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THE ROLE OF REPRODUCTION FOR PERSISTENCE OF BRYOPHYTE POPULATIONS IN TRANSIENT AND STABLE HABITATS

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ABSTRACT. Many bryophytes occur in habitats which are of limited size and duration. Consequently, a bryophyte population shows dynamics at two levels: within-habitat and between-habitat. Whereas vegetative growth and competition are primary processes at the within-habitat level, reproductive processes (including dispersal by gemmae) are crucial for the between-habitat level. Simulation studies show that knowledge of parameters of the habitat (habitat size and duration, mean distance between habitats, spatial arrangement and number of habitats) is indispensable for assessment of the role of reproduction in bryophytes. Information on these parameters is largely missing. An analysis of the British moss flora showed a strong relationship between frequency of propagule formation and habitat; mosses in small (or less contiguous) and unstable habitats show more frequent propagule formation. Without a detailed knowledge on remaining parameters of species biology and habitat, these relationships are difficult to interpret.

The method of persistence of a species is important also in evolutionary considerations. Life strategies in bryophytes are syndromes of interrelated adaptations to different habitats. These relationships to the habitat (both at within patch and between patch levels) form an intriguing subject for the study in evolution of bryophytes.

INTRODUCTION

Bryophytes typically occur in habitats which are both transient (limited in time) and patchy (limited in space). For example, more than half of the British mosses occur in habitats with a duration of several years or decades (Table 1). In contrast to vascular plants, this temporal and spatial limitation is a very conspicuous feature of the habitats occupied by bryophytes, and it is by no means limited to the fragmentation of the landscape due to human activity. The persistence of a bryophyte species in such environments is dependent on its ability to find a suitable habitat by successful dispersal, either in space (by dispersal) or in time (by dormancy). In such situations dispersal has an important stabilizing role for the population (Levin 1976) and may allow the species to benefit from habitat instability (Kuno 1981). Dispersal is attained by various means in different species (During 1992); a critical role in this process is played by reproduction by spores, gemmae or gametophyte fragments. Recently, much attention was paid to the question of the role of individual processes in bryophyte reproduction through spores (Miles & Longton 1992a, Söderström this volume). Such studies generally attempted to answer the question 'What is the potential of a given reproductive process?'. Though these studies have provided data completely unavail-

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able until now, the data should be evaluated against information on all other processes involved in the persistence of a given bryophyte population.

This paper aims to examine the potential of the reproductive processes in comparison to other population parameters. It attempts to answer the question 'What is the minimum level of reproduction by spores required to be ecologically effective in a given environment?'

DYNAMICS OF BRYOPHYTE METAPOPULATIONS

Owing to the spatial and temporal limitation of bryophyte habitats, the spatiotemporal dynamics of a bryophyte population takes place at (at least) two levels: (1) level of a habitat patch, and (2) level of a landscape (set of habitat patches). At each of these levels, there are specific processes of population dynamics each with its own parameters; i.e. vegetative growth, competition and mortality at the within habitat patch level, and propagule formation, dispersal and establishment at the landscape (between,habitat patch) level. These parameters differ widely between bryophyte species (During 1979, 1992) and in combination have been described as life strategies. The success of a bryophyte population can also be measured at these two levels, i.e. using the size of population in the occupied patches (at the within habitat level) and using proportion of habitat patches which are occupied by the species (at the landscape level; see Söderström 1988).

The dynamics of bryophyte populations are therefore well described using the metapopulation approach (Hanski 1989). Though analysis of such systems is more complex than classic population dynamics, there are techniques available. The simplest approach is the Levins's equation (Levins 1969, Hanski 1982)

$$dp/dt = mp(1-p) - ep,$$

where p is proportion of colonized habitat patches, m is colonization rate, e is extinction rate, and t is time. In this model, m is a parameter of the species, whereas e describes features of both species and habitat. However, models of this type do not take into account the processes at the within-patch level, whose dynamics may strongly interact with that at the between-patch level (Hanski 1982). Further, the spatial arrangement of the habitat patches has to be treated only implicitly, which excludes studying the importance of propagule transport. More complex models, which take both these effects into account, are generally solvable only through simulation. Though building and simulation of such models is rather easy, their behaviour may differ widely at different parameter levels, which makes generalization from the results difficult.

At any rate, these models invariably show that the survival of a species depends on the relationship between parameters of species biology and of habitat. Parameters of the habitat primarily involve mean habitat patch size and duration, the number of patches, their mean distance and their spatial arrangement. These parameters provide the context for the parameters of species biology. If there are enough data on species biology, and on the habitat parameters, models of this type permit assessment of the minimum necessary level of dispersal assuring the persistence of a given species under

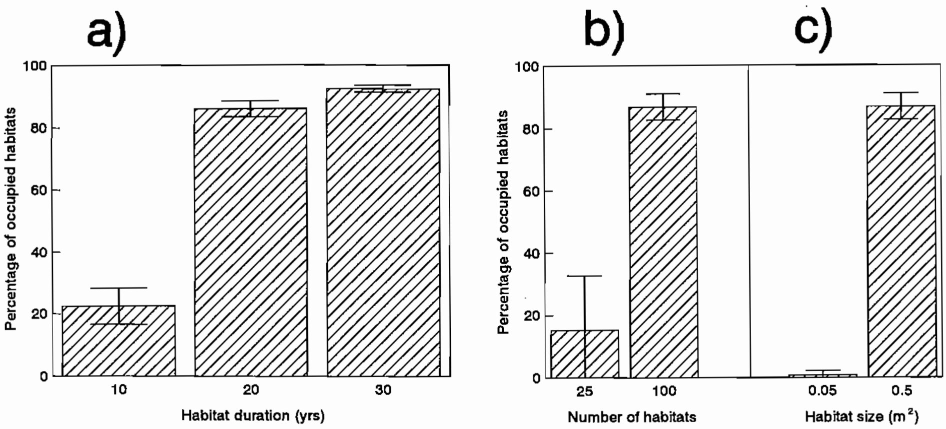

Fig. 1. Effect of habitat duration (a), number of habitat patches, (b) habitat size and (c) on proportion of habitats occupied by a species. Results from a simulation model of Herben, Rydin & Söderström (1991) with following parameters (unless indicated differently in the plot): species biology parameters: annual spore production $3.4 \cdot 10^5$ per subpopulation of maximum size, time needed to occupy available patch 4 years, dispersal 95% spores within 1 m radius, probability of a spore to establish given it reaches the habitat 10^{-6} (a, c) and 10^{-3} (b); habitat parameters: mean distance between habitats 1.46 m, habitat duration 20 yrs, habitat size 0.05 m^2. Note that within each histogram the species has identical biological parameters; only parameters of the habitat change.

Table 1. Proportion of British moss flora occurring in selected habitats/substrates. Data compiled from Smith (1978). Species occurring in several habitats contribute towards the percentages for several habitats in the left-hand column. Cases where a species occurs in a habitat "rarely" (Smith 1978) are excluded.

Habitat/Substrate	Percentage of the flora occurring there	Percentage of the flora occurring only there
Animal excrements	0.9	0.9
Arable fields, dried pond bottoms	4.9	
Bare soil	42.1	21.6
Bogs	5.2	1.6
Epiphyte	7.4	4.4
Forest floor	3.8	0.3
Grasslands	3.6	0.6
Heathlands & moors	13.8	5.4
Rocks	46.9	27.4
Rotting wood	8.7	1.2

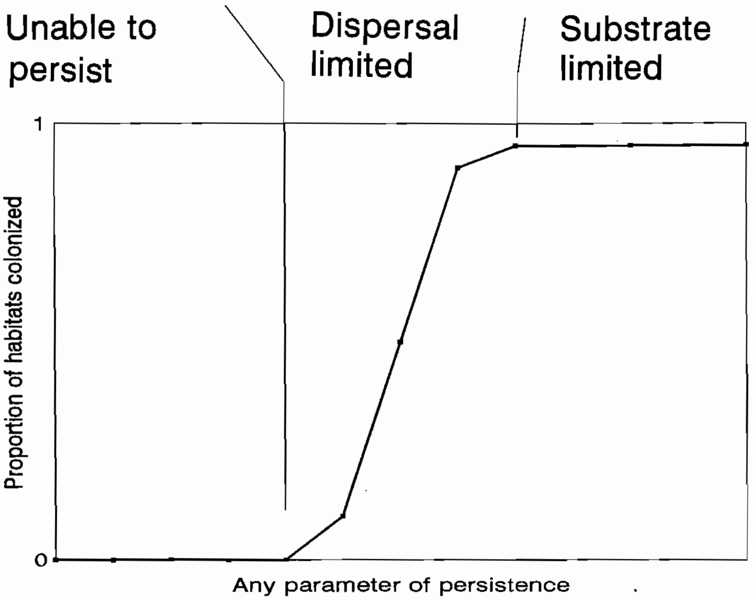

Fig. 2. Different modes of species persistence in an array of temporary habitats. In the dispersal limited area the occupation of habitat patches is not complete since the reproduction/dispersal/establishment processes do not compensate fully for the habitat loss. In the substrate limited area the dispersal is so efficient that the number of occurrences is limited by number of habitats. Redrawn from Herben & Söderström (1992).

a certain combination of habitat parameters.

Sensitivity analysis (i.e. the study of the response of the model predictions to changes in the value of one parameter) could be also used to estimate which parameter of bryophyte reproduction is most critical in determining persistence. Even small changes in habitat parameters could produce dramatic effects (Fig. 1). Further, the parameters of the habitat influence the persistence of a species in much the same way as do parameters of the species biology (Herben, Rydin & Söderström 1991). If a given dispersal or habitat parameter is high (i.e. dispersal capacity exceeds habitat dynamics), the species will colonize all available habitats and its frequency in a given landscape will be limited only by the number of available habitats. In contrast, if the given parameter is low, the species will not be able to colonize all available habitats and will persist only at a proportion of them (Fig. 2). In the first case the species is limited by number of habitats, and in the second by efficiency of the dispersal processes. Only in the second case does reproduction become limiting for species persistence. Sensitivity analysis shows that the latter state is much more sensitive to change in habitat parameters than the former.

AVAILABLE DATA ON BRYOPHYTE BIOLOGY

Population processes within the habitat patch involve growth of gametophores, interspecific competition and mortality. There is much information on these processes available for many species, coming mainly from permanent plot studies (e.g. van Tooren & During 1988). Indirect information is also provided by studies of succession (Longton 1992b).

Population processes between habitat patches involve the production of spores and other propagules, followed by their dispersal and establishment. These processes are directly related to sexual or asexual reproduction, which thus should be viewed as a critical process in assuring the survival of a species in a landscape. The information available on these processes is rather limited and, with the exception of data on spore dispersal, it cannot be drawn from studies on other fields of bryology.

Spore production is most often estimated on a per capsule basis; the use of this information is inherently limited since only spore production per area of bryophyte cover has an ecological meaning (Miles & Longton 1992a). Ecologically the most meaningful concept is the spore production per subpopulation of an ecologically defined size (e.g. maximum size attainable on a tree trunk for an epiphytic species); this indicates also how the within habitat and between habitat parameters are related. Available data on spore dispersal indicate platycurtic (i.e. with heavy tails) spatial distribution of spores, with an important proportion of spores spreading to large distances (Kimmerer 1991, Miles & Longton 1987, 1992b, Stoneburner et al. 1992). The dispersal of gemmae is generally much more short range (Kimmerer 1991, Equihua 1987). Available experimental data on spore establishment indicate that the importance of this process in species establishment varies very much among species. In some species the spore establishment seems to occur regularly (*Funaria hygrometrica*), whereas in others no such occurrence was observed (*Polytrichum strictum*: Miles & Longton 1992a).

AVAILABLE DATA ON DYNAMICS AND STRUCTURE OF BRYOPHYTE HABITATS

Mean duration of a habitat patch

Not surprisingly, this parameter depends very much on the substrate type. There are indirect data about specific substrates, such as rotten logs, tree trunks, leaves, arable land, animal excrements, dried pond bottoms (Tables 2, 3), but this information is rarely provided explicitly in studies on bryophyte ecology. There is also no review available. The habitat may have its own complex spatiotemporal dynamics (as on rotting logs or living trees), which itself could also be decribed using demographic terms (Söderström 1988). Studies of habitat patch structure are hindered by the inherent difficulty of identifying unoccupied, but available patches. This could be overcome by long term studies of bryophyte dynamics at a landscape level, but such studies are rarely done. Some information can, however, be extracted from conservation studies,, where old localities are visited again (e.g. Hallingbäck 1992). In many cases, the duration of a bryophyte habitat (i.e. the duration of its availability for the

Table 2. Duration of selected bryophyte habitats(not related to succession).

Duration (yrs)	Habitat	Source
0.5–2	Arable fields, dried bottoms	
0–2	Riparian habitats	Kimmerer & Allen 1982
2–5	Animal excrements	Marino 1991
3–5	Animal excrements	Lloret 1991
5–20	Sandstone rocks	Pujmanová & Herben unpubl.
30	Logs	Stefureac 1969
≥30	Logs	Frey 1959
21(–174)	Logs	Jonsson & Esseen 1990
50	Coniferous phorophytes	Liu & Hytteborn 1989, Hytteborn & Packham 1987
150–225	*Cedrus* and *Quercus* trunks	Tewari et al. 1985
20–500	Temperate grasslands	
≥100	Boreal forest floor	
≥100	Heaths & moors	
>5000	Peat bogs	

Table 3. Duration of selected bryophyte habitats in terms of the succession rate (rate of species replacement).

Rate	Community	Source
6–7 cm/yr	*Sphagnum* (peat bog)	Rydin 1986
3.25% cover/yr	*Leucobryum glaucum* (rock)	Paton 1956
11% cover/yr	*Hypnum cupressiforme* (rock)	Paton 1956
>50% Sörensen/time from sapling to mature tree	Epiphytes	Studlar 1982
25–30% Sörensen/3–4 months	Chalk grassland	van Tooren & During 1988
50–80% cover/4 yrs	Sandstone communities	Herben unpubl.
~100%/duration of log decomposition	Boreal forest	Söderstrom 1988
~100%/several yrs	Bare soil	Jahns 1982

bryophyte) is dependent on the rate of succession within the community since a given bryophyte species can occur only at a certain successional stage. In these cases much information can be extracted from the studies of bryophyte succession. In contrast to the shortlived habitats considered above, only minimal information is available for habitats which are more persistent and where bryophytes coexist with vascular plants (peat bogs, grasslands, heathlands, forest floor). Some data can be taken from forest succession/regeneration studies, studies on the *Calluna* cycle etc.

Mean size of a habitat patch

Again, this is very much habitat dependent, but not many data are available. Some habitats have intrinsic size limitation (rotting wood, tree trunks, boulders, excrements: Table 4), but the size of the majority of habitats depends on the structure of the landscape.

Mean distance between habitat patches, spatial arrangement and number of patches

This is the field for which almost no data are available (Table 5). This is probably due to the assumed large travel distances of spores, which seems to make these parameters unimportant. Simulation studies show, however, that under realistic sedimentation patterns these parameters will influence persistence tremendously (Herben, Rydin & Söderström 1991). In contrast to the rest of the parameters, the number of patches is an extensive parameter dependent on the landscape size. Data of this type are very rarely collected except in conservation studies (Hallingbäck 1992). Still it can affect species persistence within a landscape and also intensive parameters such as a proportion of habitats occupied by a species (Fig. 1).

HABITAT PARAMETERS AND DISPERSAL IN BRITISH MOSSES

Using the information provided by Smith's flora (Smith 1978), Longton (1992a) demonstrated a strong relationship between the frequency of spore formation and commonness in British mosses. The frequency of spore formation thus seems to promote the spreading of the moss to suitable habitats, though other explanations of this correlation are also feasible (e.g. enhanced genetic variability resulting from frequent meiosis). Using the same data source, the frequency of propagule formation is

Table 4. Approximate sizes of selected bryophyte habitats. All figures in this table are estimates by the author. In habitats with large areas the within habitat heterogeneity will be high so that few species could occur throughout.

Habitat	Area
Trunk 50 cm dbh (2 m height)	1.2 m^2
Stump	0.2–0.4 m^2
Log 50 dbh (10 m length)	15.7 m^2
Excrement	0.01 m^2
Rock	0.01–1000 m^2
Bare soil	0.01–10 m^2
Bogs	100–10^6 m^2
Boreal forest floor	10^6–10^9 m^2
Heaths	400–10^8 m^2
Temperate grasslands	400–10^6 m^2

Table 5. Between patch distances of some bryophyte habitats.

3.3 m	Decaying wood	Hedenäs et al. 1989
3.1 m	Decaying wood	Jonsson & Söderström 1988
ca. 54 m	Logs	Jonsson & Esseen 1990
ca. 28 m	Logs	Söderström 1988

also shown to differ strongly between habitats (Fig. 3). When the proportions of mosses producing diaspores regularly are compared between habitats, the lowest proportion is in grasslands (24.0%), the highest in arable land (96.8%) and animal excrements (100%, but the sample size is low here). Interestingly, this proportion correlates well with two parameters of the habitat, viz. mean duration and mean size (Fig. 4). The outlying position of arable fields may be explained as a function of an anthropogenic habitat, whose species complement comes from habitats of formerly much smaller size.

If the propagules indeed play a role in spreading the moss to suitable habitats, then species of smaller and temporary habitats rely on propagule formation more than species of larger and more stable habitats. In the latter habitats, the species survive mainly through the within habitat processes of vegetative spreading and the role of dispersal events in assuring species persistence could be much less. In addition, owing to the long duration of such habitats, even a moss with an only occasional spore production may still be successful in reaching the habitat over a longer time scale (see

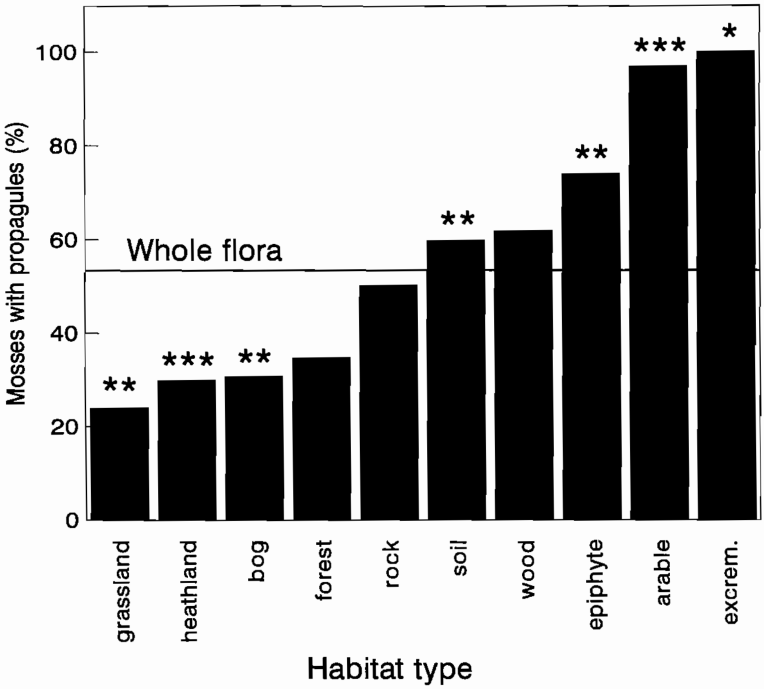

Fig. 3. Proportion of mosses regularly forming propagules (spores or gemmae) in different habitats. Data on occurrence on substrate types and on fertility are taken from Smith (1978). For the details of substrate occurrence see Table 1. A propagule forming mosses are defined as those forming spores or gemmae commonly or frequently. The horizontal line indicates proportion of propagule forming mosses in the whole moss flora of Britain. Asterisks indicate significant difference from the whole flora using the chi-square test (* – $P<0.05$, ** – $P<0.01$, *** – $P<0.001$).

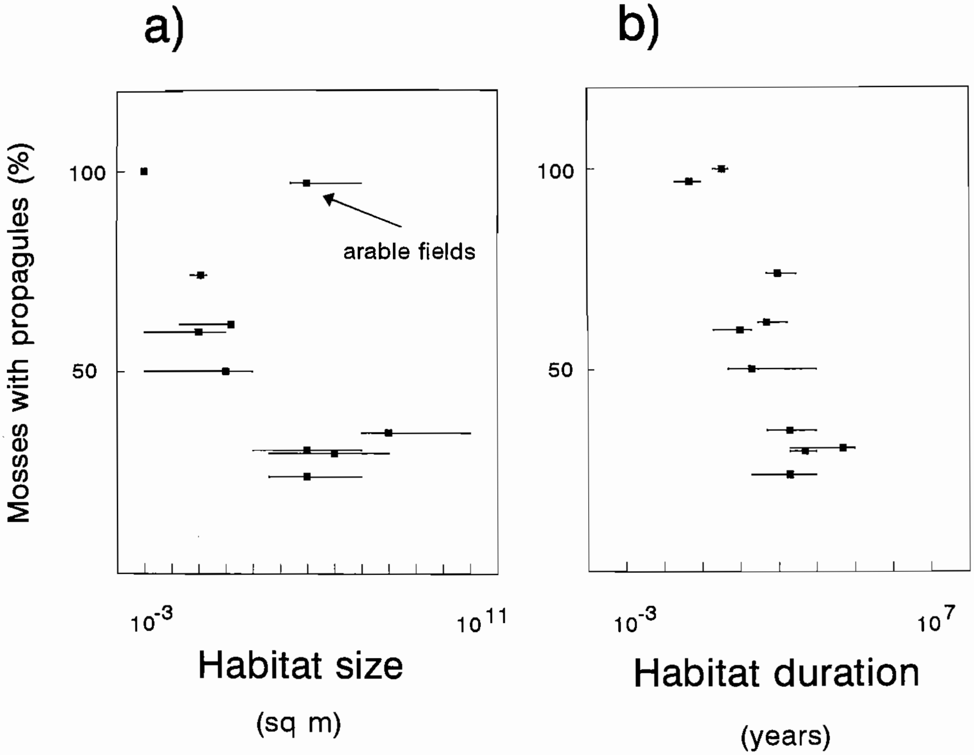

Fig. 4. Proportion of British mosses regularly forming propagules (spores or gemmae) in relation to habitat size and duration. Data on propagule formation and occurrence in habitats are taken from Smith (1978); for details see Table 1. For data on substrate duration and size see Table 4. Bars indicate ranges from the Table 4. The abscissa is in logarithmic scale.

above). However, at the scales of several thousand years or more, one has to take into account changes in environment during the Quaternary; the information which we are able to collect about the habitat now need not be relevant to its past.

CONCLUSIONS

Bryophytes of different habitats do differ in their frequency of reproduction. However, using the above arguments, role of reproduction for bryophyte persistence need not differ between transient and stable habitats. The term transient should be understood in relation to rates of reproductive and dispersal processes. Even a low frequency of propagule formation in more stable habitats (peat bogs, forest floor) may be enough for the dispersal and establishment processes of a moss to take place within the life span of the habitat, but with these processes taking much longer time than, say, for epixylics or dried pond bottom species. The minimum level of reproduction necessary to maintain a population could be only assessed if all the parameters of biology of the species in question, and the parameters of the habitat were known. Only a careful comparison of all these parameters would enable us to single out those species whose reproductive capacity does not allow them to persist in their habitat type over an indefinite time.

For further studies of role of reproduction and dispersal in bryophytes, much more attention should be paid to habitat parameters and the structure of the landscape. Even for species whose reproductive biology is well known (such as *Atrichum undulatum* or *Funaria hygrometrica*) there are almost no data on the ecological dynamics of their habitats. The effect of these parameters on persistence is very strong and the possible error in their estimation is often much higher than the error in estimation of the parameters of the species.

The method of persistence of a species is not only of primary ecological interest, but is important also in evolutionary considerations. The parameters to which persistence is most sensitive may be supposed to be under the strongest selective pressure. This has probably led to evolution of different syndromes of interrelated adaptoations in different habitats (During 1979, 1992). The degree of this interrelation and its relation to the habitat (both at within patch and between patch levels) is an intriguing subject for the study in evolution of bryophytes. Interestingly, the evolutionary interrelationship between local and regional parameters of population dynamics is contingent not only on the intensive features of the habitat patch, but also on the extensive structure of the landscape of patches.

Further, the processes operating at a patch and a landscape level may compensate each other; the persistence of a species in a given patch and landscape structure may be attained by different combination of within patch and between patch population dynamics parameters. There are also interrelations between parameters of within patch and between patch population dynamics (Hanski 1982).

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