Life Strategies of Bryophytes: A Preliminary Review
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Life strategies of Bryophytes: a preliminary review

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An attempt is made to compare bryophyte life histories with recent models of life strategies of animals and phanerogams. Important life history traits in bryophytes include the balance between sexual and asexual reproduction, the reproductive effort spent on both kinds of reproduction, the size and number of the spores, and annual production and standing crop. Age of first reproduction is generally low for asexual reproduction, but low or high for sexual reproduction, depending on the species and the population included. Density-dependent mortality appears to be rare in bryophytes; in some groups of species mortality is for the greater part caused by abiotic environmental stress, whereas in other groups biotic factors such as competition and predation are more prominent. Life expectancy varies from some weeks in extreme ephemerals to hundreds of years; in the longer lived species wide variation in life span of different individuals occurs. Tolerance and avoidance of environmental stress are two distinct alternative possibilities in bryophytes as well as in phanerogams. A preliminary system of six different bryophyte life strategies is presented. It is stressed that the choice of a fitness measure for a species or population should be made in accordance to its life strategy. Finally, some distinctive traits of bryophyte life histories are outlined.

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Резюме. Жизненные циклы бриофитов сравниваются с недавними моделями жизненных стратегий животных и явнобрачных растений (фанерогамов). Важные характерные черты жизненного цикла бриофитов включают в себя баланс между сексуальным и асексуальным воспроизведением, воспроизводительные процессы, делящиеся на оба типа воспроизведения, величину и количество спор, годовое производство и растения на корню. Обсуждаются возраст при первом воспроизведении, смертность, зависимая от плотности, вероятность жизни, выносливость и избежание стресса окружающей среды. Приводится предварительная система шести различных жизненных стратегий бриофитов. Подчеркивается, что выбор степени годности вида или популяции следует предпринять в соответствии с его/её жизненной стратегией. В заключение обрисованы некоторые различительные признаки жизненных циклов бриофитов.

1. Introduction

Much attention has been paid to life history traits and life strategies in animals (cf. Stearns 1976 for a review) and recently also in phanerogamic plants (Gadgil and Solbrig 1972, Grime 1974, Rabotnov 1975, Harper 1977). With respect to bryophytes, a few autecological case studies including some aspects of the life history of the species have been published (e.g., Saxton 1930, Romose 1940, Tamm 1953, Tallis 1959, Forman 1964, Watson 1974, Berrie 1975). Some stages in the life history of bryophytes have received special attention, such as the physiology of the sexual reproduction (Benson-Evans 1964, Sussman 1965a, Lockwood 1975), the phenology of reproduction (Grimme 1903, Greene 1960, Longton and Greene 1969b), gene flow distances in the field (Anderson and Lemmon 1974, Wyatt 1977) and dispersal (cf. Crum 1972). Growth of the plants and regulation of growth have been studied in extenso by i.a. Hagerup (1935), Pitkin (1975), Collins

(1976) and Schwabe (1976). Especially for bryophytes, water relations are crucial (Buch 1947); much work has been done in this respect on mortality by drought and desiccation tolerance (Irmscher 1912, Abel 1956, Dilks and Proctor 1976a, b). Of the life span of individual plants little is known (Reichard 1860, Wangermann 1965); the life span of spores has been investigated more thoroughly in relation to dispersal capacity (Malta 1922, Sussman 1965b, Van Zanten 1978a, b). Recently, a comprehensive study of the life histories including mortality rates of *Polytrichum alpestre* (Collins 1976), *Hylocomium splendens* and *Polytrichum commune* (Callaghan et al. 1978) has been carried out. A description of some general life strategies of bryophytes was attempted by Joenje and During (1977).

Bryophytes have some characteristics, among which the peculiar diplohaplont life cycle, the importance of vegetative reproduction in many species, the highly variable dispersal capacity of the diaspores, and their almost constantly subordinate position in ecosystems, which result in focusing points in their life histories different from angiosperms or animals. Therefore a separate consideration of their life strategies seems worthwhile. The consideration will serve to emphasize that most aspects of the life history of bryophytes are very incompletely known and that a fertile field of investigations lies open here; I also try to present a frame-work into which some results may be fitted and to discuss the fundamental strategies in bryophytes.

The system presented here might be used to get an overall picture of small and large scale fluctuations and successions in bryophyte communities and to better understand the niches of bryophytes within the communities. Also, it may generate hypotheses about the variation in life history of populations within one species in different environments, and about the role of the bryophyte synusiae in the community (e.g., with regard to their influence on the environmental factors important for the germination of phanerogams).

In discussions on fitness measures, the gross life history of the organisms in question should be known; the relative importance of number of spores (m^{-2}, yr^{-1}) and of the production (g m^2, yr^{-1}), for example, depend strongly upon the life strategy of the species studied. In fugitive species, the number of diaspores produced and their dispersability are of paramount importance; in other avoidance strategy species the possibilities of the diaspore to produce a viable new individual within the community, and therefore, the size of the spores and dormancy requirements, become more important.

In the long-lived species, there is a difference between the stress tolerant species which should have as much living biomass at the start of the growing season as possible, and the competitive species for which a high relative growth rate is very important (Grime 1974, 1977, 1978). The fitness measure to be used should in any case be chosen with care in accordance to the life strategy.

2. Life strategies

The life strategy or life history tactic of a species or population can be envisaged as a system of co-evolved adaptive traits (Stearns 1976). Many models trying to simplify the different possible strategies have been made. In Russia Ramensky (1938) described three coenotypes: violents (aggressive species), patients (tolerant species) and explerents (non-competitive species filling the space between others). Rabotnov (1975) added a fourth group, the pioneers (species able to colonize a new, for other species yet unsuitable, substrate). These concepts have had little influence in the west. There, the well-known concept of r- and K-selection (McArthur and Wilson 1967) and the continuum between these two extremes (Pianka 1970, Gadgil and Solbrig 1972) have greatly influenced the lines of thought. In this one-dimensional model, r-selected species in which reproductive rate and resource uptake are maximized are placed opposite to K-selected species in which efficiency of resource utilisation and the ability to survive in a crowded environment are the main issues. Gadgil and Solbrig (1972) related r-selection to unstable, disturbed environments and K-selection to more stable and predictable environments. A general discussion on the applicability of these concepts to bryophytes is given by Slack (1977).

Wilbur et al. (1974) and Wilbur (1976) comment on the one-dimensional character of the R-K continuum, and advocate the use of models with several environmental dimensions. They also state, that a 'life history strategy' will consist of several components, among which are reproductive effort, fecundity, reproductive life span, age of first reproduction, and juvenile and adult mortality schedules (Wilbur et al. 1974). This leads to the conception of a life history strategy as a 'region in hyperspace, the axes of the hyperspace representing the various life history traits' (Newell and Tramer 1978).

Grime (1974, 1977, 1978) proposed a triangular model for plant strategies, in which the sides of the triangle represent gradients from high to low disturbance, competition capacity (e.g., relative growth rate and litter production) and stress tolerance, respectively. The model is two-dimensional; on the first axis the extremes are competitive ability, which is mainly of importance in fertile, mesic environments, and stress tolerance, which is paramount in environments of low productivity; here often the ability to resist periods of stress and the degree to which loss of biomass in the stress period is prevented are decisive. The other axis represents the degree of disturbance, i.e. damage to the plant material, regardless of its predictability. Also for this model addition of a further dimension has been proposed (dominance, cf. Grubb 1977).

Wilbur et al. (1974) stress predictability of mortality as an important evolutionary force in the development of strategies. From a comparison of bryophyte strategies

it appears that a high predictability of continuous new establishment possibilities within the community, as opposed to locally unpredictable habitats of short duration, is another important 'template' (Southwood et al. 1974) for a group of life strategies (Joenje and During 1977). In phanerogams, such strategies often include dormancy of the seeds (Harper 1977, Thompson 1978).

Most of the strategy concepts discussed above imply adaptations to environmental fluctuations which may be variable in wave length and degree of predictability. Stearns (1976) gave a classification of such environments, together with a lucid discussion on the tactics evolved in each environment. He distinguished three main types: (1) fluctuations cyclic, period much longer than the generation time of the organisms involved; (2) fluctuations cyclic, period as long as or shorter than the generation time of the organisms; and (3) fluctuations random in time, neither cyclic nor predictable. The second type is subdivided again in: (a) cycle highly predictable; (b) start of cycle unpredictable; (c) start of cycle predictable, but conditions during the growing season unknown; and (d) start of cycle predictable, conditions only partially known.

3. Relation to life forms

The concept of life form, the 'holomorphy' (Hennig 1966) of the plants in accordance with their environments, is clearly related to the strategy concepts. The strategy refers primarily to life history traits, whereas the life form refers to morphological and physiological characters of the individuals (some authors use only morphological characters (cf. Mäkirinta 1978, Barkman 1979). The best-known life form system, that of Raunkiaer (1904, 1937) is based on the place of the perennating organs; within this system the splitting-off of the annuals is based upon other, i.e. life history characters, as was rightly remarked by Gams (1918). The subdivision of the hapaxanths by Bakker (1966) also has some characteristics of a life strategy system.

For bryophytes no practical life form system has yet been developed. The 'life form system' of Mägdefrau (1969) consists almost completely of growth forms. Bryophytes have been incorporated into the Raunkiaer system by Ellenberg and Müller-Dombois (1967) and Düll (1969, 1970); here the annual/perennial division is the only really usable one. As, however, many 'annual' bryophytes are capable of perennating a few years (pauciennials), this division presents some difficulties as a starting point in bryophytes. The division into endo-, ecto- and mixohydric species by Buch (1947), based on the water relations of the plants, might be a better one (Watson 1971), but much experimental work needs to be done yet before a really useful system can be designed.

Bryophytes may also be classified according to their growth form (Meusel 1935, Gimingham and Birse

1957, Barkman 1958, Mägdefrau 1969). Joenje and During (1977) showed, that there is a strong correlation between growth form and life strategy. Important traits are i.a., the occurrence of innovations in acrocarps, producing dense turfs which may persist for more than one year, and the capability of horizontal spread in plants with a prostrate habit or prostrate phase, which offers possibilities of crossing small distances to other suitable sites ('dispersal') and generally enhances the competitive ability of the plants (Warming 1884).

4. Some life history traits in bryophytes

4.1. General

The discussion on animal life strategies normally centers on reproduction and mortality, and on the effects of stable or fluctuating environments on both (Stearns 1976). Grime's plant strategy model is directed more towards the vegetative phase and consolidation phenomena in the individuals. In bryophytes, as in other plants, reproduction is closely allied to dispersal; in this group asexual reproduction often plays a more important role than sexual reproduction. These aspects become particularly important when correlations are drawn with fluctuations in the environment and their predictability in time and space. In the next paragraphs some aspects of reproduction, life span and mortality in the life histories of bryophytes will be discussed briefly.

Another important aspect of the life history of bryophytes concerns the timing and regulation of the stages of the life cycle. This cycle comprises several easily recognized stages; in sexually reproducing species these include spore, protonema, buds and full-grown gametophyte, gametangia, sporophyte. The 'asexual cycle' includes diaspore, protonema (often, but not necessarily), full-grown gametophyte. Within these gross stages, a finer subdivision is possible; thus, Mogensen (1978) divided spore formation, from meiosis to protonema, into five stages. The growing sporophyte of Buxbaumia aphylla goes through 12 stages from fertilisation to the shedding of the spores (Hancock and Brassard 1974).

The transition from each stage to the next is mostly governed by an interplay of environmental fluctuations and physiological traits of the plants; often long-day or short-day conditions and the phytochrome system are involved (Benson-Evans 1964, Schwabe 1976). For most transitions the exact conditions are not yet known, and it is difficult to assess their importance for the life strategies of the species now.

In all discussions on population genetics and population ecology of bryophytes one should bear in mind, that the bryophyte 'plants' usually discussed are gametophytes, i.e. haploid, and the sporophytes, which are dependent upon the gametophytes at least with respect to growing site, are the diploid phase. In the latter phase heterozygoty can occur and genes with a lower

4

fitness in one environmental constellation can be retained to some extent. Together with the limited possibilities of outbreeding, due to frequent self-fertilisation (in monoicous species), small spreading distances of gametes and high frequency of asexual reproduction, this has grave implications for the possibilities of maintaining a diverse gene pool with a certain amount of exchange. Anderson and Lemmon (1974) conclude that it is certainly not gene flow that holds together species of bryophytes; they suggest environmental pressure as an alternative mechanism.

In this context, the phenomenon of phyllodioecism, i.e. dwarf males growing on leaves and perichaetial leaves of female plants (Dening 1936) deserves special attention. Here, the female plants are thus often fertilised by their 'sons', whereas the 'daughters' of the same generation are dispersed and may form new individuals which only after some years are capable of sexual reproduction. This system has intriguing implications for the spread in time and space of new genetic combinations (I wish to thank Dr G. S. Mogensen, who pointed this out to me).

In bryophytes, as in many other groups of plants, the problem arises what to count: shoots, genetically uniform descendants from one spore, or something in between. Harper (1977) separates genets ('products of individual zygotes') and ramets, 'units of clonal growth'. For most bryophytes, the problem is even more complex than in phanerogams; on the protonema growing out of one spore, often several buds are present, thus one spore can give rise to several gametophytic shoots. Asexual reproduction may also multiply the 'individual shoots' stemming from one spore. In pleurocarpous species, the subsequent growth of the shoots and dying off of their bases will result in the separation of 'ramets'. The production of new shoots from a perennating protonema as reported by Meusel (1935) and suggested by Hancock and Brassard (1974) is another way of multiplication of 'ramets'. In a similar way, the subterranean tubers present in many small acrocarpous mosses (Whitehouse 1966) and in liverworts (Sussman 1965a) may sprout in the next growing season to produce new shoots. What then is to be called an individual? Since the concept of genet is mostly of only theoretical value, I will use the term individuals (if necessary or convenient) for all ramets resulting from spores or specialised asexual propagules that are spatially separate.

4.2. Reproduction

Sexual reproduction is one of the most prominent life history traits both in animals and in higher plants. In most groups of bryophytes, sexual reproduction plays only a minor part in the whole reproduction process (Crum 1973), and asexual reproduction by means of gemmae, tubers, flagellae, the breaking-off of leaf tips or simply by protonemal growth from leaf cells of detached plant parts or individual shoots is very common.

Asexual reproduction in hepatics is reviewed by Degenkolbe (1937) and for mosses the standard work is still Correns (1899). The physiology of asexual reproduction has been reviewed by Müller-Stoll (1965) and Sussman (1965a).

In species for which no sporophytes are known, the asexual reproduction presumably is the only method of reproduction left, but in most species the relative importance of both kinds of reproduction, clearly an important life history trait in this group, is more difficult to assess. A good example is *Grimmia laevigata* (Keever 1957). The cushions of this species often form large numbers of sporophytes and spores; however, it appeared to be nearly impossible to reproduce the plants by germination of spores, whereas new establishments through detached shoots or leaf fragments were relatively easy.

In many species there is a distinct negative correlation between asexual and sexual reproduction (Goebel 1905, Lockwood 1975). In many hepatics, sexual reproduction is induced by long day and asexual reproduction by short day conditions (Benson-Evans 1961, Lockwood 1975). In tuber-bearing *Bryum* species, the production of tubers seems to cease as soon as sporophytes are produced (Crundwell and Nyholm 1964). In the Garovaglioideae, gemmae are produced by the female plants only as long as it bears no sporophytes; once a sporophyte is formed, the plants are well supplied with dwarf males and thus will form sporophytes consistently from that time onwards, and the production of gemmae stops (During 1977). In the embanked Lauwerszee, the plants of *Bryum bicolor* and *B. argenteum* bore numerous gemmae and (in *B. bicolor*) tubers in the first years, but with the lowering of the nutrient level due to leaching from the sandy soil, the plants developed sex organs and sporophytes, and asexual reproduction ceased nearly completely (Joenje and During 1977). But there are also many species in which asexual and sexual reproduction seem to occur concomitantly (Correns 1899).

4.2.1. Age of first reproduction

In considerations on reproduction, it is often necessary to treat sexual and asexual reproduction separately. In discussions on the determination of 'r', the relative reproduction parameter in the population growth models, the 'age of first reproduction' needs to be known (Stearns 1976). For sexual reproduction, this age is related to, (1) the time lapse between dispersal and germination of the spore, which depends on the duration of the dispersal period and the occurrence of a dormancy period; (2) the time lapse between germination of the spores and the formation of ripe gametangia, and (3) the duration of the development of the sporophyte, i.e. the time between fertilisation and the shedding of the spores. This period is mostly rather fixed for each species and correlates strongly with seasonal fluctuations in the environment (Arnell 1875, Grimme 1903,

Lackner 1939, Jendralski 1955). For different species it may vary from ca. 4 months to 24 months (Grimme 1903); however, Watson (1971) supposes that in *Phascum cuspidatum* this period (estimated by Grimme to 7–10 months) might be as short as a few weeks. Berrie (1975) showed in a life history study of *Riccia nigrosquamata,* that this period lasts only 4–5 wk. Within each species, the length of the period seems to be very stable within local populations, but variable according to the climate of the region (Lackner 1939).

Few data are available on the time lapse between germination of the spore and the first appearance of gametangia. Berrie (1975) showed for *Riccia nigrosquamata,* that in the favourable season the first gametangia appear 2–3 wk after germination and the first ripe spores occur after 6–8 wk. In temperate regions, many species need long or short days for the initiation of gametangia (Benson-Evans 1964); here the span between germination of the spore and the first appearance of gametangia will be much longer, often more than one year. Casual observations indicate that in many annual or ephemeral species this span is a few months but seldom more, whereas in most perennial species it can be delayed considerably and, in some, development of the sex organs occurs rarely at all. For the species of the Garovaglioideae my impression is that several years of vegetative growth precede the first development of sex organs.

When the stage of ripe gametangia is reached, fertilisation and sporophyte development are necessary for sexual reproduction. In monoicous species this may pose little problems, but in many dioicous species sporophytes are rare. The causes of this are discussed by, i.a., Longton and Greene (1969a, b), Wyatt (1977), and Newton (1971, 1978).

For asexual reproduction, the age of first reproduction will often be lower than in sexual reproduction; however, there is a wide, environmentally-induced variation in this respect. The asexual diaspores are usually fewer in number than the spores, but, as demonstrated for *Grimmia laevigata* (Keever 1957), they have a better chance to survive and give rise to new 'individuals'. Sometimes, the effect may be a rapid local spread and so a high reproduction rate.

Some species, such as *Bryum bicolor, B. argenteum* and *Marchantia polymorpha,* show an interesting combination of both kinds of reproduction: once established in a new, yet bare, relatively fertile region (in the case studied, the former Lauwerszee after embankment) they reproduce solely by gemmae in the first year and partly in the second, whereas in later years, in situations of complete vegetation cover, the asexual reproduction stops and many of the plants develop sporophytes (Joenje and During 1977). This combination of rapid asexual reproduction and, later on, when resources become scarcer, sexual reproduction is also known in some marine animals, living in environments with predictable long-term fluctuations (Stearns 1976).

4.2.2. Reproductive effort

By reproductive effort is meant 'the proportion of resources diverted to reproduction, summed over the time interval in question' (Stearns 1976). When applying this concept to bryophytes one meets again the problem of the distinction between asexual and sexual reproduction. An interesting field of investigations concerns, how the reproductive effort is divided between sexual and asexual reproductive parts. Lockwood (1975) showed, for instance, that many amino acids and other metabolites have a strong effect on the regulation of amount and developmental speed of sex organs and gemmae.

The proportion of resources directed towards the asexual diaspores depends largely upon environmental factors. For example in moist, undisturbed environments *Campylopus flexuosus, Orthodicranum montanum* and several other species form large tufts nearly without propagula, whereas in dry forests they may form dense cushions consisting nearly wholly of short, easily detached branchlets.

In general, the reproductive effort spent on sporophytes is high in ephemeral and annual species and much lower in perennial ones. Especially in the small, cleistocarpous annuals of open soils such as *Ephemerum* spp., *Phascum* spp. and *Acaulon* spp., sporophyte frequency is very high and the plants consist mostly of sporophytes. In the larger, perennial pleurocarps the reproductive effort will depend strongly on the frequency of the sporophytes, which again varies between the species as well as with the environment. *Ptilium crista-castrensis,* for example, sporulates very rarely, but where sporophytes are produced they can be rather abundant (2–5 per frond). The same applies to species with dwarf males like *Dicranum scoparium, Leucobryum glaucum* (Woesler 1935) and the Garovaglioideae (During 1977). In a few of such 'phyllodioicous' species of the genus *Macromitrium,* part of the reproductive effort is seemingly directed to special 'nesting places' for the dwarf males, mainly parts of the leaves clad densely with a rhizoid felt (Ernst-Schwarzenbach 1939). Probably this part, though interesting, is not very important numerically.

4.2.3. Size and number of spores

Spore size and spore number may form an important part of the reproduction tactics of a bryophyte species (Joenje and During 1977). Spore size is not only relevant in relation to the number of spores that a sporophyte can produce. Schmidt (1918) calculated, that spores of 20μm or smaller will have the best chances of long-range dispersal, whereas for larger spores the probable dispersal distance decreases rapidly with size (cf. Crum 1972). Small spores thus offer the possibilities of large spore numbers and long-range dispersal. Disadvantages of small spore size probably include the long time that many spores will have to stay in the harsh environments of the upper air layers, as their

6

fall-out is nearly wholly dependant on air currents and rain (Geiger 1965).

Spore size is usually constant within the species; in some species, however, anisospory occurs (Vitt 1968) and in a few others the size is more variable, perhaps under influence of the environment (e.g., *Phascum cuspidatum*: 24–36 μm, Nyholm 1956). In *Cinclidium*, about 50% of the spores die at a certain stage in the spore development, which gives rise to 'false anisospory' (Mogensen 1978). *Dawsonia* spp. (5–10 μm), *Buxbaumia aphylla* (10 μm) and *Polytrichum commune* (10–12 μm), have very small spores whereas the small cleistocarpous acrocarps especially often have large spores, about 30–50 μm. The largest spores occur in *Archidium alternifolium* (100–200 μm) and in some hepatics, especially within the genus *Riccia* (60–120 μm); the very large, multicellular spores occurring in some groups, such as the family Dicnemonaceae, which is due to precocious germination within the theca (Parihar 1961) deserve special mention.

Spore numbers vary enormously, depending on the species; whereas *Archidium alternifolium* has only 1–20 spores per sporophyte, many species have 100000 or more, and a sporophyte of *Buxbaumia aphylla* may produce 5.5 million spores (Kreulen 1972). The largest number known is that of *Dawsonia beccarii* var. *limbata*: 80 millions spores per theca (Kreulen 1972)! Within a species, the number is variable, but within the same order of magnitude; thus, Kreulen (1972) estimated for *Tortula muralis* sporophytes from different habitats numbers ranging from 500000 to 1 million, and in *Cinclidium stygium* the number of spores ranged from 4600 to 9600 (Mogensen 1978). In pleurocarps and some polysetous acrocarps, the number of spores per time unit depends also on the number of sporophytes produced on the plants.

4.2.4. Dormancy of the spores
In most species of bryophytes, germination of the spores is inhibited as long as they remain in the operculate theca (Buch 1920, Oppenheimer 1922). This might be due to lack of light or water inside the theca (Sussman 1965a); the presence of chemical substances emanating from the wall of the theca and inhibiting germination has been shown (Oppenheimer 1922). However, there is also a group of species in which the spores are reported to germinate inside the theca (Parihar 1961).

Once shed, the spores of many species are able to germinate immediately. In *Riella*, however, the spores first have to pass through a dormant stage (Howe and Underwood 1903, Thompson 1941). The same was shown for *Riccia trichocarpa* by Campbell (1918). Von Gaisberg (1921) reported, that although mature spores of *Riccia glauca* germinated only after a rest period, this could be shortened considerably by freezing the spores. Dormancy of the spores has also been found for *Riccia nigrosquamata* (Berrie 1975), but it was not established which factor would break this dormancy.

Servettaz (1913) reported such a dormant stage of the spores for some mosses as well, but von Ubisch (1913) and others showed rapid germination of the spores in the species mentioned by him. Partly, this might be due to the differences in germination capacity of spores from different sporophytes of the same species (cf. Servettaz 1913, Heitz 1942, Sussman 1965a).

In *Riccia glauca*, von Gaisberg (1921) also found that, while mature spores needed a rest period before germination, immature spores germinated immediately. Woesler (1933) reported the same for *Bryum argenteum*. In *Barbula unguiculata*, the spores showed distinct seasonality of germination which might also indicate the need for a resting period (Hoffmann 1957). Kinugawa and Nakao (1965) state, that in *Bryum pseudotriquetrum* germination of the spores is only possible under long-day conditions, which may be important in view of the dispersal season (July-autumn, Lackner 1939).

In some germination experiments with several treatments of the spores, carried out by H. H. T. Prins (unpubl.), the spores of *Splachnum vasculosum*, *Orthotrichum anomalum*, *Plagiothecium denticulatum*, and *Hypnum cupressiforme*, and to a lesser extent also *Leucodon sciuroides*, germinated well after a few days' freezing at −5°C, but not if sown directly on the same substrate, whereas spores of 6 other species germinated well if sown directly. The *Splachnum* spores germinated better if the intact sporophyte had been frozen than if the spores were first dispersed in distilled water and then frozen.

Van Zanten (1978a, b) carried out many germination experiments, with and without previous freezing treatment; he does not report any example of such a dormancy. According to Sussman (1965a: 982) 'the presence of dormant spore stages is not correlated necessarily with the ecological niche occupied by an organism although it may be in some cases'.

Clearly, a consistent and comprehensive investigation into the distribution and ecological role of spore dormancy in bryophytes would be worthwhile.

4.2.5. Standing crop and annual production
In the strategy model of McArthur and Wilson (1967), high standing crop is considered an important trait of the K-strategy. Annual production plays a primary role in the models of Grime (1974, 1978). Unhappily, on both characteristics only scattered data exist, and since there are large differences between methods of different authors, the results may be not directly comparable. Still, a broad comparison might be possible (Tab. 1).

High values of standing crop are shown particularly by open vegetation in which bryophytes comprise 50% or more of the community biomass (Forman 1969). The productivity of *Sphagnum* bogs is surprisingly high; this might partly be explained by the continuously high moisture content and therefore continuous photosynthesis possibility, whereas most terrestrial communities

Tab. 1. Standing crop and/or annual production of some bryophyte communities from literature data.

Author	Vegetation type	Bryophyte standing crop (ton ha⁻¹)	Bryophyte annual production (ton ha⁻¹)
Forman 1969	alpine	1.7–2.4	
	krummholz	0.5	
	coniferous woodland	0.6	
	coniferous deciduous woods	0.25	
	ecotone	0.08	
	northern hardwoods	0.03	
	oak woods	0.02	
Whittaker 1963	several heath and forest types in Great Smoky Mts	0.007–0.4	
1966	mosses in forests in Great Smoky Mts	0.02–3	
Rodin and Bazilevich 1967	arctic tundra	0.35–0.55	
	alpine tundra	0.1–1	
	shrub tundra	1.1–1.3	
Clymo 1964	*Sphagnum* bogs		(1–)3–5 (–12)
Clymo and Reddaway 1974	*Sphagnum rubellum* (=10–40% of comm. prod.)	1.4	
Tamm 1953, 1964, Romell 1939	*Hylocomium splendens* in Scandinavian forests	ca 2	0.5–1
Romose 1940	*Homalothecium sericeum*		0.5
	Philonotis fontana	6.4	
Callaghan et al. 1978	*Hylocomium splendens* in Swedish Lapland	0.57–1.75 mean 1.2	0.5–0.9
	Polytrichum commune in birch forest	0.006–0.4 mean 0.1	ca 0.2
Collins 1976	antarctic *Polytrichum* alpestre heath		4–6.5
Jacobsen 1978	S-African epiphytes (in 10 × 10 m² plots)		0.004–0.005
Munshi 1974	*Hydrogonium/Hyophila* community	0.2–0.95	0.73 max.
	Physcomitrium community	0.11	0.11
Joenje and During 1977	*Funaria* community in embanked polder	5	
Ketner 1972	salt marsh, above ground production, all plants		3–6
	idem, below ground		3–15
Willems 1979	limestone grassland, above ground standing crop, all plants		ca 3
	idem, heavily manured		ca 9

often experience prolonged periods of drought stress when photosynthesis is nil (Romose 1940; for a thorough account of problems of xerophytism in bryophytes, cf. Patterson 1964). Still, the figures for *Sphagnum* are high compared to the above ground biomass production of salt marshes (Ketner 1972) and limestone grasslands (Willems 1979); there, however, a large part of the production is transferred to the plant

parts below the soil surface (Ketner 1972), and the difference between gross production and net production is high due to, i.a., loss to animals between the harvests. In this context one may note the high leaf area ratio (LAR; leaf surface area per unit ground area) of bryophytes; Romose (1940) estimated the LAR for *Mnium hornum* turfs as 26, for *Physcomitrium* turfs as 25! For temperate forests this is 4 to 6 (Whittaker 1975).

In dry terrestrial communities, the highest standing crops are reached in open, stable communities, whereas open, unstable communities also have a rather high annual production but a distinctly lower standing crop, except for extraordinary situations as in the recently embanked Lauwerszee, which for a short time was very rich in nutrients (Joenje 1974). The needle forest communities in general show lower figures. In deciduous forests the bryophyte layer contains only a fraction of 1% of the community biomass (Forman 1969) and the production and standing crop of the bryophytes are very low; even lower figures are given by Jacobsen (1978) for epiphytes in South African forests.

The difference between r- and K-selected species with respect to maximum standing crop appears thus to be largely overshadowed by environmental influences. Still, the results of Callaghan et al. (1978) suggest that the more K-selected *Hylocomium splendens* has a higher standing crop than *Polytrichum commune*, whereas the more r-selected species of Munshi (1974) show a rather high annual production but a comparatively low standing crop.

4.3. Life span and mortality

The life cycle can be completed in less than one year in some ephemerals, such as *Funaria hygrometrica*, whereas plants of other species can live for many decades without reproducing. In *Riccia nigrosquamata*, the individuals can live for some years while the life span of each part of the thallus is only 7–10 wk in the growing season (Berrie 1975). In *Ceratodon purpureus* and others the plants mostly reach an age of 2–5 yr (Doignon 1949); the plants of *Campylopus introflexus* in the Netherlands reach 5–10 yr. Individuals of many long-lived species in relatively unchanging environments show a characteristic pattern: only the parts produced during the last few years are alive (Molisch 1929, Wangermann 1965, Collins 1976). Callaghan et al. (1978) found, that in *Hylocomium splendens* the plants might produce new shoots nearly infinitely provided the apex is not accidentally killed, and that the plant parts remained active little more than 2 yr, whereas in *Polytrichum commune* the shoots have a finite life expectancy and remain active for ca. 3–4 yr. The plants can be traced back through the dead shoots for a considerable time; a cushion of *Leucobryum glaucum* has been followed for 50 yr (Vallin 1974), and individual *Hylocomium splendens* plants reached an age of 80 yr

(Amann 1928). The age of some individuals of *Hymenostylium recurvirostre* in calcareous tufa was estimated as 2800 yr by Reichard (1860)!

The life span of the plants is rather plastic and often strongly determined by the environment. E.g., the normally annual *Physcomitrium pyriforme* regularly produces new shoots and lives for several years under cultivation conditions (During 1973a). In nature, regeneration from buds, protonema or leaf parts presumably is not rare (Correns 1899, Müller-Stoll 1965). For some species claimed to be annuals, evidence has been collected that they produce new shoots from a perennating protonema (*Buxbaumia:* Dening 1928, Hancock and Brassard 1974; *Ephemerum:* Meusel 1935). In a number of species the plants die off in times of stress, but leave tubers or gemmae (many hepatics in our regions) for the next growing season; in such cases the concept of individual becomes problematical.

Mortality of the gametophytes may have many different causes; a thorough study on this subject might be worthwhile. One of the very few species studied in this respect is *Polytrichum alpestre;* in antarctic populations mortality is partly restricted to the winter season and probably caused by freezing or drought, in addition to a non-seasonal component which is caused mainly by small catastrophes: droppings of large sea birds, debris falling, etc. (Collins 1976). The replacement rate of the shoots was positively correlated with their density. Mortality depends also on the age of the turfs: in young turfs the annual replacement rate varied around a mean of 32%, in older turfs this rate, averaged over 5 yr, was 13%. Since the main part of mortality took place during winter, the correlation with shoot density is not easily explained by intraspecific competition.

Kimmel (1962) and Van Laar and During (unpubl.) followed some permanent quadrats for a few years. The speed of the changes occurring on seemingly 'stable', unchanging forest soils and steep earth walls in forests was surprisingly high; after one year more than half of the plants had disappeared and where replaced by others of the same or another species. Also, there was large variation in life expectancy between the species even in one plot; species such as *Dicranella heteromalla* and *Campylopus flexuosus* had a much higher rate of replacement than, for example, *Dicranum scoparium* or *Leucobryum glaucum*. More detailed information is not yet available.

The experiments of Lipman (1936) shed some light on the reaction to drought stress, often considered one of the main causes of mortality (Clausen 1952, Abel 1956, among others). Living material of eight bryophytes, viz. *Dicranella heteromalla, Dicranum scoparium, Bartramia pomiformis, Hypnum patientiae, Thelia asprella, Entodon seductrix, Atrichum angustatum* and *Brachythecium cyrtophyllum*, was dried over H_2SO_4 under vacuum for 2 months; then half of each specimen was kept in liquid air (−190°C) for 50 h. Upon investigation after this treatment, the material of all

species looked healthy and alive, and though five species succumbed to fungal attacks after plantation in moist soil, the plants of Brachythecium cyrtophyllum, Hypnum patientiae and Thelia asprella grew as well as the dried but unfrozen plants for more than a year.

The sensitivity of plants to drought varies strongly according to species (Irmscher 1912); some species characteristically gain a high resistance to drought after several short drought treatments (Clausen 1952, Abel 1956, Patterson 1964, Dilks and Proctor 1976a, b).

The experiments mentioned show that severe drought and cold itself need not be lethal to the species studied. However, I still think that a combination of intermittent periods of drought and cold might be harmful. It is quite possible that this is an indirect cause, since the species become sensitive to other attacks. For other species, a surplus of water may be lethal, presumably because of the greater vulnerability for fungal attacks.

Such attacks by fungi, lichens or algae constitute another possibly important cause of death. Bryophytes can also be eaten by animals. Mice have both hepatics and mosses on their diet (Ferns 1966), and Smith (1977) found that some beetles on the Marion Islands ate 37% of their body weight per day of Brachythecium rutabulum. Predation by animals seems not to be particularly important, however (Crum 1973). Indirect influence of animals, for example the scattering of dense cushions by birds, thus causing a severe drying-out, probably has greater influence.

Lack of light will be one of the main causes of death below dense stands of phanerogams in nutrient-rich environments, and in forest litter accumulations. In one of my quadrats, the pattern of living and dead bryophyte material was mainly determined by the pattern of litter lying on it in a quiet autumn period after a spell of windy weather.

Overgrowing by individuals of other species will be a significant mortality factor in the course of successions, such as the succession of epiphyllous liverworts (Sjögren 1975) and during the vegetation changes on boulders in Norway (Lye 1967). This cause might well be indirect also through shadowing effects.

An obvious indirect cause of mortality is displacement or other changes of the substrate; falling down of tree branches or whole trees means for the epiphytes a significant change in water and light conditions, chances of litter cover, etc.

Recently much attention has been given to the theoretical negative effects of reproduction on the survival of the 'adults' (Stearns 1976). The idea is, that the efforts done to produce progeny, i.e. sporophyte production or production of asexual diaspores, have to be drawn from vegetative growth possibilities and thereby limit the chances of survival through a harsh season. The only information I could find on this subject in bryophytes are the observations of Callaghan et al. (1978) on Hylocomium splendens and Polytrichum commune; in the first species, shoots bearing

sporophytes grew much better than sterile shoots of the same degree of branching, and in the latter species shoot parts with male inflorescences die after ca. 4 yr (mean), whereas sterile shoot parts die after 2–3 yr. It might well be possible that in some species the formation and sprouting of new buds (innovations) is suppressed by a developing sporophyte; whether this has any influence on mortality is not clear.

Five categories of life spans of gametophytes can be distinguished, four of which have been mentioned earlier (Joenje and During 1977).

Ephemerals – life cycle generally shorter than one year, events in the cycle not restricted to a particular season; mortality mostly determined by abiotic factors.

annuals – life cycle normally one year, mostly strongly seasonal with a resting stage in which only spores are alive. Here, too, mortality is determined abiotically.

pauciennials – life cycle normally one or a few years, mostly strongly seasonal. Mortality has often partly biotic causes.

pluriennials – life cycle normally several years, few specimens reaching a higher age than 5–10 yr (short lived perennials); seasonality of the gametophyte less distinct. Mortality (indirectly) caused by competition of phanerogams or change of habitat.

long-lived perennials – life cycle many years, age of specimens often much higher than 5 yr; seasonality of the gametophyte less distinct. Several mortality causes all play some part, among which predation by animals and small habitat catastrophes.

The life span of spores has been investigated by Malta (1922). There is large variation in the time that spores of different species survive herbarium storage conditions, ranging from a few hours to decades (Malta 1922, Sussman 1965b). The spores of some species also appear to be very resistant to desiccation and low temperatures (Rabe 1905); Becquerel (1932) showed that spores of Atrichum undulatum, Brachythecium rutabulum, Ctenidium molluscum, Dicranella heteromalla, Funaria hygrometrica, Homalothecium sericeum, and Leucobryum glaucum survived when exposed to the temperature of liquid helium (–271°C), if dried and placed into evacuated tubes. Recently, Van Zanten (1978a, b) investigated the endurance of spores of different species under possibly lethal conditions such as extreme drought, freezing, and ultraviolet light, in comparison to the distributions of the species involved. Such a tolerance of extreme environmental conditions is especially meaningful in relation to spore size and number.

According to Correns (1899), asexual propagules such as gemmae and tubers may survive adverse conditions significantly longer than the gametophytic shoots, but mostly not as long as the spores; the less-specialised

10

propagules such as flagellae and broken-off leaf tips mostly did not survive much longer than the shoots.

4.4. Avoidance and tolerance

Individual plants and populations regularly experience periods of severe stress; in the Netherlands this is the dry summer period for most species, but periods of heavy snow cover or severe frosts in winter may also have strong effects. Adaptations to these periods is a crucial point in life strategies (Raunkiaer 1937, Grime 1974, Stearns 1976). In general, two alternative strategies occur: the plants die off and leave only highly stress-tolerant diaspores for the next growing season (avoidance), or the plants endure the stress period with as much of their vegetative parts as possible (tolerance) (cf. e.g. Thompson 1978).

The species showing the 'avoidance strategy' can be divided again into two groups: one with small to very small spores (less than 20 µm) and one with larger spores. Joenje and During (1977) suggest, that the first group is adapted to environments which are highly unpredictable. Woodland clearings fall into this category. The second group should then be adapted to habitats which also disappear, i.e., become unsuitable for the species, within a short period but which predictably reoccur on different spots in the same community stand, such as hoof prints along a brooklet, reindeer dung along a reindeer path in a bog, and (with a longer cycling period) bare tree branches. Among phanerogamic plants, species with a similar strategy often have a bank of dormant seeds in the soil (Harper 1977, Thompson 1978). Whether the bryophytes of this group have a similar 'spore bank' in the soil is not known to me; seed bank experiments of Willems (unpubl.) give the impression that especially for the small cleistocarpous annual acrocarps in limestone grasslands this might well be so. In a few occasions, dormancy of bryophyte spores seems to exist.

This tactic might be called the 'shuttle-strategy', as it is very characteristic of many species in 'shuttle'-situations (Van Leeuwen 1966, During 1973b).

The longer lived species of the tolerance strategy might be classified according to the size of their spores as well; another possibility is a classification according to their competitive ability and tolerance to stress (Grime 1974, 1978). For such a classification more should be known of relative growth rate and other characteristics of the species (Grime 1974). At present such data are known for only very few species, among which *Racomitrium lanuginosum* (Tallis 1959), *Sphagnum rubellum* (Clymo and Reddaway 1974), and *Polytrichum alpestre* (Collins 1976).

5. A preliminary system of life strategies in bryophytes

When we consider the distribution of life history traits within the bryophytes, it is clearly possible to distinguish some more or less consistent life strategies based upon traits that often occur together. Some suggestions in this direction were given by Joenje and During (1977); here I will elaborate the preliminary system somewhat, using the life history traits discussed above. I will focus on the reactions to fluctuations in the environment, especially their amplitude and predictability, because the variation in most life history traits seems to be connected strongly with such factors. The habitats have been compared to the classification of fluctuating environments of Stearns (1976). The growth forms mentioned are according to Gimingham and Birse (1957). The following strategies can be distinguished.

(1) *Fugitives*
The species with the fugitive life strategy have the following characteristics in common (Fig. 1):
  short life span; ephemeral-annual.
  high sexual reproductive effort; a very large proportion of the plants producing sporophytes.
  no asexual reproduction, innovations mostly absent.
  low age of first reproduction, within one year.
  spores small, less than 20 µm, very persistent and long-lived.
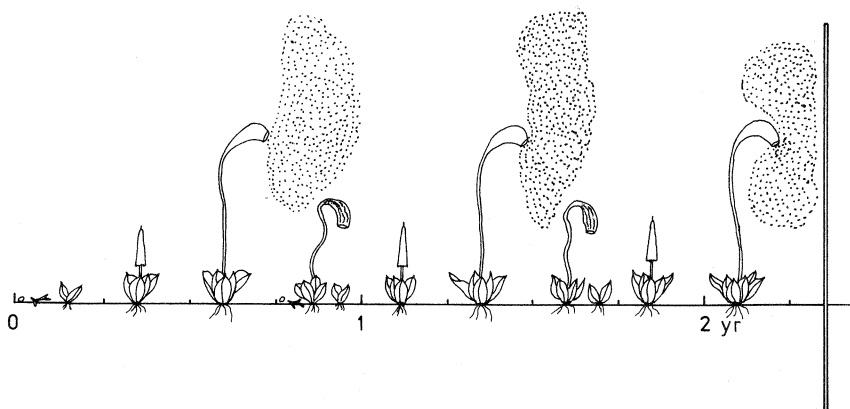 growth form predominantly Open Turf.

Fig. 1. The fugitive life strategy, schematically. Note non-seasonal reproduction, the small, widely dispersed spores, and absence of innovations and asexual propagation. The vertical bar symbolizes the end of the period when the habitat is suitable for the species.

Fig. 2. The colonist life strategy, schematically. Note initial importance of gemmae and tubers, the small spores and the presence of innovations.

The fugitive strategy fits in highly unpredictable environments that exist for only a short time, approaching environment type 3 (Random) of Stearns. The fugitives are often the first species in a secondary succession series. In the phanerogams this strategy is very rare; among the bryophytes *Funaria hygrometrica* is one of the few examples. It occurs most often in bacteria, algae and fungi (Stearns 1976). In Joenje and During (1977) this strategy is called '*Funaria hygrometrica* type'.

(2) *Colonists*
The life strategy of the colonists is characterized by (Fig. 2):

moderately short life span; (annual-) pauciennial-pluriennial.

high reproductive effort both in asexual and sexual diaspore production; asexual reproduction mostly concentrated in the early life stages, sporophytes later, then frequent.

innovations normally present.

age of first asexual reproduction low, often a few months; age of first sexual reproduction at least one year, mostly 2–3 yr.

spores small, less than 20 μm, and very persistent in most species; asexual propagules much larger.

growth form predominantly Short Turf, in some species Open Turf or Thalloid Mat.

The colonist strategy is often met with in environments the start of which is unpredictable in time and space, but that more or less predictably will last for some years (a few generations). This type of environment has some characteristics of type 1 (predictable long cycles) of Stearns. Examples of the species fitting in this group, called '*Bryum bicolor* group' by Joenje and During, are *Bryum argenteum*, *B. bicolor*, *Ceratodon purpureus*, and *Marchantia polymorpha*. According to the data presented by Keever (1957) and Hancock and Brassard (1974), respectively, also *Grimmia laevigata* and *Buxbaumia aphylla* would have this strategy.

Within this strategy now fall truly colonizing species such as *Bryum argenteum* and *B. bicolor* as well as species with a 'pioneer'-character (Rabotnov 1975) such as *Andreaea* and *Grimmia* species. A separation of these groups might be possible if their relative growth rates were known. In the cultivation experiments with *Grimmia pulvinata* mentioned above, the plants appeared to grow very slowly (5 mm in one year), whereas *Bryum bicolor* had a much higher growth rate.

The colonists often appear early in secondary succession series, together with or shortly after the fugitives (Joenje and During 1977). As the name indicates, the pioneers occur early in primary succession series, often on bare rocks.

A number of species have a life strategy that seems to be derived from this one but shows some characteristics of the 'shuttle'-strategies. The difference with the colonists is mainly the absence or at least rarity of the sporophytes and the strong reliance on asexual reproduction. The life span of the 'individuals' is mostly less than one to a few years. Examples are the species of the *Bryum erythrocarpum* complex, reproducing mainly by their subterranean tubers; *Zugodon viridissimus*, reproducing mainly by axillary gemmae; *Orthodicranum montanum*, *Campylopus fragilis* and *Dicranum tauricum*, with fragile shoots, leaves and leaf tips respectively. Still producing sporophytes, though rarely, are for example *Blasia pusilla*, *Leptobryum pyriforme* (depending on the strain under study), *Cephaloziella divaricata*, *Isopaches bicrenatus* and many other gemmiferous hepatics.

Especially the strategy of the *Bryum* '*erythrocarpum*' species and many of the liverworts, in which seasonal fluctuations sometimes play an important part, has a strong resemblance to the next category.

(3) *Annual shuttle species*
This strategy and the next ones are not bound to certain succession stages; they may occur in any stage, but different species may be restricted more rigidly in this re-
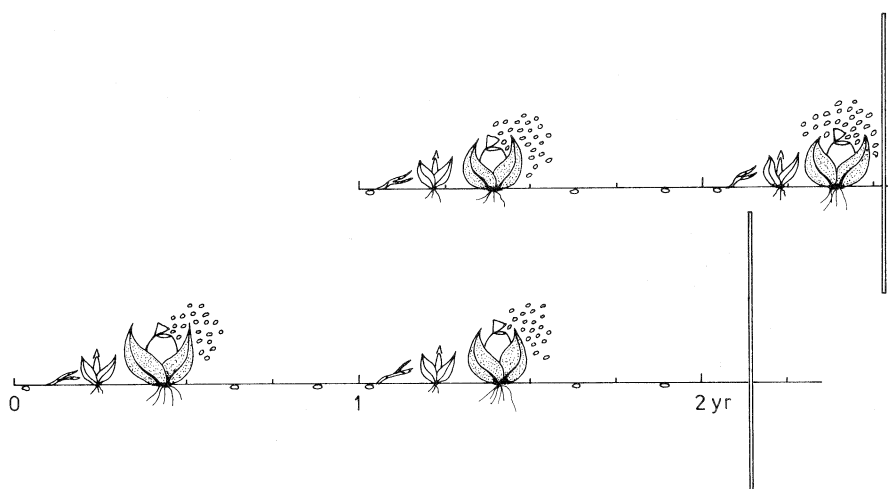
12

Fig. 3. The annual shuttle life strategy, schematically. Note seasonality of reproduction, large spores with small dispersal capacity and the absence of innovations and asexual propagation. The upper series symbolizes the possibility to shift to another gap in the same community.

spect. The relative importance of the different strategies mostly depends on frequency and variability of small disturbances within the communities studied. The annual shuttle strategy is characterized by (Fig. 3):

short life span; (ephemeral-) annual-pauciennial.

sexual reproductive effort high, sporophytes very frequent.

asexual reproduction absent, innovations mostly absent.

age of first reproduction low, normally less than 1 yr. spores large, 25–50 (–200) μm, life span mostly several years.

growth form Open Turf or Thalloid Mat, rarely Short Turf.

This strategy fits into a habitat which is present for only a short period (1–2 yr or less) on each spot but which predictably reappears frequently within the same community or in the neighbourhood ('gaps' cf. Grubb 1977). The life cycle is often strongly determined by seasonal fluctuations and a severe stress period which is 'avoided' by being present in the spore stage only. In Stearns' classification the habitat might be compared with type 2d: cyclic, period short, start predictable, conditions partially known.

The annual shuttle strategy is met with in many agricultural weeds, both angiosperms and bryophytes, and in such environments as hoof prints near drinking places, on steep sides along brooklets, on animal paths, on dung of large animals, and on several kinds of gaps in dry calcareous grasslands. Examples of the group, called '*Physcomitrium pyriforme* group' by Joenje and During, are *Physcomitrium pyriforme, Phascum cuspidatum, Ephemerum serratum, Riccia bifurca, Fossombronia incurva, Splachnum ampullaceum.*

(4) *Short lived shuttle species*

This strategy has much in common with the former one. It is characterized by (Fig. 4):

life span longer, pauci-pluriennnial.

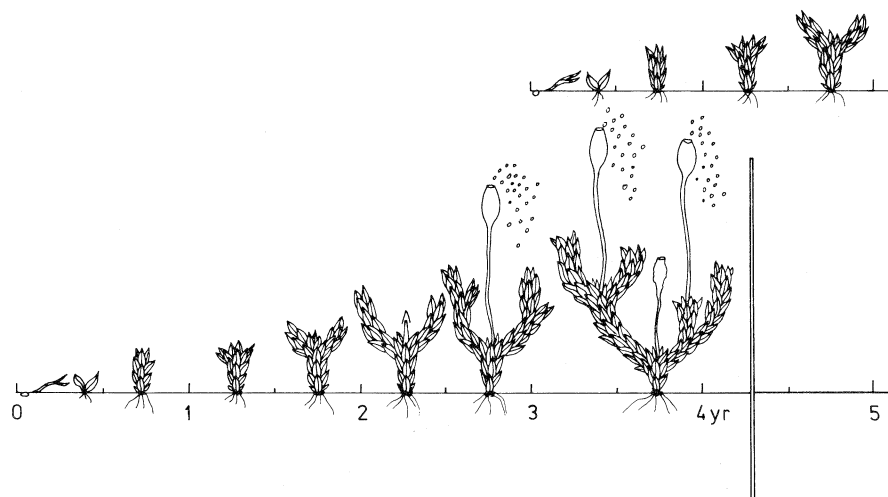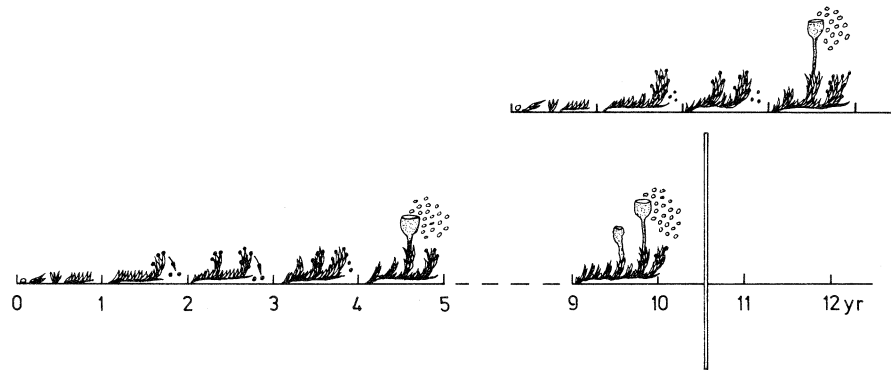sexual reproductive effort rather high, sporophytes ± frequent.

Fig. 4. The short-lived shuttle life strategy, schematically. Note large spores, presence of innovations and absence of asexual propagation.

Fig. 5. The perennial shuttle
life strategy, schematically.
Note large spores and
importance of asexual
propagation.

asexual reproduction rare or absent; innovations
normally present.
age of first reproduction ca. 2–3 yr.
spores large, 25–50 (–100) μm; life span probably
several years.
growth form Short Turf or Thalloid Mat.
The environments in which the species of this strategy
can be found are also much like those of the annual
shuttle species, but the strong avoidance of seasons with
severe stress is absent and the time during which the
habitat remains suitable is longer, 2–3 yr or slightly
more. Several species occur on temporarily open spots
on high parts of salt marshes (*Bryum marratii, B. war-
neum, Pottia heimii,* for instance); other possible
habitats include animal bones (*Tetraplodon mnioides*)
and calcareous grasslands. The strategy is called '*Bryum
angustirete* group' by Joenje and During (1977).

(5) *Perennial shuttle species*
This strategy was not mentioned by Joenje and During
(1977). It is characterized by (Fig. 5):
    long life span; pluriennial-perennial.
    sexual reproductive effort moderate, sometimes low
    to absent.

asexual reproductive effort moderate, rather high in
cases with rare or no sexual reproduction. Innova-
tions present.
age of first asexual reproduction variable, normally
exceeding 1–2 yr; age of first sexual reproduction
rather high (estimation: more than 5 yr).
spores (in regularly sporulating species) large,
25–200 μm, life span often short; asexual diaspores
large, too.
growth form Cushions, Rough Mats, Smooth Mats or
Tufts mostly.
The environments fit for this strategy are 'stable' (un-
changing, constant) and numerous within the com-
munity, but predictably end after a certain period. In
Stearns' classification they come near to category 2a.
Good examples are provided by many epiphytic
habitats. In the tropics many beautiful species have this
strategy, such as *Dicnemon* spp., the species of the
Garovaglioideae and *Macromitrium* spp. In Europe,
one might think of *Leucodon sciuroides, Antitrichia
curtipendula,* and several *Orthotrichum* and *Ulota*
species; here strategies intermediate between this one
and the colonist strategy are not rare. The distinction
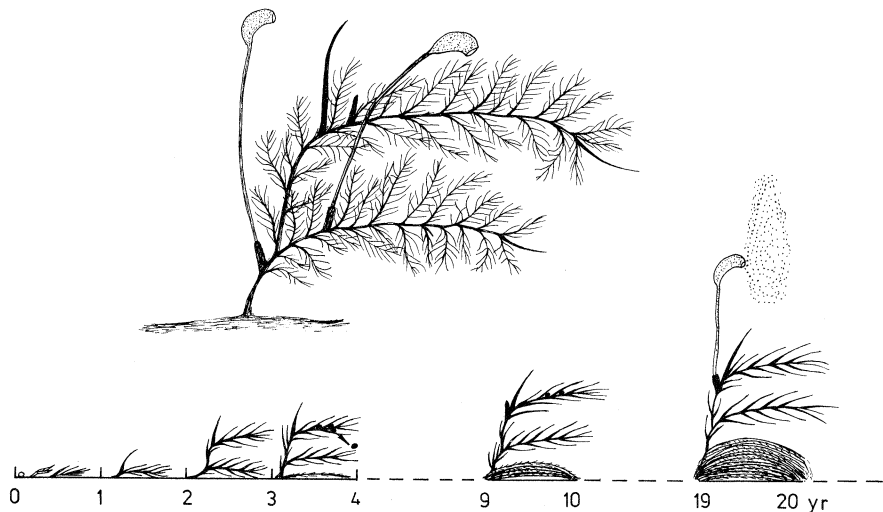between this strategy and the next one is not always
clear.

Fig. 6. The perennial stayer
strategy, schematically.
Spores small, annually new
shoots, asexual and sexual
propagation less important
than vegetative persistence.

14

(6) Perennial stayers

This strategy, called 'Brachythecium rutabulum group' by Joenje and During (1977), is most frequent in later successional stages. It is characterized by (Fig. 6):

> long life span; perennials.
>
> sexual and asexual reproductive effort rather low to nearly absent, sometimes very localized in small areas.
>
> age of first reproduction variable, several years at least.
>
> spores small, less than 20 μm; life span variable.
>
> growth form Wefts, Dendroids, Mats, also Large Cushions.

This strategy fits in more or less constant environments, or such, which may last very long (the tufa of Reichard 1860!), or in regularly fluctuating environments in which the fluctuations are tolerated by the plants (category 2a of Stearns). Most species of fens, bogs and forest floors belong here; examples are Sphagnum spp., Drepanocladus spp., Brachythecium spp., Leucobryum glaucum. A distinction of strategies within this group might be possible using the model of Grime (1974).

6. Discussion

6.1. Life history traits

The bryophytes as a group show widely diverging strategies. Still, in some respects they are more or less clearly distinct from the (equally diverging) strategies of phanerogamic plants.

Firstly, the diplohaplont life cycle with haploid gametophytes and dependent diploid sporophytes is a constant peculiarity of bryophytes, which has far-reaching implications for many aspects of population genetics and population biology. The extremely small gene flow distance, in dioicous species especially important for sexual reproduction, is related to this configuration of the life cycle and constitutes a second prominent difference with phanerogams.

In phanerogams as well as in bryophytes many species rely partly or sometimes wholly on asexual reproduction. In bryophytes, however, this reproduction without changing the genetic outfit is much more common and important for the persistence of the species, which again has implications for the rate of genetic recombination and evolution. The asexual reproductive units often serve as propagules for dispersal over moderate distances as well, which is decidedly rare in phanerogams.

The spores of bryophytes often reach a dispersal capacity as large as the pollen of the flowering plants, and even the largest spores of the shuttle species (and, for that matter, all asexual propagules) are miniatures compared to the large and heavy seeds of most phanerogams.

The small size and the absence of roots are indications that most bryophytes react in a different way to environmental stresses such as short periods of drought and cold in that they cannot draw upon reserves in the substrate even for a short period; even very xerotolerant species are not really xerophytic, but poikilohydric (Watson 1971). Moreover, some sensitive liverworts show distinct drought-avoidance in that the plants die, but leave resistant gemmae for the next favourable season. In this respect, the enormous regenerative capacity of bryophytes must be mentioned (Müller-Stoll 1965). The life span of (bi-)annual and ephemeral bryophytes is less strictly fixed physiologically than is the case in large groups of phanerogams (Harper 1977).

Finally, mortality has partly other causes in bryophytes than in phanerogams. In many phanerogams, mortality is highest in periods of active growth of the survivors, i.e. is often density-dependent (Harper 1977); as a result of this competition often a few large and many small plants grow together. The mean plant size is rather small and again density-dependent; in denser stands the mean plant size is smaller. In bryophytes, this intraspecific competition generally plays a much smaller role; in Polytrichum alpestre, Collins (1976) found the same relation between mean shoot size and shoot density, but here the shoots do not differ strongly in size, and mortality is nearly wholly caused by external influences such as frost damage, droppings of birds, debris etc. (Collins 1976). Predation is a second important cause of death in phanerogams (Harper 1977); in bryophytes, data are scarce, but many have the strong impression that the role of predation in mortality of the individuals is rather low (e.g., Crum 1973).

6.2. Strategies

One of the problems with the life form system of Raunkiaer (1937) is, that bryophytes and other cryptogams cannot easily be accomodated into it; moreover, nearly all species fall into one or two categories. The same holds more or less for the coenotypes of Ramensky (1938) and Rabotnov (1975). Bryophytes are nearly all explerents; a few species can be classified as pioneer. Grime's (1974) triangular model is better suited for bryophytes. Since information on competitive ability (relative growth rate, annual production) is only known for very few species, and the predictability of the microhabitats in my opinion plays a prominent role in bryophyte strategies, it is difficult at the moment to fully evaluate the usability of this model for bryophytes.

Conversely, of the life strategies described in this paper, the fugitive strategy hardly occurs among phanerogams. Also, the differentiation in the shuttle strategy is only partly found in phanerogams. In the r-K continuum of McArthur and Wilson (1967) and Pianka (1970), the K-selected species were thought to be characteristic of 'stable' situations, more or less the end points (climax) of succession seres (Gadgil and Solbrig 1972); this may be true for phanerogams, a 'stable', complicated climax community offers mainly life pos-

sibilities for different kinds of shuttle species of bryophytes (epiphytes, species on rotten wood and others), apart from the few species on the forest floor which show K-selected traits.

Consequently, productivity is a usable fitness measure for only a small group of bryophyte species, whereas in phanerogams it is by far the most important fitness measure (Harper 1977). In most bryophytes, fitness is related more to numbers and size of propagules, longevity and resistance of shoots and propagules, depending on the life strategy adopted. As, moreover, density dependent mortality plays a much smaller role, selection through competition is much less effective in bryophytes in an evolutionary perspective; selection operates mainly upon tolerance and avoidance of environmental stress, and is thus a force more apt to fixation of genotypes than to diversification of these. Together with the large role of asexual propagation, this might account for the slow evolutionary rate ascribed to bryophytes (e.g., Steere 1958).

References

Abel, W. O. 1956. Die Austrocknungsresistenz der Laubmoose. – Österr. Akad. Wiss. Wien, Math. naturw. Kl. Abt. I, 165: 619–707.

Amann, J. 1928. Bryogéographie de la Suisse. – Zürich.

Anderson, L. E. and Lemmon, B. E. 1974. Gene flow distances in the moss, *Weissia controversa* Hedw. – J. Hattori Bot. Lab. 38: 67–90.

Arnell, H. W. 1875. De skandinaviska löfmossornas kalendarium. – Akad. Avhandl. Uppsala.

Bakker, D. 1966. On life forms of hapaxanths in the Dutch flora. – Wentia 15: 13–24.

Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. – Assen.

– 1979. The investigation of vegetation texture and structure. – In: Werger, M. J. A. (ed.), The study of Vegetation, The Hague-Boston-London, pp. 123–160.

Becquerel, P. 1932. La vie latente des spores de mousses aux basses températures. – C. R. Acad. Sci. Paris 194: 1378–1380.

Benson-Evans, K. 1961. Environmental factors and bryophytes. – Nature, Lond. 191: 255–260.

– 1964. Physiology of the reproduction of bryophytes. – Bryologist 67: 431–445.

Berrie, G. K. 1975. The biology of a West African species of *Riccia* L. – J. Bryol. 8: 443–454.

Buch, H. 1920. Physiologische und experimentell morphologische Studien an beblätterten Laubmoosen I, II. – Oefv. Finska Vet.-Soc. Förh. A 62, no 6.

– 1947. Über die Wasser- und Mineralstoffversorgung der Moose I, II. – Soc. Sci. Fenn., Comm. Biol. IX, 16 + 20.

Callaghan, T. V., Collins, N. J. and Callaghan, C. H. 1978. Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polvtrichum commune* in Swedish Lapland. – Oikos 31: 73–88.

Campbell, D. H. 1918. The structure and development of mosses and ferns. – 3d ed., New York.

Clausen, E. 1952. Hepatics and Humidity. – Dansk Bot. Arkiv 15: 1–80.

Clymo, R. S. 1964. The origin of acidity in *Sphagnum* bogs. – Bryologist 67: 427–431.

– and Reddaway, E. J. F. 1974. Growth rate of *Sphagnum rubellum* Wils. on Pennine Blanket Bog. – J. Ecol. 62: 191–196.

Collins, N. J. 1976. Growth and population dynamics of the moss *Polytrichum alpestre* in the maritime Antarctic. Strategies of growth and population dynamics of tundra plants 2. – Oikos 27: 389–401.

Correns, C. 1899. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. – Jena.

Crum, H. 1972. The geographic origin of the mosses of North America's eastern deciduous forest. – J. Hattori Bot. Lab. 35: 269–298.

– 1973. Mosses of the Great Lakes Forest. – Contrib. Uni. Michigan Herb. 10: 1–404.

Crundwell, A. C. and Nyholm, E. 1964. The european species of the *Bryum erythrocarpum* complex. – Trans. Brit. Bryol. Soc. 4: 597–637.

Degenkolbe, W. 1937. Brutorgane bei beblätterten Lebermoosen. – Ann. Bryol. 10: 43–96.

Dening, K. 1928. Entwicklungsgeschichtliche Untersuchungen am Gametophyten von *Buxbaumia aphylla* (L.). – Verh. naturh. Ver. Preuss. Rheinl. Westphalens 85: 306–444.

– 1936. Untersuchungen über sexuellen Dimorphismus der Gametophyten bei heterothallischen Laubmoosen. – Flora 30: 57–86.

Dilks, T. J. K. and Proctor, M. C. F. 1976a. Seasonal variation in desiccation tolerance in some British bryophytes. – J. Bryol 9: 239–247.

– and Proctor, M. C. F. 1976b. Effects of intermittent desiccation on bryophytes. – J. Bryol. 9: 249–264.

Doignon, P. 1949. L régénération naturelle du peuplement muscinal dans les parcelles brûlées de la Forêt de Fontainebleau. – Rev. Bryol. Lich. N. S. 18: 160–168.

Düll, R. 1969. Moosflora von Südwestdeutschland. Allgemeiner Teil. – Mitt. Bad. Landesver. Naturk. Naturschutz N.F. 10: 39–138.

– 1970. Id. II. Teil: Die Laubmoose (Musci). – Ibid. 10: 301–329.

During, H. J. 1973a. On the difference between *Physcomitrium pyriforme* and *Funaria fascicularis*. – Lindbergia 2: 94–98.

– 1973b. Some bryological aspects of pioneer vegetations in moist dune valleys in Denmark, the Netherlands and France. – Ibid. 2: 99–104.

– 1977. A taxonomical revision of the Garovaglioidea (Pterobryaceae, Musci). – Bryophyt. Bibl. 12.

Ellenberg, H. and Müller-Dombois, D. 1967. A key to Raunkiaer plant life forms with revised subdivisions. – Ber. geobot. Inst. ETH, Stftg. Rübel 37: 56–73.

Ernst-Schwarzenbach, M. 1939. Zur Kenntnis des sexuellen Dimorphismus der Laubmoose. – Arch. Julius-Klaus Stiftung 14: 361–474.

Ferns, P. N. 1976. Diet of a *Microtus agrestis* population in south west Britain. – Oikos 27: 506–511.

Forman, R. T. T. 1964. Growth under controlled conditions to explain the hierarchical distribution of a moss, *Tetraphis pellucida*. – Ecol. Monogr. 34: 1–25.

– 1969. Comparison of coverage, biomass and energy as measures of standing crop of bryophytes in various ecosystems. – Bull. Torrey Bot. Club 96: 582–591.

Gadgil, M. and Solbrig, O. T. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. – Am. Nat. 106: 14–31.

Gaisberg, E. von 1921. Beiträge zur Kenntnis der Lebermoosgattung *Riccia*. – Flora N.F. 14: 262–277.

Gams, H. 1918. Prinzipienfragen der Vegetationsforschung. Ein Beitrag zur Begriffsklärung und Methodik der Biocoenologie. Vierteljahrsschr. Naturf. Ges. Zürich 63: 293–493.

Geiger, R. 1965. The climate near the ground. – 4th ed., Harvard, Cambridge.

Gimingham, C. H. and Birse, E. M. 1957. Ecological studies on growth-form in bryophytes I. Correlations between growth-form and habitat. – J. Ecol. 45: 533–545.

Goebel, K. C. 1905. Organography of plants II. – Oxford.

Greene, S.W. 1960. The maturation cycle or the stages of development of gametangia and capsules in mosses. – Trans. Brit. Bryol. Soc. 3: 736–745.

Grime, J. P. 1974. Vegetation classification by reference to strategies. – Nature, Lond. 250: 26–31.

– 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – Am. Nat. 111: 1169–1194.

– 1978. Interpretation of small-scale pattern in the distribution of plant species in space and time. – In: Freijsen, A. H. J. and Woldendorp, J. W. (ed.), Structure and Functioning of Plant Populations, Amsterdam, pp. 101–124.

Grimme, A. 1903. Über die Blütezeit deutscher Laubmoose und die Entwicklungsdauer ihrer Sporogone. – Hedwigia 42: 1–75.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. – Biol. Rev. 52: 107–145.

Hagerup, O. 1935. Zur periodizität im Laubwechsel der Moose. – Kgl. Danske Vidensk. Selsk. Biol. Medd. 11, 9.

Hancock, J. A. and Brassard, G. R. 1974. Phenology, sporophyte production and life history of Buxbaumia aphylla in Newfoundland, Canada. – Bryologist 77: 501–513.

Harper, J. L. 1977. Population biology of plants. – Academic Press, London.

Heitz, E. 1942. Die keimende Funaria-spore als physiologisches Versuchsobjekt. – Ber. Deutsch. Bot. Ges. 60: 17–27.

Hennig, W. 1966. Phylogenetic systematics. – Urbana.

Hoffmann, A. 1957. Untersuchungen über die Geschlechtsdifferenzierung bei haploiden und diploiden Gametophyten von Barbula unguiculata (Hudson). – Z. indukt. Abstamm. Vererb. Lehre 88: 374–387.

Howe, M. A. and Underwood, L. M. 1903. The genus Riella, with descriptions of new species from North America and the Canary Islands. – Bull. Torrey Bot. Club 30: 214–244.

Irmscher, E. 1912. Über die Resistenz der Laubmoose gegen Austrocknung und Kälte. – Jb. f. wiss. Botanik 50: 387–449.

Jacobsen, N. H. G. 1978. An investigation into the ecology and productivity of epiphytic mosses. – J. S-Afr. Botany 44: 297–312.

Jendralski, U. 1955. Die Jahresperiodizität der Entwicklung der Laubmoose im Rheinlande. – Decheniana 108: 105–163.

Joenje, W. 1974. Production and structure in the early stages of vegetation development in the Lauwerszee-polder. – Vegetatio 29: 101–108.

– and During, H. J. 1977. Colonisation of a desalinating Wadden-polder by bryophytes. – Vegetatio 35: 177–185.

Keever, C. 1957. Establishment of Grimmia laevigata on bare granite. – Ecology 38: 422–429.

Ketner, P. 1972. Primary production of salt-marsh communities on the island of Terschelling in the Netherlands. – Thesis, Univ. Nijmegen.

Kimmel, U. 1962. Entwicklung einiger Moose und Flechten auf Dauer-Untersuchungsflächen. – Ber. Oberhess. Ges. Natur- u. Heilk. Giessen, N.F. Naturw. Abt. 32: 151–160.

Kinugawa, K. and Nakao, S. 1965. Spore germination and protonemal growth of Bryum pseudo-triquetrum as a long day plant. – Bot. Mag. Tokyo 78: 194–197.

Kreulen, D. J. W. 1972. Spore output of moss capsules in relation to ontogeny of archesporial tissue. – J. Bryol. 7: 61–74.

Lackner, L. 1939. Über die Jahresperiodizität in der Entwicklung der Laubmoose. – Planta 29: 534–616.

Leeuwen, C. G. van 1966. A relation theoretical approach to pattern and process in vegetation. – Wentia 15: 25–46.

Lipman, C. B. 1936. The tolerance of liquid air temperatures by dry moss protonema. – Bull. Torrey Bot. Club 63: 515–518.

Lockwood, L. G. 1975. The influence of photoperiod and exogenous nitrogen-containing compounds on the reproductive cycles of the liverwort Cephalozia media. – Am. J. Bot. 62: 893–900.

Longton, R. E. and Greene, S. W. 1969a. The growth and reproductive cycle of Pleurozium schreberi (Brid.) Mitt. – Ann. Bot. 33: 83–105.

– and Greene, S. W. 1969b. Relationship between sex distribution and sporophyte production in Pleurozium schreberi (Brid.) Mitt. – Ann. Bot. 33: 107–126.

Lye, K. A. 1967. Studies in the growth and development of oceanic bryophyte communities. – Svensk Bot. Tidskr. 61: 297–310.

MacArthur, R. H. and Wilson, E. O. 1967. Theory of island biogeography. – Princeton Univ. Press, Princeton.

Mägdefrau, K. 1969. Die Lebensforme der Laubmoose. – Vegetatio 16: 285–297.

Mäkirinta, U. 1978. Ein neues ökomorphologisches Lebensformen-system der aquatischen Makrophyten. – Phytocoenologia 4: 446–470.

Malta, N. 1922. Über die Lebensdauer der Laubmoossporen. – Latv. Augstk. Raksti (Acta Univ. Latvi) 4: 235–246.

Meusel, H. 1935. Wuchsformen und Wuchstypen der europäischen Laubmoosen. – Nova Acta Leopoldina N.F. 3 (12): 123–277.

Mogensen, G. S. 1978. Spore development and germination in Cinclidium (Mniaceae, Bryophyta), with special reference to spore mortality and false anisospory. – Can. J. Bot. 56: 1032–1060.

Molisch, H. 1929. Die Lebensdauer der Pflanze. – Jena.

Müller-Stoll, W. R. 1965. Regeneration bei niederen Pflanzen (in physiologischer Betrachtung). – In: Ruhland, W. (ed.), Handbuch der Pflanzenphysiologie XV/2: 92–155.

Munshi, J. D. 1974. Seasonal changes in standing crop and annual net production of two moss communities at Varanasi. – Trop. Ecol. 15: 23–38.

Newell, S. J. and Tramer, E. J. 1978. Reproductive strategies in herbaceous plant communities during succession. – Ecology 59: 228–234.

Newton, M. E. 1971. A cytological distinction between male and female Mnium undulatum Hedw. – Trans. Brit. Bryol. Soc. 6: 230–243.

– 1978. Environmental factors controlling sexual reproduction in mosses of the genus Mnium. – Bull. Br. Bryol. Soc. 31: 11.

Nishida, Y. 1978. Studies on the sporeling type in mosses. –. Hattori Bot. Lab. 44: 371–454.

Nyholm, E. 1956. Illustrated Moss Flora of Fennoscandia II, 2. – Lund.

Oppenheimer, H. 1922. Das unterbleiben der Keimung in den Behälter der Mutterpflanze. – S-B. Akad. Wiss. Wien, math-nat. w. Kl. Abt. I, 131: 279–312.

Parihar, N. S. 1961. An introduction to Embryophyta Vol. 1. Bryophyta (ed. 4). – Allahabad.

Patterson, P. M. 1964. Problems presented by bryophytic xerophytism. – Bryologist 67: 390–396.

Pianka, E. R. 1970. On r- and K-selection. – Am. Nat. 104: 592–597.

Pitkin, P. H. 1975. Variability and seasonality of the growth of some corticolous pleurocarpous mosses. – J. Bryol. 8: 337–350.

Rabe, F. 1905. Über die Austrocknungsfähigkeit gekeimter Samen und Sporen. – Flora 95: 253–324.

Rabotnov, T. A. 1975. On phytocoenotypes. – Phytocoenologia 2: 66–72.

Ramensky, L. G. 1938. (Introduction to the geobotanical study of complex vegetations). – Selkhozgiz, Moscow.

Raunkiaer, C. 1904. Om biologiske Typer, med Hensyn til Planternes Tilpasning at overleve ugunstige Aarstider. – Bot. Tidsskr. 26: XIV.
– 1937. Plant life forms. – Oxford.
Reichard, H. W. 1860. Über das Alter der Laubmoose. – Verh. Zool. bot. Ges. Wien 10: 589–598.
Rodin, L. E. and Bazilevich, N. I. 1967. Production and Mineral cycling in terrestrial vegetation. – Oliver and Boyd, Edinburgh.
Romell, L. G. 1939. Den nordiske Blåbärsgranskogens produktion av ris, mossa och förna. – Svensk Bot. Tidskr. 33: 366–382.
Romose, V. 1940. Ökologische Untersuchungen über Homalothecium sericeum, seine Wachstumsperioden und seine Stoffproduktion. – Dansk Bot. Arkiv 10 (4): 1–134.
Saxton, W. T. 1930. The life history of Lunularia cruciata (L.) Dum. – Trans. Roy. Soc. S.-Africa 19: 259–268.
Schmidt, T. 1918. Die Verbreitung von Samen und Blütenstaub durch die Luftbewegung. – Österr. Bot. Z. 67: 313–328.
Schwabe, W. W. 1976. Photoperiodism in liverworts. – In: Smith, H. (ed.), Light and Plant Development, London: 371–382.
Servettaz, C. 1913. Recherches expérimentales sur le développement et la nutrition des Mousses en milieux stérilisés. – Ann. Sci. nat. Bot., Sér. IX. 17: 11–223.
Sjögren, E. 1975. Epiphyllous bryophytes of Madeira. – Svensk Bot. Tidskr. 69: 217–288.
Slack, N. G. 1977. Species Diversity and Community Structure in Bryophytes: New York State Studies. – Bull. N.Y. State Museum 428: 1–70.
Smith, V. R. 1977. Notes on the feeding of Ectemnorrhinus similis Waterhouse (Curculionidae) adults on Marion Island. – Oecologia (Berl.) 29: 269–273.
Southwood, T. R. E., May, R. M., Hassell, M. P., and Conway, G. R. 1974. Ecological strategies and population parameters. – Am. Nat. 108: 791–804.
Stearns, S. C. 1976. Life history tactics: a review of the ideas. – Qu. Rev. Biol. 51: 3–47.
Steere, W. C. 1958. Evolution and speciation in mosses. – Am. Midl. Nat. 92: 5–20.
Sussmann, A. S. 1965a. Physiology of dormancy and germination in the propagules of cryptogamic plants. – In: Ruhland, W. (ed.), Handbuch der Pflanzenphysiologie XV/2: 933–1025.
– 1965b. Longevity and resistance of the propagules of bryophytes and Pteridophytes. – Ibid.: 1086–1093.
Tallis, J. H. 1959. Studies in the biology and ecology of Rhacomitrium lanuginosum Brid. II. Growth, reproduction and physiology. – J. Ecol. 47: 325–350.
Tamm, C. O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). – Medd. Skogsforskn. Inst. Stockholm 43: 1–140.
– 1964. Growth of Hylocomium splendens in relation to tree canopy. – Bryologist 67: 423–426.
Thompson, K. 1978. The occurrence of buried viable seeds in relation to environmental gradients. – J. Biogeogr. 5: 425–430.

Thompson, R. H. 1941. The morphology of Riella affinis I. Germination of the spore and development of the thallus. – Am. J. Bot. 28: 845–855.
Ubisch, G. von 1913. Sterile Mooskulturen. – Ber. Deutsch. Bot. Ges. 31: 543–552.
Vallin, H. 1974. Vegetation changes in a moss cushion during 50 years. – Svensk Bot. Tidskr. 68: 169–191.
Vitt, D. H. 1968. Sex determination in mosses. – Michigan Botanist 7: 195–203.
Wangermann, E. 1965. Longevity and ageing in plants and plant organs. – In: Ruhland, W. (ed.), Handbuch der Pflanzenphysiologie XV/2: 1026–1057.
Warming, E. 1884. Über perenne Gewächse. – Bot Centralbl. 18, no 19.
Watson, E. V. 1971. The structure and life of bryophytes. – London.
Watson, M. A. 1974. The population biology of six species of closely related Bryophytes (Musci). – Ph. D. thesis, Yale Univ.
Whitehouse, H. L. K. 1966. The occurrence of tubers in european mosses. – Trans. Brit. Bryol. Soc. 5: 103–116.
Whittaker, R. H. 1963. Net production of heath balds and forest heaths in the Great Smoky Mountains. – Ecology 44: 176–182.
– 1966. Forest dimensions and production in the Great Smoky Mountains. – Ecology 47: 103–121.
– 1975. Communities and Ecosystems. – 2nd ed., Macmillan New York.
Wilbur, H. M. 1976. Life history evolution in seven milkweeds of the genus Asclepias. – J. Ecol. 64: 223–240.
– , Tinkle, D. W. and Collins, J. P. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. – Am. Nat. 108: 805–817.
Willems, J. H. 1979. Experiments on the relation between species diversity and above ground plant biomass in chalk grassland. – Acta Bot. Neerl. 28: 235.
Woesler, A. 1933. Entwicklungsgeschichtliche und cytologische Untersuchungen an den Vorkeimen einiger Laubmoose, sowie einiger Beobachtungen über die Entwicklung ihrer Stämmchen. – Beitr. Biol. Pflanzen 21: 59–116.
– 1935. Zur Zwergmännchenfrage bei Leucobryum glaucum Schpr. I. – Planta 24: 1–13.
Wyatt, R. 1977. Spatial pattern and gamete dispersal distances in Atrichum angustatum, a dioicous moss. – Bryologist 80: 284–291.
Zanten, B. O. van 1978a. Experimental studies on trans-oceanic long-range dispersal of moss spores in the southern hemisphere. – In: Suire, C. (ed.), Congrès international de bryologie Bordeaux 21–23 Novembre 1977, Comptes rendus. Bryophyt. Bibl. 13: 715–733.
– 1978b. Experimental studies on trans-oceanic long-range dispersal of moss spores in the southern hemisphere. – J. Hattori Bot. Lab. 44: 455–482.