Review

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Living together and living apart: the sexual lives of bryophytes

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Haploid gametophytes of bryophytes spread by clonal growth but mate locally, within an area defined by the range of sperm movement. Rarity of establishment from spores or vegetative competition can result in unisexual populations unable to reproduce sexually. Females typically outcompete males, probably because females expend fewer resources than males on the production of gametes. Extreme sexual dimorphism—tiny males growing as epiphytes on much larger females—has evolved many times. Haploid selfing is common in bryophytes with bisexual gametophytes, and results in completely homozygous sporophytes. Spores from these sporophytes recapitulate the genotype of their single haploid parent. This process can be considered analogous to 'asexual' reproduction with 'sexual' reproduction occurring after rare outcrossing between haploid parents. Ferns also produce bisexual haploid gametophytes but, unlike bryophytes, haploid outcrossing predominates over haploid selfing. This difference is probably related to clonal growth and vegetative competition occurring in the haploid but not the diploid phase in bryophytes, but the reverse in ferns. Ferns are thereby subject to stronger inbreeding depression than bryophytes.

This article is part of the themed issue 'Weird sex: the underappreciated diversity of sexual reproduction'.

1. Sexual lives of bryophytes

Animal life histories are characterized by multicellular diploid individuals that produce haploid gametes by meiosis. Gametes are the only haploid cells of such life cycles. The life histories of bryophytes (mosses, liverworts and hornworts) are fundamentally different. Multicellular haploid gametophytes (gamete-producing plants) produce gametes by mitosis. The fertilization of an ovum by a sperm produces a zygote that develops into a short-lived multicellular diploid sporophyte (spore-producing plant) that grows attached to the maternal gametophyte on which it depends for nutrients. Sporophytes produce haploid spores by meiosis that germinate to produce new gametophytes (figure 1). Mating is restricted to the distance over which sperm can find ova, usually in the millimetre to centimetre range [1]. Clonal expansion occurs via vegetative spread of gametophytes into neighbouring space and production of gemmae (asexual propagules) that disperse gametophytic clones to new sites [2].

Gametophytes of *dioecious* bryophytes are unisexual, producing either eggs or sperm, but not both. Males and females compete for space but require close proximity for sexual reproduction. By contrast, gametophytes of *monoecious* bryophytes are bisexual, able to produce both eggs and sperm. A bisexual gametophyte that fertilizes its own eggs engenders homozygous sporophytes all of whose spores are genetically identical (excepting meiotic errors and post-zygotic mutations). Roughly 70% of liverworts, 60% of mosses and 40% of hornworts are dioecious [3]. Bryophyte life cycles are not only fascinating in themselves, but also provide us a mirror for viewing better-known systems from a different angle. Among other topics, this paper explores the question when are males and females sexual collaborators who tolerate each other's presence and when are they asexual competitors who exclude each other from contested space?
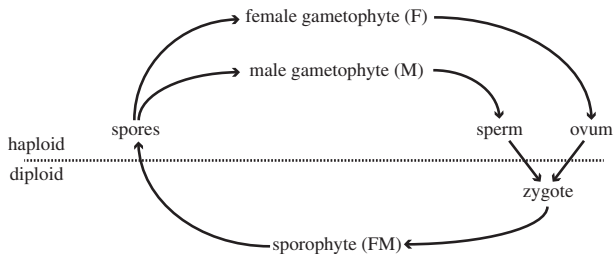
Figure 1. Life cycles of mosses, liverworts and hornworts possess multicellular haploid gametophytes that produce gametes by mitosis. Fertilization of an ovum by a sperm produces a multicellular diploid sporophyte that develops while attached to, and nutritionally dependent upon, its haploid mother (attachment is represented by shaded rectangle). Sporophytes produce haploid spores by meiosis. Spores germinate after dispersal to form the next generation of gametophytes. In species with chromosomal sex determination, male gametophytes possess an M chromosome and female gametophytes possess an F chromosome. In these species, sporophytes are obligate FM heterozygotes.

(a) Sex determination

The sex of unisexual gametophytes is determined by the segregation of sex chromosomes at meiosis, or at least, it is in the few species in which the question has been investigated. Such chromosomes have traditionally been called X and Y but I use F (for female) and M (for male) to distinguish them from chromosomes that determine sex in the diploid phase. In the F/M system of haploid sex determination, all sporophytes are FM heterozygotes, and each meiotic tetrad contains two F-bearing spores that develop into female gametophytes and two M-bearing spores that develop into male gametophytes (figure 1). As a corollary, the sex ratio is balanced at the completion of meiosis.

Heteromorphic sex chromosomes have been reported in several dioecious liverworts [4,5] but in relatively few dioecious mosses [6]. For most dioecious mosses, genetic sex determination is an assumption awaiting evidence. In recent years, molecular markers that segregate with sex have been identified in a few dioecious mosses [7,8]. The M chromosome of the liverwort *Marchantia polymorpha* has been sequenced, and the F chromosome partially sequenced [9,10]. These M and F chromosomes comprise, respectively, about 4% and 8% of the base pairs of a haploid genome [11]. In the moss *Ceratodon purpureus*, 35% of anonymous loci were sex-linked, consistent with the cytogenetically determined size of sex chromosomes in this species [12].

Gametophytes of most liverworts possess 8–10 chromosomes [13] and are unisexual [14,15]. The bisexual gametophytes of some monoecious liverworts possess 16 or more chromosomes and are therefore considered to be diploid descendants of haploid dioecious ancestors [16,17]. A similar association of monoecy with polyploidy occurs in mosses: some monoecious species have twice as many chromosomes as related dioecious species [18,19], and monoecious species, on average, have higher chromosome numbers than dioecious species [20]. The association of monoecy with polyploidy suggests diploid bisexual gametophytes originated from unreduced spores of FM diploid sporophytes of dioecious species and thus possessed all the genes necessary for both male (M) and female (F) sexual functions. Despite this attractive scenario, some bisexual gametophytes are haploid, and some unisexual gametophytes are polyploid [17,21,22]. Sex chromosomes have been reported from dioecious hornworts [23], but

most hornworts are monoecious [24]. Monoecious and dioecious hornworts have similar chromosome numbers [3]. Therefore, changes in ploidy do not appear to have been a major factor in changes of sexual systems in hornworts.

2. Sessile sex

Sexual reproduction is rare for many dioecious mosses but common for most monoecious mosses [25]. For example, sporophytes are rare, very rare, or unknown for 262 of 380 (69%) dioecious moss species in the British moss flora but for only 22 of 260 (8%) monoecious moss species. These numbers include 108 dioecious species (41%) and eight monoecious species (3%) for which sporophytes are unknown in Britain, including species in which sporophytes have never been observed anywhere [26]. The rarity of sexual reproduction for many dioecious bryophytes appears to be a consequence of mature male and female gametophytes rarely growing together within the range of sperm movement.

Spatial isolation of the sexes could be explained by rarity of establishment from spores, such that most local populations are established from a single spore, together with minimal subsequent intermingling of the sexes via asexual reproduction. Spatial isolation of the sexes could also be explained by competitive exclusion of one sex by the other within local populations. The most likely timing of competition would be during local establishment from spores, or gemmae, before the appearance of macroscopically visible plants. Competition could also be expressed in the inability of newly arrived spores or gemmae to become established in a macroscopic patch of the opposite sex. Rare establishment or intersexual competitive interactions are not mutually exclusive explanations of sexual isolation. If sexual reproduction is uncommon because of intersexual competition, then mixed-sex populations become less likely because of the rarity of spores. This paper focuses on the hypothetical effects of intersexual competition.

Vegetative competition among haploid clones, combined with short-range fertilization, means that local mating populations will often be small and that unisexual gametophytes will sometimes have no individuals of the opposite sex within the range of sperm movement. Even if local populations contain more than one clone, sometimes all clones will be one sex. The frequency of single-sex populations will increase as the number of clones in the local population decreases and as the sex ratio, in the general population from which the local population is recruited, deviates further from an equal balance of the sexes. The size of local mating populations will be determined, in part, by the growth habits of clones and their tendency to exclude other clones or to intermingle. Polytrichaceous mosses that exclude other species also exclude the other sex of their own species from their clumps [27].

If males and females occupy the same niche and undergo prolonged clonal growth without sexual reproduction, then whichever sex is the superior competitor would be expected to exclude the other sex from their shared habitat [28]. Sexual reproduction facilitates coexistence, because it resets the sex ratio among spores to equality, thus disproportionately benefitting the less competitive sex. When long-term clonal persistence is not an option, the sexes depend on each other for spore production. Thus, the relative importance of asexual and sexual reproduction will be a key determinant of intersexual relations. Long periods of sexual abstinence favour the

vegetatively competitive sex, but frequent sexual liaisons favour coexistence of the sexes, even sexual cohabitation.

Although each sex requires the other for reproduction via spores, this mutual dependence does not eliminate intersexual conflict. The genetic diversity of a gametophyte's sexual progeny is greater the larger the number of the opposite sex in the local mating population, but the gametophyte's expected fitness is greater the smaller the number of the same sex. In other words, gametophytes benefit from the company of multiple members of the other sex, but from being the only representative of their own sex. The absence of sexual competition between individuals of opposite sex does not necessarily translate into reduced vegetative competition between the sexes. Sex-specific attenuation of competition requires that other individuals be distinguishable by sex, but tolerance of the opposite sex could create evolutionary incentives for gametophytes to dissemble their sex when at a competitive disadvantage.

(a) Female advantage

Female-only populations of bryophytes outnumber male-only populations [29] and archegoniate (egg-producing) shoots often outnumber antheridiate (sperm-producing) shoots in mixed-sex populations [30]. The observed excess of female-only populations could result from a female bias in the sex ratio among spores, lower survival of male clones founded from a single spore or gemma, greater production of gemmae by females, or competitive exclusion of males by females when the sexes grow together [31,32]. The archegoniate bias could be explained, in principle, by fewer male shoots than female shoots producing gametangia [33]. However, an excess of female shoots generally persists when sex can be assigned to sterile shoots [34–38].

If sex is determined by the segregation of F and M chromosomes, or the segregation of male-specific and female-specific alleles at a sex-determining locus, then the sex ratio among spores should be 1 : 1 and observed biases would be postmeiotic in origin (although possibly influenced by different germinability of male and female spores). Genetic sex determination has been reported in several dioecious bryophytes [4–12], but information on more species would be desirable. I will assume as a working hypothesis, until contrary evidence becomes available, that there are equal numbers of male and female spores immediately after meiosis.

The best-supported hypothesis for explaining female biases in bryophytes is that females grow faster than males, because males invest more in unsuccessful sexual reproduction [33,39]. Females invest in sexual progeny via expenditures on archegonia before fertilization and sporophytes after fertilization. The cost of producing a few archegonia, in case sperm are present, is cheap compared with the cost of producing enough sperm to search the local area for archegonia that may or may not be present. Therefore, females can reinvest photosynthate in growth until an archegonium is fertilized, enjoying the advantages of compound interest, and then switch to investment in a costly sporophyte. By contrast, males invest in antheridia without a guarantee that an archegonium will be fertilized. Sperm that fail to find archegonia are sunk costs.

Female biases are predicted to decrease with the frequency of sexual reproduction, because sporophytes are provisioned exclusively by females. Indeed, in the clonal moss *Hylocomium*

splendens, females without sporophytes grow faster than males but females with sporophytes grow slower than males [40]. Stronger female biases are associated with fewer sporophytes, both in a phylogenetic comparison between two families of wetland mosses [41] and in a comparison between coastal and epiphytic populations of the liverwort *Frullania tamarisci* [42]. Sporophytes, of course, are necessarily absent in populations that lack males.

An additional factor that could contribute to a female advantage will briefly be mentioned. Chloroplasts and mitochondria of bryophytes are inherited via eggs but not sperm [12,43]. Strict maternal inheritance would mean that the evolutionary lineage of an organellar gene in dioecious taxa has spent all previous generations in female gametophytes and encounters each male gametophyte as an evolutionarily novel environment. Therefore, organellar genomes will have evolved to maximize female fitness without regard for effects on male fitness. This asymmetry might contribute to a growth advantage of female over male gametophytes, but the evolutionary lineages of nuclear genes will have repeatedly encountered organelles in gametophytes of both sexes, and will have been strongly selected to exploit organelles in male gametophytes.

The preponderance of archegoniate gametophytes in dioecious bryophytes contrasts with a preponderance of staminate sporophytes in dioecious angiosperms (with interesting exceptions) [44,45]. A factor that may contribute to female biases being more common in bryophytes than in angiosperms is that pollen can be transferred to ovules over much greater distances than sperm can be transferred to archegonia. Therefore, male angiosperms need not invest extensively in asexual reproduction as a form of mate search, and female angiosperms will more frequently experience the postzygotic costs of seed and fruit production.

(b) Sex, why bother?

Relative allocation to asexual and sexual reproduction should evolve to match the historical rates of return on investment. More should be invested in asexual reproduction when fewer opportunities exist for sexual reproduction, because marginal returns from investment in antheridia decline when fewer sperm fertilize archegonia and marginal returns from investment in archegonia decline when fewer are fertilized. This evolutionary dynamic has the potential for positive feedback. Less sex favours less investment in gametangia that favours further declines in the frequency of sex. If returns from sexual investment are sufficiently low relative to returns from clonal expansion, lineages that dispense altogether with sexual investment may have higher clonal fitness than lineages that retain sexual function.

An evolutionary tension exists between sexual and asexual reproduction in dioecious bryophytes. Some haploid genets may live for hundreds, perhaps thousands, of years. During clonal growth, natural selection is inoperative against mutations that impair strictly sexual functions and may even favour such mutations if resources can be reallocated from gametangia and sporophytes to vegetative growth and asexual propagules. For both these reasons, mutations that degrade sexual functions will accumulate in long-lived clones [46,47]. Successful reproduction via spores, on the other hand, is only possible for subclones that retain sexual functions. Thus, gametophytic populations are expected to contain older clones

comprising subclones, some of which are no longer sexually competent, and younger genets that are sexually competent. If sexual reproduction is sufficiently rare, then sexual competence may be lost from the population by a combination of drift and selection for vegetatively vigorous subclones.

Female gametophytes pay the full cost of sporophytes even though only one spore in two inherits any particular female-derived gene. By contrast, every asexual propagule inherits the female's entire genome. Thus, investment in asexual propagules yields twice the return of an equivalent investment in spores, other things being equal. For this reason, natural selection will tend to favour functions of dispersal and perennation being performed by asexual propagules rather than by spores. Investment in archegonia and sporophytes should be reserved for those functions that depend on the unique attribute of spores as the genetically variable products of sexual reproduction.

A bisexual gametophyte always has itself as a potential mate. Gametophytic selfing produces sporophytes, all of whose spores are genetically identical to each other and to the subtending bisexual gametophyte. These spores are not subject to twofold dilution with alleles of another gametophyte and may evolve functions performed by asexual propagules in dioecious species. Gametophytic selfing is, in effect, a form of asexual propagation, but one that requires the maintenance of the genetic machinery of antheridia, archegonia and sporophytes. Monoecious species are therefore less subject than dioecious species to mutational meltdown of sexual functions.

3. Intersexual relations

Intersexual relations undoubtedly vary among bryophytes. Many gametophytes occur in single-sex populations. Mating systems have not been studied in species with strong female biases and rare sporophytes. Perhaps females in these species can be conceptualized as 'black widows' that spend long periods without partners, produce sporophytes with males when they meet, then promptly eliminate their mate to wait and grow, until their next brief sexual encounter. For other dioecious species with abundant sporophytes, males and females grow intertwined [48] or males grow as minute dwarfs on female leaves (see §3b). Sporophytes are also abundant in monoecious species in which bisexual gametophytes mate with themselves.

(a) Promiscuity and fidelity

Two studies of dioecious peat mosses suggest a range of possible mating systems. A population of *Sphagnum lescurii* from North Carolina, USA, contained many different male and female genotypes. The sporophytes on a single female shoot had, on average, four different haploid fathers [49]. This suggests a promiscuous mating system. By contrast, all sampled shoots of *Sphagnum fuscum* from a large bog (Fuglmyra) in Norway were assigned to one of two major haplogroups interpreted as two clones. Both clones occurred on transects 250 m apart and both were detected in 50 year old peat, with one detected in 450 year old peat [50,51]. Abundant sporophytes at Fuglmyra suggest that the clones are of opposite sex. These clones are intermingled over many metres and have coexisted for at least 50 years, perhaps much longer, without one competitively excluding the other within the mire. Under this interpretation, *Sphagnum fuscum* at

Fuglmyra consists of a monogamous couple in a long-term sexual relationship. Because *Sphagnum fuscum* creates and maintains its own hummock habitat [52], the bog at Fuglmyra could be considered the extended phenotype of a 'diploid' pair of haploid gametophytes producing trillions of spores over hundred of years for the chance that a few lucky spores establish new bogs.

(b) Dwarf males

Tiny males grow epiphytically on much larger females in many moss species [53,54]. Males are sometimes reduced to no more than a few leaves sheathing a single antheridium [55]. Male dwarfs are facultative in some species but obligate in others. In one survey, dwarf males were detected in 72 out of 162 (44%) dioecious mosses, with full-sized males unknown in 18 of these species [54]. Male dwarfism appears to have evolved many times independently [54,56]. Taxa in which full-sized males are unknown are puzzling. Why should males abandon the option of growing to substantial size in the absence of females? Dwarfing probably occurs on a continuum from taxa in which tiny males grow on female leaves to taxa in which males facultatively produce antheridia at smaller size in the presence of females.

Males that exhibit facultative dwarfing appear to modify their growth in response to contact with females. Males of *Leucobryum juniperoideum* develop as dwarfs on female leaves. But when a dwarf male is detached from a female leaf and grown in culture, he grows to large size [57,58]. Full-sized males produce much larger antheridia, and presumably many more sperm, than dwarf males [58]. Sporophyte-bearing cushions of this species always contain males, either as large leafy stems or epiphytic dwarfs, whereas cushions without sporophytes lack males [57].

Female colonies with sporophytes are rare in many species with dwarf males [57–59]. However, once the first male arrives and sires the first generation of sporophytes, spores from these capsules can fall onto maternal leaves and produce a second generation of dwarf males that are both offspring and mates of their mum [60,61]. The second generation of sporophytes can then produce a third generation of dwarf males who mate with a female who is simultaneously both their mum and their grandmum. ('Mum' is used to refer to haploid egg-producers to distinguish them from diploid 'mothers' [62].)

A study of 1399 shoots of *Homalothecium lutescens* found 465 fertile female shoots and two full-sized males, with dwarf males on eight female shoots. Several dwarf males were present on five of these shoots, suggesting local recruitment [63]. In other populations of this species, most female shoots carried dwarf males, sometimes numbering in the hundreds [64]. Genotypes of dwarf males showed that many were closely related to the female shoot on which they grew, probably her offspring, but some appeared to have been dispersed from other colonies [65]. Genotypes of sporophytes revealed that multiple paternity was common on a single shoot with some sporophytes homozygous for every one of 68 single-nucleotide polymorphisms [66]. Multiple generations of haploid males mating with a longer-lived haploid mum is an extreme form of inbreeding, but complete homozygosity at so many loci is somewhat puzzling, because heterozygosity should be maintained at sex-linked loci if sex is genotypically determined.

(c) Intra-tetrad mating

A few dioecious liverworts disperse spores as persistent meiotic tetrads [1]. Each tetrad contains two male spores and two female spores. Thus, male and female gametophytic 'siblings' disperse together and potentially mate with each other. Such matings have unusual genetic properties that maintain substantial heterozygosity. Sex chromosomes and homologous centromeres segregate at meiosis I and are reunited by intratetrad mating. Therefore, this form of mating maintains heterozygosity at all centromeres and all loci for which there is no crossover between the locus and its centromere [67,68]. Heterozygosity is lost in 50% matings at loci for which there is exactly one crossover between the locus and its centromere but in less than 50% of matings for two or more crossovers [69].

The dispersal of two male and two female spores to a single site is seemingly inefficient. Would it not be better to break each tetrad into two dyads, each a male with a female, and disperse spores to two sites rather than one? There may be developmental reasons why bisexual dyads are difficult to evolve. Sex chromosomes are believed to segregate at anaphase I, with spores formed after simultaneous cytokinesis at the end of telophase II. The formation of bisexual dyads would require mechanisms to ensure that non-sister spores are dispersed together. Persistent dyads have been reported in three species of *Haplomitrium* [70–73]. There are two interpretations of the sexuality of these dyads. The first interprets the two spores as of opposite sex, ensuring the joint dispersal of the sexes and allowing intra-dyad matings [70,74]. The second interprets the two spores of a dyad as same-sexed products of meiosis II [73]. This question will be resolved empirically, but the first interpretation makes more adaptive sense.

Males are much smaller than females in some liverworts that disperse spores in persistent tetrads [75]. Growth of male thalli of *Riccia curtisii* and *Sphaerocarpos stipitatus* initially keeps pace with growth of female thalli but falls behind once males start to produce antheridia [75,76]. Slow growth of males once archegonia are fertilized, whether these are conventional dwarf males or males dispersed in persistent tetrads, may be a form of paternal care in which males limit their own growth to increase the resources females can invest in the male's sporophytic offspring [54]. Within a male–female couple, jointly procreated spores are a common good, but asexual propagules are private goods. Cooperation between the sexes will be most stable when neither sex has other reproductive options including asexual propagation. Gemmae are generally absent in species that disperse spores as persistent dyads or tetrads (for the sole reported exception, see [77]). I have found no reports of dwarf males producing gemmae, although gemmae are reported from females of species with dwarf males [60,78].

(d) Monoecious mating

The existence of abundant sporophytes on bisexual gametophytes, compared with rare sporophytes on unisexual female gametophytes, has been interpreted as evidence for frequent gametophytic selfing in monoecious bryophytes [1,25,59,79]. However, one would expect sporophytes to be more common on bisexual gametophytes, even in the absence of gametophytic selfing, because all possible combinations of bisexual gametophytes can produce sporophytes on each and every gametophyte whereas sporophytes never occur on male gametophytes nor on female gametophytes in single-sex groups.

Recombination is often considered more common in dioecious than monoecious bryophytes, because spores produced by gametophytic selfing are genetically uniform, whereas spores produced by outcrossing are genetically variable. However, one must compare the number of outcrossed sporophytes, not the proportion of outcrossed sporophytes, to determine the relative rates of recombination, because monoecious taxa produce more sporophytes than dioecious taxa. When two unisexual gametophytes occur together, and are of opposite sex, then sporophytes produced on the female gametophyte are always outcrossed. By contrast, when two bisexual gametophyte occur together, self-sperm compete with other-sperm to fertilize archegonia on both gametophytes. Clearly, the general belief that recombination is less common in monoecious taxa depends on an implicit assumption that self-sperm outcompete other-sperm when both are present, perhaps because archegonia are closer to self-antheridia than other-antheridia, because antheridia and archegonia develop in synchrony or because archegonia and self-sperm exchange a 'secret handshake' unknown to other-sperm.

The twofold dilution of maternal alleles in outcrossed sporophytes compared with gametophytically selfed sporophytes suggests natural selection should favour fertilization by self-sperm over other-sperm. An advantage of self-sperm has been demonstrated in at least one monoecious moss. When pairs of *Funaria hygrometrica* gametophytes were grown together, 98% of capsules were produced by gametophytic selfing [80]. Direct evidence of frequent selfing by bisexual gametophytes comes from findings of genetic identity between gametophytes and associated sporophytes. Different clumps of monoecious *Weissia controversa* had different numbers of supernumerary chromosomes, but numbers were uniform within clumps. All sporophytes had karyotypes consistent with mating within a clonal clump [79,81]. Allozyme and microsatellite studies in monoecious mosses find that most sporophytes are homozygous, consistent with frequent gametophytic selfing [82–84], although one study of monoecious liverworts found that 5% of sporophytes of *Pellia borealis* and 25% of sporophytes of *Pellia epiphylla* were sired by mating between gametophytes [85,86].

4. Comparisons with ferns

Fern gametophytes are sessile haploid organisms that reproduce sexually by short-range fertilization, with diploid progeny (sporophytes) developing at the site of fertilization. All these features are shared with bryophytes. Despite these similarities, somewhat more than half of all bryophytes, but no homosporous ferns, are dioecious [3]. Universal monoecy of homosporous ferns is probably related to vegetative competition among sporophytes, rather than among gametophytes, and increased genetic loads relative to bryophytes.

Clonal propagation of bryophytes is restricted to the haploid phase. An archegoniate clone may produce multiple mature sporophytes, in multiple years, at multiple sites. Each sporophyte is short-lived, without asexual reproduction, remains attached to and nutritionally dependent upon its mum, and occupies an area much smaller than the range of sperm movement. Sporophytes do not directly compete with each other for space. By contrast, clonal propagation of ferns occurs in the diploid phase and sporophytes compete for space. Fern sporophytes become nutritionally independent from and

typically outlive, their mum. A mature sporophyte can vegetatively dominate an area much greater than the range of sperm movement. Although many young sporophytes may be conceived within a local mating population, only one occupies that space at reproductive maturity. Bryophytic gametophytes achieve high fitness by producing many sporophytes, whereas pteridophytic gametophytes achieve high fitness by producing a single successful sporophyte.

Gametophytes of many bryophytes are perennial, produce asexual propagules, and can therefore afford to delay sexual reproduction until propitious circumstances. By contrast, most fern gametophytes are short-lived and lack asexual propagules. Rapid production of a fern sporophyte is at a premium. Bisexuality gives a fern gametophyte two options—via an egg and a sperm—of contributing genes to the sporophyte that triumphs in competition within its local neighbourhood [87]. These considerations may explain why dioecious mating systems, with genetically determined sex, are unknown among homosporous ferns. Gametophytes of some fern species precociously produce antheridia in the presence of larger archegoniate gametophytes, but the existence of local populations of unisexual gametophytes is a labile response of potentially bisexual gametophytes [88–90].

(a) Inbreeding depression

Many monoecious bryophytes produce most sporophytes by gametophytic selfing. Although gametophytes of some ferns regularly self-fertilize [91], this is the exception rather than the rule. Some ferns have mixed mating systems in which outcrossed sporophytes are provisioned preferentially but selfed sporophytes mature in the absence of outcrossed sporophytes [92], whereas others appear to be almost exclusive outcrossers [93]. A bisexual gametophyte doubles its genetic representation in a sporophyte by fertilizing its own archegonia. Why should fern gametophytes forgo this immediate benefit of haploid selfing? A possible answer is that relatively small reductions of vigour greatly diminish an inbred sporophyte's prospects in winner-takes-all competition with neighbouring sporophytes, thus outweighing the twofold cost of outbreeding.

Inbreeding depression may be less of a problem for bryophytes than for ferns. Mutations that impair gametophyte functions, including functions shared by gametophytes and sporophytes, will be eliminated by within-clone selection during gametophytic growth. Moreover, mutations with diploid-specific effects will be immediately exposed to selection in homozygous sporophytes produced by gametophytic selfing [94]. For these reasons, the genetic load among spores of monoecious bryophytes is expected to be low. Similar arguments apply to dioecious bryophytes, except that recessive mutations with sporophyte-specific effects are shielded from selection in heterozygous sporophytes. The limited data currently available find little evidence of inbreeding depression in monoecious bryophytes but hints of inbreeding depression in some, but not all, dioecious bryophytes [49,80,95].

Most ferns undergo prolonged vegetative growth as diploid sporophytes. Recessive mutations that impair haploid functions will accumulate during prolonged clonal propagation of sporophytes. Such mutations are shielded from natural selection until spore production, when gametophytic growth remains an effective filter for mutations with essential functions in the haploid phase. Most mature fern sporophytes are the products of gametophytic outcrossing rather than

selfing. Therefore, recessive sporophyte-specific mutations are not immediately exposed to selection [96]. As a consequence, outbreeding ferns may accumulate substantial genetic loads for loci with sporophyte-specific effects [97].

Inbreeding depression has been inferred from smaller size of inbred moss sporophytes [49,80] and from failures of isolated fern gametophytes to produce sporophytes by gametophytic selfing [98–100]. Because mature moss sporophytes and early fern embryos obtain much of their nutrition from their mum, these measures of 'inbreeding depression' reflect an interaction between the genotypes of haploid mums and diploid offspring. Early losses of inbred sporophytes could be interpreted as adaptive behaviour of maternal gametophytes if resources can be reallocated from lower-quality to higher-quality sporophytes [87]. Fern gametophytes that fail to mature sporophytes in one experiment may subsequently produce a viable homozygous sporophyte. This phenomenon has been called 'leaky lethality' [101], but could also be interpreted as strategic behaviour by maternal gametophytes who first wait for an outcrossed sporophyte but then switch to default provisioning of a selfed sporophyte [87,92].

(b) Asexual comparisons

Many ferns possess apogamous life cycles in which gametophytes develop from unreduced spores (diplospory) then bud sporophytes directly from these gametophytes (apogamy) [102]. Such life histories are unknown in bryophytes, although apogamy can be induced experimentally [103]. Thus, there seems to be no fundamental developmental constraint that prevents the evolution of apogamic life histories in bryophytes; rather, bryophytes achieve the same 'asexual' ends by different means. Bisexual gametophytes of bryophytes frequently produce homozygous sporophytes by gametophytic selfing which then produce haploid spores genetically identical to the haploid parent. By contrast, heterozygous sporophytes of apogamic ferns produce heterozygous spores and heterozygous gametophytes, all replicating the same diploid or higher-ploid genotype. The prevalence of apogamic life histories among ferns may be a consequence of the accumulation of genetic load in sexual ancestors that habitually outcrossed.

Apogamous ferns are common in xeric habitats. Apogamy has been proposed to be advantageous when free water is rare because it eliminates the need for sperm to fertilize archegonia [104,105]. Free water, however, is occasionally present in most habitats occupied by fern gametophytes, and some monoecious mosses of xeric habitats regularly produce sporophytes despite the absence of apogamy. Apogamy may nevertheless provide advantages when opportunities for fertilization are rare, and local populations of fern gametophytes compete to produce a single mature sporophyte, because apogamy gives a gametophyte a head start over sexual competitors that must wait for fertilization in the race to produce this sporophyte.

Many dioecious bryophytes propagate by clonal growth of gametophytes, with sexual reproduction rare or absent. In some taxa, sporophytes are unknown. Most ferns, by contrast, propagate as perennial sporophytes and possess gametophytes that lack means of asexual reproduction. Gametophytic production of gemmae, however, has evolved in three families of predominantly epiphytic ferns [106]. Some of these ferns exist as self-perpetuating populations of gametophytes with rare, short-lived sporophytes. In some cases, sexual reproduction

has been lost altogether and populations are maintained exclusively by clonal proliferation of gametophytes [107–109].

5. Conclusion

Distinctive features of bryophyte sexuality are consequences of clonal proliferation of sessile haploid organisms that mate within small local neighbourhoods. Sexual reproduction is rare in many species with unisexual gametophytes, because mixed-sex populations are rare. Such populations must rely on asexual forms of reproduction for their short-term persistence.

Gametophytic selfing is common in species with bisexual gametophytes and is functionally equivalent to 'asexual' reproduction. In such species, spore production can serve a dual function of 'clonal' spread via spores produced by gametophytic selfing and genetic recombination in spores produced by gametophytic outcrossing. Gametophytic selfing is rarer in ferns, probably because of higher genetic loads secondary to clonal proliferation as diploid sporophytes.

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