

adults of both sexes. Considering only the Hyaenidae, Frank postulates that when the ancestral *Crocota* moved from a *Hyaena*-like niche of scavenging and solitary foraging to one of active predation and communal feeding on a limited and very localized resource, feeding competition increased dramatically. The result was intense selection pressure for females to have priority of access at kills and ensure the same for their cubs. As a consequence, females became more and more aggressive and ultimately, this increased aggressiveness (mediated by androgen levels) resulted in females' dominance over males.

It has been suggested that in primates, competition for clumped, high-quality resources has not only

resulted in clear-cut dominance relations, but has favoured long-term alliances among relatives, enabling them to outcompete other conspecifics¹⁴, and in some cases leading to a system of inheritance of rank. The similarities in social organization between *Crocota* and Old World primates could be due partly to similarities in the importance of being dominant in feeding competition, and the value of cooperation in such competition.

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Recent Developments in Bryophyte Population Ecology

H.J. During and B.F. van Tooren

Bryophytes abound in a wide variety of habitats, and despite their low stature play a significant role in many ecosystems. Earlier views of bryophytes as being 'evolutionary failures' are being questioned since the discovery of high genetic variability in those species and populations which have been studied. At the same time, there is growing evidence that in many taxa the maintenance of populations is almost completely dependent on asexual propagation; sexual reproduction may result in an enormous spore output, but establishment from spores in the field seems to be very difficult. The remarkably rapid fine-scale dynamics found in many bryophyte populations may play a role in the maintenance of genetical variability; it may also partly determine community diversity.

Bryophytes are encountered in almost all habitats on land and in many freshwater habitats. They may be apparent for only a few weeks of the year, as in deserts¹, or compose permanent banks more than 5000 years old². In bogs and many polar ecosystems they are the main primary producers, and in montane rain forests the large biomass of epiphytic bryophytes decisively influences water retention in whole watersheds³. In the temperate zones bryophytes are usually less prominent, but they may still decisively affect seedling emergence and establishment⁴,

nutrient relationships⁵, and other processes in an ecosystem.

In recent years, a number of significant contributions have been made in the fields of ecophysiology and population biology of bryophytes. Since several excellent reviews on physiological ecology have appeared recently (e.g. Ref. 6, and see Box 1), our main focus will be on population ecology.

Sexual reproduction

About half of all bryophyte species are dioecious. Among the monoecious plants, the sexual organs may be distributed in a variety of ways, sometimes even within the same species⁸. Gamete dispersal distances are very low; different methods yield estimates of 2–5 cm for most species tested; only in species with specialized 'splash-cup' male inflorescences (Fig. 3) may dispersal reach 0.2–1.0 m (Ref. 8).

Monoecious species clearly run a high risk of inbreeding. Self-incompatibility has not yet been shown to occur in bryophytes, but several less absolute mechanisms promoting outbreeding have been found, mostly involving temporal separation of the sexes⁸.

Studies using isoenzymes and chromosome markers show that genetic variability within populations may be considerable, in fact as large as in flowering plant populations^{9–11}. If a species has recently invaded a new area, however, variation is much lower¹⁰ and genets occur in a coarse-grained pattern¹¹. Apparently, the fine-grained pattern of many genets growing closely intermingled is reached only after a long time.

Reproductive allocation has never been measured for a bryophyte. Qualitatively, however, obvious differences exist. Small acrocarpic (erect-growing) genera (Fig. 5) such as *Ephemerum* and *Pottia* usually bear a sporophyte many times heavier than the supporting gametophyte, whereas many large pleurocarps (mosses with prostrate growth form; see Fig. 4) occasionally produce a few sporophytes.

Spore output per sporophyte is in the range of 50 000–600 000 in many moss species with spores of 15–25 μm ; in mosses with somewhat larger spores, numbers are in the range 5000–10 000 per sporophyte. Among hepatics (liverworts), spore output is low in many Marchantiales (with spores of

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Box 1. Structure and life history of bryophytes

The structure and life history of bryophytes differ in several ecologically important aspects from those of phanerogamic plants. Their life cycle is fairly complex: from a germinating (haploid) spore a mostly filamentous protonema develops on which one or, more commonly, several buds arise. These buds grow out to green plants, the gametophytes, which may be either thallose or consist of stems and leaves (Figs 1 and 2). Sexual organs on these gametophytes produce gametes, and after fertilization a (diploid) sporophyte develops (Fig. 3) that remains connected with and dependent on the gametophyte. In the sporophyte, meiosis occurs and spores are produced.

Bryophytes are poikilohydric: in nearly all species, the plants frequently desiccate completely but rapidly resume photosynthesis and growth upon rewetting (Fig. 4). Even so, the variation in anatomical characters, growth form of individual shoots and of shoot complexes is largely interpreted in terms of adaptations to their water economy. Although bryophytes do not have real roots, in some, so-called endohydric species (Figs 2, 3 and 5) transport of water is partially internal; in most other (ectohydric) species (Fig. 4) water is taken up over the whole surface of the plant⁶. Nutrients are acquired along the same route, which may partially explain the high sensitivity of many species to air and water pollution. This makes them useful both as indicators and as integrating samplers ('moss bags') of pollution⁷.

Finally, transport of spermatozoids in bryophytes is only possible in water; therefore, gamete dispersal distances are very restricted and sexual reproduction is rare or absent in many habitats and taxa. Conversely, asexual propagation of the gametophyte is very common, either by specialized propagules such as gemmae (one- to many-celled structures of various shapes that break off easily) or simply by protonemata growing out of broken-off fragments.

50–200 μm), but may reach five million in other groups¹².

Spore dispersal

For the majority of bryophytes, particularly those with small spores, wind is assumed to be the main dispersal agent. The travelling distance of spores will partly de-

pend upon spore size. Recent spore trap studies show that even of small ($< 20 \mu\text{m}$) spores, 15–90% fall within 2 m of the source^{8,13}. In *Sphagnum subtile*, a species with slightly larger spores (19–29 μm), no spores were recovered beyond 0.75 m (Ref. 14).

Since small spores are produced in great numbers, even the escape of only a few per cent from the direct surroundings of the source means that considerable numbers of spores are subject to long-distance dispersal, particularly if they are lifted high enough into the air to become caught in jet streams. This raises the question of whether spores are able to survive the extreme conditions of drought, cold and UV radiation that characterize this environment. Laboratory experiments with spores from a large number of species showed much interspecific variation with regard to resistance to low temperatures and drought, and revealed a significant correlation between survival in these conditions and the area presently occupied by the species¹⁵. More realistic experiments exposing spores to high-altitude environments on wings of aeroplanes are now under way.

Asexual propagation

Asexual propagation is very common, particularly in dioecious taxa¹². In culture, protonemata of many species produce abundant gemmae¹⁶. Gametophytes may bear propagules on the rhizoids, on short specialized rhizoids on the

stem, on leaf lamina or costa, on leaf tips, even on specialized 'splash-cup' gemma heads as in *Tetraphis pellucida*. In some Polytrichaceae, rhizoid 'wicks' consisting of several parallel rhizoid strands may extend from the 'parent' shoot for several centimetres and then produce new buds and gametophytes¹⁷. Many species that do not possess such specialized propagula show indeterminate growth and branching followed by a gradual falling apart of the ramets.

Asexual propagation in bryophytes may serve several functions^{8,12,18}, including the following:

1. In weedy species, such propagules may serve to colonize an area very rapidly following disturbance, because they can generally be produced earlier and faster than spores. Usually, in the period following the colonizing phase sporophytes are produced.

2. In many epilithic species, populations are maintained by asexual propagation only; sporophytes are rare or absent, or spore germination and establishment is extremely rare¹⁹. The greater success of gemmae in such situations has been ascribed to their larger size and nutrient store²⁰.

3. Asexual propagation reduces the chance of extinction of genotypes in an environment with mortality occurring in a fine-grained pattern (i.e. affecting only isolated shoots or small clumps of shoots)²¹.

4. In dioecious species, establishment from spores hardly ever results directly in gametophores occurring closely enough in time and space for sexual reproduction to occur. Maintenance and local spread of the plants by asexual propagation considerably increases this possibility¹².

Diaspore bank

In many ecosystems, the soil contains a store of propagules of bryophytes consisting of spores, tubers, gemmae, and leaf and stem fragments. In some Dutch chalk grassland sites, the below-ground species composition appeared to be rather different from that above ground²². Some species were present only above ground, often even common there, with only rarely some stem fragments in the soil (mainly pleurocarps and hepatics).



Fig. 1. Two hepatics, the leafy species *Ptilidium ciliare* (left) and the thallose species *Riccia glauca* (right). Photographed in the Netherlands by B.F. van Tooren (left) and J.H. Willems (right).

Other species occurred locally in temporary gaps, but were present below ground in larger numbers, presumably as spores (*Ephemerum* spp., *Pottia* spp.). Most common below ground were some tuber-bearing *Bryum* species, that occurred very rarely in the above-ground vegetation, mostly on ant hills. Only one species, *Fissidens taxifolius*, which also possesses tubers on the rhizoids, was very abundant both above ground and in the diaspore bank.

In Antarctic soils, similar discrepancies between above- and below-ground vegetation were observed²³; here, hepatics were more abundant in the diaspore bank. Some samples yielded several species not known from the study area or even from the Antarctic at large – which probably attests to the effectiveness of long distance dispersal in some species.

In general, the diaspore bank of bryophytes differs from that of most phanerogam populations in the predominance of asexual propagules. Tubers of several species appear to be long-lived in the soil: at the chalk grassland site, even more so than spores of, for example, *Pottia* species²². Buried stem fragments also seem to maintain some viable cells for quite some time; there is a recent report of regrowth from cells in *Sphagnum* stems from a depth of 30 cm in peat²⁴.

Germination and establishment

Recruitment of new genotypes to the population of gametophytes after spore dispersal is of course dependent on subsequent germination and establishment. Unfortunately, we know very little about these processes in the field. Under laboratory conditions, spores of nearly all species germinate rapidly, and gametophytes develop freely on the protonema. Species of severely disturbed habitats, such as *Funaria hygrometrica*, appear to follow this pattern in the field. In more 'stabilized' habitats however, field experiments have shown that the production of new plants from spores is extremely rare, in spite of the large numbers of spores released^{13,19}. Most spores probably never germinate at all, and in the rare cases when they do,

as in *Atrichum undulatum* (Fig. 5), the protonemata did not grow beyond the three-celled stage¹³. In this species, and in the epilithic *Grimmia laevigata*¹⁹, production of new shoots was not rare, but they could be traced back to asexual propagation only – rhizoid wicks in the first, leaf fragments in the second case.

In this context, it should be pointed out that several rare or locally extinct species have recently re-established small populations, presumably from spores, in Dutch polders that have been reclaimed from the sea in the past decades²⁵. These species are characteristic of late-successional stages: epiphytes of forest trees, species of soil, humus and rotten logs in old forests, rich fens. Outside the new polders, most of them had not been observed for many years.

These observations suggest that germination and establishment are controlled by a complex network of relations, which has not yet been fully developed in the new polders and which can be disturbed by taking samples to the lab and putting them under a different set of conditions. Microorganisms may be essential elements in such a network, as has been suggested for tropical epiphyllous ecosystems²⁶. That establishment is not (yet?) controlled in this way in all species is shown by the rapid expansion in western Europe of some species originating from the southern hemisphere, such as *Orthodontium lineare* and *Campylopus introflexus*¹⁵.



Fig. 2. *Rhodobryum roseum*, an acrocarpic moss of shaded habitats, as the large leaves and open growth form indicate. Photographed in The Netherlands by J.H. Willems.



Fig. 3. *Polytrichum juniperinum* with 'splash-cup' male inflorescences and young sporophytes. Photographed in The Netherlands by H.J. During.

Fig. 4. *Abietinella abietina*, a pleurocarpic moss of exposed habitats. The leaves are appressed when dry (below) but rapidly spread when moistened (left). Photographed in The Netherlands by J.H. Willems.





Fig. 5. Two acrocarpic mosses of different growth-form: *Conostomum tetragonum* (left) forms dense cushions in dry boreal-arctic environments; the loose turfs of *Atrichum undulatum* (right) are found in more mesic habitats in temperate regions. Photographed by H.J. During in Greenland (left) and The Netherlands (right).

Growth rate, life span and 'strategies'

The relative growth rates of bryophytes may vary considerably between species²⁷; while some species may reach values as high as some fast-growing flowering plants, others have inherently low growth rates. These results facilitate the accommodation of bryophytes into Grime's triangular model²⁸ of primary plant strategies as main avenues of ecological specialization in response to the combined effects of various intensities of stress, disturbance and competition; differences in growth rates constitute a major element of this model²⁸.

In a different approach, six life history strategies were described based on spore size, life span, estimated reproductive allocation and relative investment in asexual propagation¹⁸. The species with

small spores and life spans exceeding one year were divided into a group with relatively short life spans, high reproductive allocation and often high investment in asexual propagation (Colonists) and a group with potentially much longer life spans and lower reproductive allocation (Perennials). Among the Colonists, some species appear to have inherently low growth rates and possibly longer life spans (Pioneers), whereas the Colonists *sensu stricto* such as *Bryum bicolor*, *B. argenteum* and *Ceratodon purpureus* have much higher growth rates. Among the Perennials, the strategy of the Competitors such as *Brachythecium rutabulum* may be separated from the slow-growing Stress-tolerators such as *Clenidium molluscum*²⁷.

In such models of life history strategies, life span and age of first reproduction play an important role. In fact, very little is known about mortality rates and life span in the field. Population history studies of *Polytrichum* species revealed that the life span of an individual shoot is limited to 2–5 years²⁹; however, innovations from the shoot bases generally result in a very long life span of genets. A similar pattern was found for *Atrichum undulatum*^{13,17}.

Repeated micro-charting of plots in forest and chalk grassland stands indicated that turnover rates of several species of lower stature than the *Polytrichaceae* were high, and that mortality occurred in a very fine-grained pattern³⁰. In these plots mortality hardly varied between seasons. The data now avail-

able suggest that mortality is usually not density-dependent^{30,31}.

Very little is known about mortality causes in this group of plants. Bryophytes are seldom grazed to an appreciable extent, although they may represent an important part of the diet of a few animal species, such as lemmings and some invertebrates⁵. Sporophytes are often taken preferentially, presumably because of the high lipid content of the spores⁵.

Competition and niche differentiation

The commonness of fine-grained, density-independent mortality may seem to imply that competitive exclusion is rare in the field. However, interspecific competition certainly occurs among Perennials; for example, it has been shown to be a partial determinant of the species sequence of *Sphagna* along the hummock-to-hollow gradient in bogs³². But even in that case, other factors such as priority seem to be involved as well³².

In a study of colonization by the recently introduced species *Orthodontium lineare* (Fig. 6), including repeated micro-charting and dissecting of turfs to reveal possible overgrowing of other species, three different patterns emerged³³. In some coarse-grained communities, competition seemed to be strongly hierarchical and resulted in competitive exclusion of several species and a low diversity of the vegetation. In fine-grained communities competitive replacement did occur, but competitive relations were non-hierarchical and no species was excluded from the plots; diversity remained high. In a third group of communities, the pattern was coarse again, but overgrowing was not observed, mortality being regulated mainly by fluctuations in the inhospitable environment.

An analysis of differences in ecology between six closely related *Polytrichaceae* showed much niche overlap between some, and clear separation between other species³¹ (in this and the subsequent references, 'niche' refers to the habitat niche³⁴). A similar result was obtained for a number of stream-inhabiting bryophytes³⁵. Competitive exclusion may be prevented by niche differentiation between the taxa involved. Niche differentiation between perennial



Fig. 6. *Orthodontium lineare*, a southern-hemisphere species that was introduced into Europe early this century and has since spread far and wide. Photographed in The Netherlands by H.J. During.

Sphagnum species is fairly clear³²; a mathematical model of the competitive relationship between two *Sphagnum* species differing slightly in growth rate and water economy proved to be consistent with field data³⁶. If, however, mortality is density-independent in species with other life history strategies, niche differentiation is not necessary to explain coexistence between species in many situations. This has already been postulated and shown to be consistent with field data for epiphytic phanerogams³⁷, and supports non-equilibrium models of origin and maintenance of high species diversity³⁸.

Conclusion

Knowledge about life history variation in bryophytes is rapidly increasing. A better understanding of shoot mortality and its causes would be a major step forward in this field. More information is also urgently needed about factors regulating germination and establishment from spores under field conditions¹³. There is increasing evidence that interactions with microorganisms are important for growth and nutrition of bryophytes in many ecosystems³; it may well be that such interactions also play a crucial role in the establishment from spores.

The combination of high genetic variability with the predominance of asexual propagation and the rarity of successful reproduction via spores in the same species is something of a paradox. If the fined-grained pattern of density-independent mortality observed in some communities proves to be a more general phenomenon, this might provide a clue; then, asexual propagation might indeed be a safeguard to prevent local extinction of genets²¹. Together with very occasional establishment from spores, this would result in a gradual accumulation of different genotypes in the population. Such mechanisms would support the use of expected time to extinction³⁹ as a (derived) fitness parameter.

It is clear that a study of the ecology of bryophytes is not only interesting for its own sake. Due to their relatively simple anatomical structure and lack of roots, bryophytes are also very suitable for experimental tests of more

general hypotheses concerning the role of competition, niche differentiation, and the origin and causes of diversity in ecosystems.

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