most maritime species, *Schistidium marinum* and *Ulotia phyllantha*, to the least maritime, *Grimmia trichophylla*, *Hypnum cupressiforme* var. *resupinatum* and *Isoetecium myosuroides*. Associated with damp rocks and sah spray are *Tortella flavovirens*, *Trichosomum brachydonium* and *Schistidium marinum* whilst *Ulotia phyllantha* occurs on drier rocks. Inland species fall

into two groups: associated with shelter and shaded sites are *Isoetecium myosuroides*, *Frullania germana*, *F. tamarisci*, *Plagiochila spinulosa* and *Scapania gracilis*; species of exposed sites are *Frullania dilatata*, *Grimmia trichophylla*, *Hedwigia ciliata*, *Hypnum cupressiforme* var. *resupinatum* and *Polyptrichum piliferum*. Neither of these, however, form discrete associations.

It has long been known that some bryophytes are calcicole, some calcifuge and some neutral and that the composition of saxicolous communities depends upon the chemical nature of the rocks but the precise reasons for the calcicole-calcifuge situation is obscure.

In the Chichibu Mountain area of Japan (Nagano, 1969, 1972) there are a number of different rock types including limestone, calcareous conglomerate, calcareous graywacke, blackslate and chert. At a number of sites some of these rock types abut and since, at any one locality, macro-environmental conditions are uniform, differences in the structure and composition of the bryophyte communities can be attributed to differences in the rock substrate upon which they grow. Such differences exist and are most marked between the limestone and the chert communities. The communities on calcareous conglomerate, calcareous graywacke and blackslate each have their own characteristics but show much greater affinities with the limestone associations than with the chert. Clearly, rock type has a marked effect on species composition of communities, although not necessarily on the life-form spectra. It is considered (Nagano, 1969) that the differences may be attributed to pH controlled by the quantities of calcium, silicon and sometimes aluminium in the substrate.

A similar example is provided by the different rock types on the Islands of Rhum and Skye off the west coast of Scotland (Bates, 1978). Rock types include Duress limestone, (calcareous sedimentary), Torridonian sandstone (acid sedimentary), basalt (basic igneous) and peridotite and allivahite (ultrabasic igneous). Table 7.11 shows the number of species common to the different rock types. The flora of the limestone is clearly

Table 7.11 Bryophyte and macrolichen taxa common to the four rock types on Skye and Rhum (the number of bryophyte species is in brackets). Only taxa for which there were more than five records in the 121 sample grids are included. From Bates, 1978.

	Duress limestone	Torridonian sandstone	Basalt	Ultrabasic rocks
Duress limestone	23(14)	1(1)	0	1(1)
Torridonian sandstone	1(1)	26(11)	19(10)	13(9)
Basalt	0	19(10)	24(14)	13(9)
Ultrabasic rocks	1(1)	13(9)	13(9)	22(12)

markedly different from those of the other rock types whereas the floras of the non-calcareous rocks have many species in common. Analyses of data suggest that it is the high availability of calcium that plays the predominant role in determining the species differences between the limestone and other rocks. There are some differences between the acid Torridonian sandstone and the basic non-calcareous igneous rocks but it is not considered likely that these are due to chemical differences in the rocks and it is also unlikely that the physical nature of the substrate is important.

In the bryophytes from Rhum and Skye, calcicole species had a calcium content 17 times that of species from non-calcareous rocks (Bates, 1978). In the Chichibu Mountains (Nagano, 1972) although the situation is not so extreme, calcicole species contained far more calcium than calcifuge ones. Thus, the calcicole *Torrella toruosa* contained 9 times as much calcium as the calcifuge *Barranliopsis lescurei*. In the Hebridean species, differences in iron and aluminium content are not related to amounts in the substrate rocks and similarly with quantities of nitrogen, magnesium, potassium and phosphorous in the Japanese species. It is evident that the distribution of calcicole and calcifuge species is determined by the high solubility of calcium in calcareous rocks. A possible reason for this is discussed in Chapter 11, pp. 414-17.

#### 7.4.5 Nutrition

Little is known about the nutrition of saxicolous bryophytes. Bates (1978) points out that the high iron and aluminium contents of *Andreea rohii* growing on Torridonian sandstone, which has low contents of these elements, suggests that they may come from external sources. Also the levels of potassium and phosphorus in bryophytes are remarkably constant and bear no relation to the levels in the substrate rock (Nagano, 1972; Shacklette, 1965). Bates (1978) suggests that the various elements may be derived from rain, dust, salt spray and animal excrement. He also observes that on ultrabasic rocks on Skye and Rhum bryophytes and lichens are often limited to the upper surface of boulders which may serve as bird perches and hence receive supplies from that source.

In the five commonest lichen and moss species that cover 80-90% of the bare granite rock surface of the Piedmont Plateau in Georgia, USA (Snyder and Wullstein, 1973), nitrogen fixation by *Azotobacter* is greater in *Grimmia laevigata* than in the four lichen species. This is probably because the bacteria are associated with soil particles trapped in the moss tufts. It is not possible to quantify the nitrogen fixation by soil bacteria in mosses but the activity of *Azotobacter* in such mosses may well contribute to the nitrogen pool of the communities concerned.

#### 7.5 CONCLUSIONS

Most of the studies of epiphytic and epilithic bryophytes have been carried out in temperate regions, but even these present a picture more of what is not known than what is, especially with regard to epiliths. Most emphasis has been placed on phytosociological studies, relatively little on the life-form in relation to habitat and the significance of micro-environmental factors in determining occurrence and frequency of species. Many of the conclusions concerning the latter point are speculative and require experimental confirmation. Modern quantitative techniques have proved valuable in suggesting the possible significance of various environmental features (e.g. Bates, 1975, 1978; Yarranton, 1967a-d; Yarranton and Beasley, 1968) and these are likely to prove of similar value with respect to epiphytes.

#### REFERENCES

- Barkman, J.J. (1958). *Phytosociology and Ecology of Cryptogamic Epiphytes*. Assen.
- Bartholomew, F.P. (1980). *Some observations on the relationship between bryophyte community structure and environment in north-west Wales*. MSc. Thesis, Univ. Wales.
- Bates, J.W. (1975). *J. Ecol.*, **63**, 143-62.
- Bates, J.W. (1978). *J. Ecol.*, **66**, 457-82.
- Beals, W. (1965). *Oikos*, **16**, 1-8.
- Billings, W.D. and Drew, W.B. (1938). *Am. Midl. Nat.*, **20**, 302-30.
- Coleman, B.B., Muehsner, W.C. and Charles, D.R. (1956). *Am. Midl. Nat.*, **56**, 54-87.
- Cooper, W.S. (1928). *Ecology*, **9**, 1-5.
- Cuberson, W.L. (1955). *Ecol. Monogr.*, **25**, 215-31.
- Duncan, U.K. (1965). *Trans. Br. Bryol. Soc.*, **4**, 828.
- Du Rietz, G.E. (1925). *Svensk Växsvoc. Sullis Handl.*, **2**, 1-65.
- Engle, M.J. (1960). *Bryologist*, **63**, 238-41.
- Foote, K.G. (1966). *Bryologist*, **69**, 265-72.
- Fridriksson, S. (1975). *Sursey: Evolution of Life on a Volcanic Island*. Butterworth, London.
- Gams, H. (1932). In: *Manual of Bryology* (Verdoon, F., ed.), pp. 323-66. The Hague.
- Gimingham, C.H. and Birse, E.M. (1957). *J. Ecol.*, **45**, 533-45.
- Gimingham, C.H. and Robertson, E.T. (1950). *Trans. Br. Bryol. Soc.*, **1**, 330-44.
- Gough, L.P. (1975). *Bryologist*, **78**, 124-45.
- Grebe, F.C. (1911). *Festschr. Vereins f. Naturkunde zu Cassel*, **1911**, 195-258, 259-83.
- Greig-Smith, P. (1964). *Quantitative Plant Ecology*. Butterworth, London.
- Grubb, P.J., Flint, O.P. and Gregory, S.C. (1969). *Trans. Br. Bryol. Soc.*, **5**, 802-17.
- Hale, M.E. (1952). *Ecology*, **33**, 398-406.

- Hale, M.E. (1955). *Ecology*, **36**, 45-63.
- Hoffman, G.R. (1971). *Bryologist*, **74**, 413-27.
- Hoffman, G.R. and Boe, A.A. (1977). *Bryologist*, **80**, 32-47.
- Hoffman, G.R. and Kazmierski, R.G. (1969). *Bryologist*, **72**, 1-19.
- Horiikawa, Y., Ando, H. and Kawai, I. (1961). *Ecological Studies of Hakusan Quasi-National Park*. Tokyo.
- Horiikawa, Y. and Nakanishi, S. (1954). *Bull. Pl. Ecol. (Jap.)*, **3**, 203-10.
- Hosokawa, T. and Kubota, H. (1957). *J. Ecol.*, **45**, 579-91.
- Hosokawa, T. and Odani, N. (1957). *J. Ecol.*, **45**, 901-5.
- Hosokawa, T., Odani, N. and Tagawa, H. (1964). *Bryologist*, **67**, 396-411.
- Hosokawa, T. and Omura, M. (1959). *Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.)*, **3**, 43-50.
- Hübschmann, A. von (1955). *Mit. For.-soz. Arbeitsgem N.F.*, **5**, 50-7.
- Iwatsuki, Z. (1960). *J. Hattori bot. Lab.*, **22**, 159-350.
- Iwatsuki, Z. and Hattori, S. (1956). *J. Hattori bot. Lab.*, **16**, 106-116.
- Iwatsuki, Z. and Hattori, S. (1966). *J. Hattori bot. Lab.*, **29**, 223-37.
- Iwatsuki, Z. and Hattori, S. (1970). *Mem. Nat. Sci. Mus., Tokyo*, **3**, 365-74.
- Jackson, T.A. (1971). *Pacif. Sci.*, **25**, 22-32.
- Jacobsen, N.H.G. (1978). *Jl. S. Afr. Bot.*, **44**, 297-312.
- Johnsen, A.S. (1969). *Bryologist*, **72**, 397-403.
- Johnson, J. and Sächting, W. (1976). *Bryologist*, **79**, 86-92.
- Jones, E.W. (1959). *Trans. Br. Bryol. Soc.*, **4**, 611-12.
- Keever, C. (1957). *Ecology*, **38**, 422-9.
- Keever, C., Oosting, H.J. and Anderson, L.E. (1951). *Bull. Torrey Bot. Club*, **78**, 401-21.
- Klement, O. (1950). *Ber. Bayer. Bot. Gesell.*, **28**, 1-26.
- Klement, O. (1959). *Dreheriana*, **7**, 5-56.
- LeBlanc, F. (1963). *Can. J. Bot.*, **41**, 591-638.
- Martin, N.M. (1938). *J. Ecol.*, **26**, 82-95.
- McVaugh, R. (1943). *Ecol. Monogr.*, **13**, 121-66.
- Miyata, J. and Hosokawa, T. (1961). *Ecology*, **42**, 766-75.
- Miokendo, L. (1865). *Jahresber. Naturhist. Verein Augsburg*.
- Miotsuka, J. (1925). *Bull. Acad. Bot. Sci. Lett.*, **B 1924**, 835-50.
- Nagano, I. (1969). *J. Hattori bot. Lab.*, **32**, 155-203.
- Nagano, I. (1972). *J. Hattori bot. Lab.*, **35**, 391-8.
- Nakanishi, S. (1966). *Jap. J. Bot.*, **19**, 231-54.
- Olsen, C. (1917). *Bot. Tidsskr.*, **34**, 313-42.
- Omura, M. and Hosokawa, T. (1959). *Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.)*, **3**, 51-63.
- Omura, M., Nishikawa, Y. and Hosokawa, T. (1955). *Rev. bryol. lichenol.*, **24**, 50-68.
- Oosting, H.J. and Anderson, L.E. (1939). *Bot. Gaz.*, **100**, 750-68.
- Paton, J.A. (1956). *Trans. Br. Bryol. Soc.*, **3**, 103-14.
- Patterson, P.M. (1953). *Bryologist*, **56**, 157-9.
- Pfeffer, W. (1871). *Neue Denkschr. der allgem. Schweizer Ges.*, **24**, 1-42.
- Phillips, E.A. (1951). *Ecol. Monogr.*, **21**, 301-16.
- Pike, L.H., Denison, W.C., Tracy, D.M., Sherwood, M.A. and Rhoades, F.M. (1975). *Bryologist*, **78**, 389-402.

- Pike, L.H., Rydell, R.A. and Denison, W.C. (1977). *Can. J. For. Res.*, **7**, 680-99.
- Pike, L.H., Tracy, D.M., Sherwood, M.A. and Nielson, D. (1972). In: *Research on Coniferous Forest Ecosystems* (Franklin, J.F., Dempster, L.J. and Waring, R.H., eds), pp. 177-187. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Pitkin, P.H. (1973a). *J. Bryol.*, **7**, 522-3.
- Pitkin, P.H. (1973b). *Aspects of the Ecology and Distribution of some Widespread Corticolous Bryophytes*. D.Phil. thesis, Univ. Oxford.
- Pitkin, P.H. (1975). *J. Bryol.*, **8**, 337-56.
- Rasmussen, L. (1975). *Lindbergetia*, **3**, 15-38.
- Rasmussen, L. and Herring, J. (1977). *Rev. bryol. lichenol.*, **43**, 207-17.
- Rasmussen, L. and Johnson, I. (1976). *Oikos*, **27**, 483-7.
- Richards, P.W. (1938). *Ann. Bryol.*, **11**, 108-30.
- Schade, F.A. (1912). *Bot. Jahrb.*, **48**, 19.
- Shacklette, H.T. (1965). *U.S. Geog. Surv. Bull.*, **1189-D**, 1-21.
- Simon, T. (1974). *Acta Bot. Acad. Sci. Hung.*, **20**, 241-8.
- Sjögren, E. (1961). *Acta phytogeog. succ.*, **48**, 1-149.
- Slack, N.G. (1975). *XIII Int. Bot. Congr. Absir.*, Leningrad, **1**, 87.
- Slack, N.G. (1976). *J. Hattori bot. Lab.*, **41**, 107-32.
- Slack, N.G. (1977). *Bull. N.Y. St. Mus. Sci. Surv.*, **428**, 1-70.
- Smith, A.J.E., ed. (1978). *Provisional Atlas of the Bryophytes of the British Isles*. Natural Environmental Research Council, London.
- Snyder, J.M. and Wulstein, L.H. (1973). *Bryologist*, **76**, 196-9.
- Staxang, S. (1969). *Oikos*, **20**, 224-30.
- Stotler, R.E. (1976). *Bryologist*, **79**, 1-15.
- Syratt, W.J. and Wanstall, P.J. (1968). In: *Air Pollution: Proc. First European Congress on the Influence of Air Pollution on Plants and Animals*, pp. 79-85. Tagawa, H. (1959). *Jap. J. Ecol.*, **9**, 178-84.
- Tobiasen, P.L., Mott, K.A. and Slack, N.G. (1978). *Bryophytorum Biblioth.*, **13**, 253-77.
- West, V. and Stotler, R.E. (1977). *Bryologist*, **80**, 612-18.
- Whitehouse, E. (1933). *Ecology*, **14**, 391-405.
- Yarranton, G.A. (1967a). *Lichenologist*, **3**, 392-408.
- Yarranton, G.A. (1967b). *Can. J. Bot.*, **45**, 93-115.
- Yarranton, G.A. (1967c). *Can. J. Bot.*, **45**, 229-47.
- Yarranton, G.A. (1967d). *Can. J. Bot.*, **45**, 249-58.
- Yarranton, G.A. and Beasleigh, W.J. (1968). *Can. J. Bot.*, **46**, 1591-9.