ULTIMATE COSTS OF SPOROPHYTE PRODUCTION IN THE CLONAL MOSS *HYLOCOMIUM SPLENDENS*

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Abstract. A richly sporophyte-producing population of the dioecious perennial clonal moss *Hylocomium splendens* was followed for five years in order to investigate the long-term costs of sporophyte production. Female mature segments were divided into two subpopulations: sporophyte producing and reference without sporophytes. Ultimate (long-term) population growth rates of $\lambda = 1.091$ and 1.258, respectively, were found for the two subpopulations by building separate deterministic transition matrix models. By bootstrapping each subpopulation, the difference in λ between subpopulations was found to be significant ($P < 0.001$). Life-table response experiment analysis attributed the lower population growth rate of the SP subpopulation to inferior ramification rates, lower survival, and inferior size development of mature segments. Considerable variation in *H. splendens* sporophyte production among years indicates large among-year variation in investment in sexual reproduction, probably related to resource status. Establishment of *H. splendens* from spores in natural habitats has never been observed. Nevertheless, sexual spores may play a role in establishment of *H. splendens* populations on new substrates.

Key words: bootstrapping; boreal forest (southeastern Norway); bryophyte; clonal plant; elasticity; Hylocomium splendens; *life-table response experiment; matrix models; models, transition matrix; population growth rate; sexual reproduction; somatic costs.*

INTRODUCTION

Trade-offs between investment in sexual reproduction and vegetative growth imply costs of sexual reproduction that are paid in terms of decreased growth or survival or future reproduction (Williams 1966, Syrjänen and Lehtilä 1993, Reznick et al. 2000). However, short-term effects of reproductive events on growth and survival have long-term population consequences only if reproductive costs more than outweigh the long-term (ultimate) fitness benefits (Calvo and Horvitz 1990, Calvo 1993). The balance between benefits and costs of reproduction can be assessed quantitatively by use of a formal demographic model (Ackerman and Montalvo 1990, Ehrlén and Eriksson 1995), e.g., a population transition matrix model, in which the contribution from each component of the life cycle to long-term fitness is integrated into a single value, the population growth rate (λ; Caswell 2001). While a wide range of ecological issues have been addressed by matrix population modeling (Caswell 2001), this approach has rarely been used to study the cost of reproduction in plants (e.g., Sohn and Policansky 1977, Calvo and Horvitz 1990, Calvo 1993, Ehrlén and Eriksson 1995, Silvertown and Dodd 1999). Recent developments in

population matrix modeling provide opportunities for evaluating the reliability of population growth rate estimates (Kalisz and McPeek 1992, Alvarez-Buylla and Slatkin 1994, Caswell 2001) and for statistically testing the significance of differences in long-term population growth due to costs of reproduction. This opens the door for comparative studies of population growth rates, necessary to validate ecological and evolutionary theory (Lenski and Service 1982).

Bryophytes are attractive organisms for tests of theory in reproductive biology because of their simpler structure compared with vascular plants. Notably most bryophytes lack belowground structures that allow a more flexible use of energy and nutrients. Furthermore, costs of bryophyte sexual reproduction are not likely to be offset by photosynthesis of reproductive structures (Proctor 1977, Renault et al. 1992). Nevertheless, while costs of sexual reproduction have been demonstrated for many vascular plants, problems with nondestructive identification of the tiny ''individuals'' (Rydgren and Økland 2002*a*) have hampered studies of bryophytes (Ehrlén et al. 2000). Using a colored-ring tagging technique (Økland 1995), this obstacle has been overcome, at least for larger-sized species.

This study aims at testing whether sexual reproduction in females of *Hylocomium splendens* has long-term demographic costs. We approached this aim by carrying out a demographic study of an abundantly fertile population over a five-year period. Population growth

PLATE 1. *Hylocomium splendens* mat in spring (May) at the study site. In the middle of the photograph, some female segments carry almost mature sporophytes. A male segment with antherida on the branches appears directly beneath this. Approximate height of the female segment from where it emerges is 15 mm. Photograph by K. Rydgren.

rates (λ) of the sporophyte-carrying subpopulation and the subpopulation of females without sporophytes were calculated and compared statistically by use of population matrix modeling in combination with resampling techniques. In addition, we quantified the contribution of different life-stage transitions to the observed difference in λ by performing a life-table response experiment (Horvitz et al. 1997, Caswell 2001) analysis.

MATERIALS AND METHODS

Hylocomium splendens, a pleurocarpic moss with modular growth (see Plate 1), is widely distributed in the northern hemisphere (Persson and Viereck 1983). New modules develop annually, most often in spring, from the main axis of one-year-old segments. Segment chains remain connected until they decompose from below (after 2–20 yr) or are injured (Tamm 1953, Økland 1995). Growing points become mature segments in their second autumn. *H. splendens* is dioecious and gametangia develop in spring on growing points that develop into mature segments the subsequent autumn (Bakken 1994). Fertilization is followed by seta elongation in autumn and sporophytes reach maturity the next spring or summer (van der Wijk 1960, Bakken 1994). *H. splendens* shares with many vascular plants (Lacey 1986, Wesselingh et al. 1997) and some lichens (Hestmark 1992) a size threshold for sexual reproduction (Rydgren et al. 1998*b*, Rydgren and Økland 2002*b*). Sporophyte production in *H. splendens* varies strongly both between habitats and between years (Cal-laghan et al. 1978, Økland 1995, Rydgren and Økland 2001, 2002*b*).

Data collection

Data were collected over a five-year period (1995–1999) in a small *Picea abies* forest valley north of Stampetjern, Skedsmo municipality, Akershus County, Southeastern Norway (11°09′ E, 59°59′ N), 170 m above sea level, on a boulder (area: ~0.8 m²; average slope: 38°) that was almost completely covered by *Hylocomium splendens*. A rectangle of 0.4 × 0.9 m was placed at the center of the top surface of the boulder and divided into 36 grid plots, 10 × 10 cm each. Annual census of all *H. splendens* shoots was performed for five years (1995–1999) in the nine plots that contained two or more sporophyte-carrying segments at the start of the study in 1995. At each annual census (see Økland [1995] for details), we carefully searched for all growing points present at the previous census, and all new growing points were mapped and nondestructively tagged, using plastic rings. Presence of sexual structures (archegonia and antheridia) and, for female segments, the number of sporophytes on each mature segment, were recorded. The population had a 4:1 female-biased sex ratio (Rydgren and Økland 2002*b*). Sporophytic and non-sporophytic individuals grew intermingled on the boulder, reducing possible environmental effects on size. The size (dry mass, DM, expressed as base-2 logarithms whereby one unit corresponds to doubling of the size, and sizes becomes
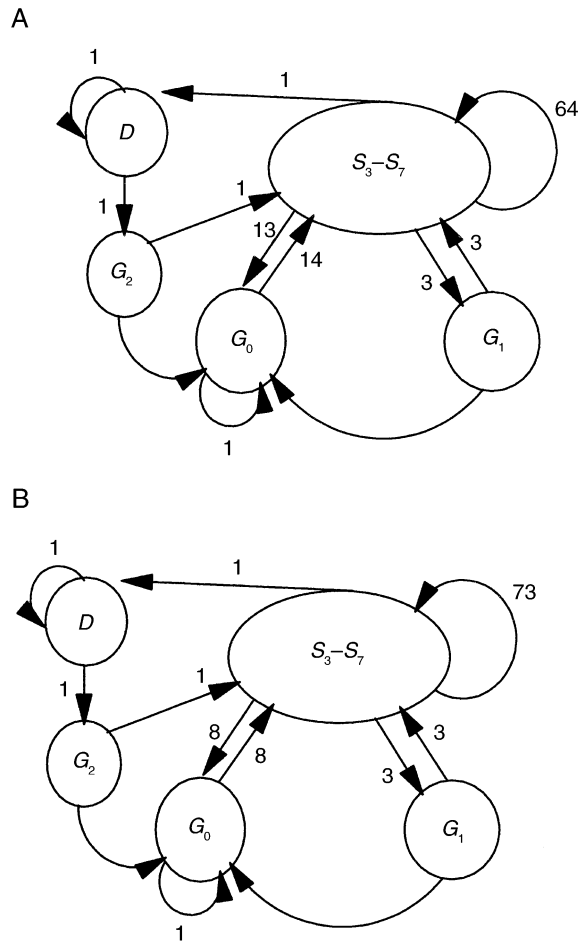
A

B

FIG. 1. Life-cycle graphs for (A) the reference subpopulation and (B) the sporophyte subpopulation of *Hylocomium splendens*. The numbers on the figure are the elasticities (only shown where $\geq 1\%$). For simplicity, the five classes of mature segments (S classes S_3–S_7) were lumped. The classification into life stages (D = diaspore bank; G = growing points) is explained in *Materials and methods: Construction of transition matrices.*

normally distributed) of all mature segments was estimated from in situ morphological measurements (segment length, number of branches, and length of the longest branch) by a nonlinear regression model (R^2 = 0.913, n = 328 mature segments; see Økland 1995).

Construction of transition matrices

Female *H. splendens* segments were classified into nine life-stage classes (Fig. 1): five S classes for mature segments according to estimated dry masses (S_3, $\log_2$ DM < 4; S_4, $4 \leq \log_2$ DM < 5; up to S_7 ($\log_2 \geq$ DM 7); three G-classes to account for growing points that have not yet developed into mature segments, arising by other branching processes than the normal, single ramification from the one-year-old main shoot axis (G_0 for the second and further ramifications from the one-year-old shoot axis; G_1 and G_2 for growing points re-

generating from two- and from three-year-old tissue [or older, or from detached fragments of indeterminable age], respectively); and a "diaspore bank" (D), included for technical reasons to account for the emergence of G_2 growing points (Fig. 1). The half-life of D individuals was fixed to 1 yr because a segment's regenerative ability is approximately halved each year after maturation (Økland 1995). In cases of multiple ramifications, the largest daughter segment (upon maturity) was placed in the appropriate S class, while the other(s) were recorded as G_0. The number of mature segments one year before the start of the first transition period was estimated according to Økland (1995), and used as the initial number of "individuals" in the diaspore bank.

All transitions recorded in the four transition periods, from female life stages in one year (t) to offspring life-stages in the next year ($t + 1$), were pooled in order to obtain a large data set in which short-term variation between years, not of interest in the context of the present study, was averaged out. Next, we classified the transitions into two subpopulations, the reference subpopulation (REF) and the sporophyte subpopulation (SP), according to the presence or absence of young sporophytes on the maternal segment at time t.

G_0 and G_1 growing points were classified to subpopulation according to the sporophyte status of their source segment. A G_1 growing point was allocated to the SP subpopulation if and only if its source segment carried sporophyte(s) the previous year. G_1 growing points emerging in 1995 were not included in matrix models because information on the source segment was not available. For G_2 growing points and the diaspore bank D the sporophyte status of the source segment was generally not known and all recorded segments were therefore included in both subpopulations. The resulting matrix models are expected to provide conservative estimates, because of negative effects of sporophyte production on population growth rates (K. Rydgren and R. H. Økland, *unpublished data*).

For each subpopulation, the full set of transitions were bootstrapped to estimate means and confidence intervals for λ (Kalisz and McPeek 1992, Caswell 2001). Resampling was made separately for mature segments, G_1 and G_2 growing points. By keeping the relative proportions of segments from each of these three categories invariant among the resampled matrices, we avoided introducing variation into the sets of bootstrapped matrices that was irrelevant to, and hence might obscure, the costs of sporophyte production per se. The ratio of G_2 "individuals" to the total number of mature segments was fixed for each resampled data set to equal that in the pooled data (both subpopulations taken together). For the SP subpopulation with 260 mature segments and 14 G_1 growing points, every bootstrapped sample included 26 G_2 growing points. The corresponding figures for the REF subpopulation were 456 mature segments, 23 G_1 growing points, and 44 G_2
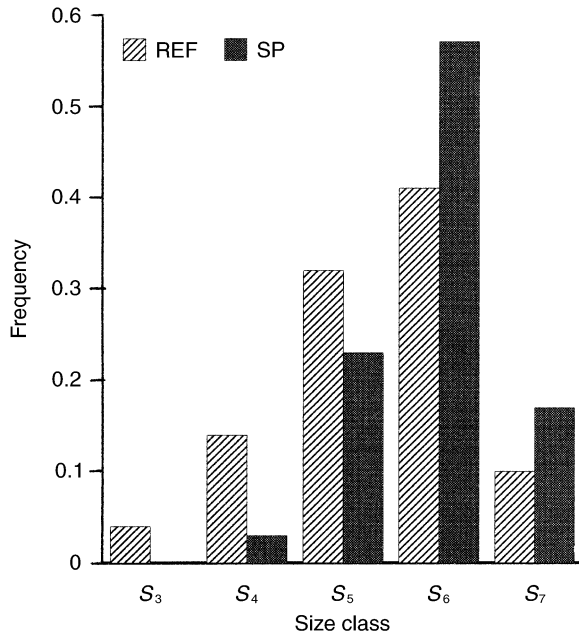
FIG. 2. Size distributions of mature female *Hylocomium splendens* segments of the reference (REF; $n = 456$) and sporophyte (SP; $n = 260$) subpopulations at the start of the transition period. Size is given in $\log_2$ dry mass (DM) units; see Materials and methods: Data collection for information on size-class estimation.

growing points. Stochastic variation in the frequency by which G_2 growing points arises from the diaspore bank, the D–G_2 transition probability, was introduced for each pair of bootstrapped matrices (one from each subpopulation) by drawing a G_2 regeneration frequency f with replacement from a sample with 500 randomly distributed numbers in the range 0.020–0.056. A scaling factor x was drawn from a normal distribution with mean $\pm$ 1 SD = 1.00 ± 0.06 and truncated range 0.80–1.20. The D–G_2 transition probabilities for the REF and SP bootstrap matrices were then obtained as fx and $f(2 - x)$, respectively. The D–D transition was kept constant at 0.500 in all matrices. Altogether 1000 pairs of bootstrapped data sets were generated.

Matrix analyses

Transition matrix models (Caswell 2001) of the form $\mathbf{d}_{t+1} = \mathbf{A} \cdot \mathbf{d}_t$ were used, where $\mathbf{d}_t$ and $\mathbf{d}_{t+1}$ are 9×1 column vectors, containing the distribution of mature segments among nine life-stage classes in years t and $t + 1$; $\mathbf{A}$ is a 9×9 matrix, each matrix element a_{ij} giving the probability of transition from class j to class i between t and $t + 1$.

The population growth rate (λ), sensitivities, and elasticities (de Kroon et al. 1986, 2000) were calculated from the transition probability matrices for REF and SP subpopulations (the matrices in which every element in the sample used for bootstrapping was included

once). Furthermore, λ was calculated for the 2000 bootstrap matrices (in 1000 pairs).

Bootstrap estimates for the mean λ and its 95% confidence interval (CI) were obtained by the percentile method (Caswell 2001). The quotient $(x + 1)/(n + 1)$ was used as α in a one-tailed, nonparametric test of the hypothesis that λ for REF and SP subpopulations were equal (where x is the number of bootstrap matrix pairs for which $\lambda_{SP} > \lambda_{REF}$, n is the total number of bootstrap matrix pairs).

We applied life-table response experiment (LTRE; Horvitz et al. 1997, Caswell 2001) analysis to the two transition probability matrices to quantify the contributions of different vital rates to the difference in population growth rate between the REF and the SP subpopulations. Our data represent a fixed treatment (Horvitz et al. 1997, Caswell 2001) so that the difference in λ between the treatment (λ^t) and the control (λ^c) is given as

$$\lambda^{(t)} - \lambda^{(c)} \approx \sum_{ij} (a_{ij}^{(t)} - a_{ij}^{(c)}) \times \left(\frac{\partial \lambda}{\partial a_{ij}} \bigg| \frac{(\mathbf{A}_t + \mathbf{A}_c)}{2} \right)$$

where $(a_{ij}^{(t)} - a_{ij}^{(c)})$ is the difference in transition probability a_{ij} between a treatment matrix and a control matrix, and $\delta\lambda/\delta a_{ij}|(\mathbf{A}_t + \mathbf{A}_c)/2$ is the sensitivity of transition a_{ij} in the mean matrix (the matrix "halfway" between $\mathbf{A}_t$ and $\mathbf{A}_c$).
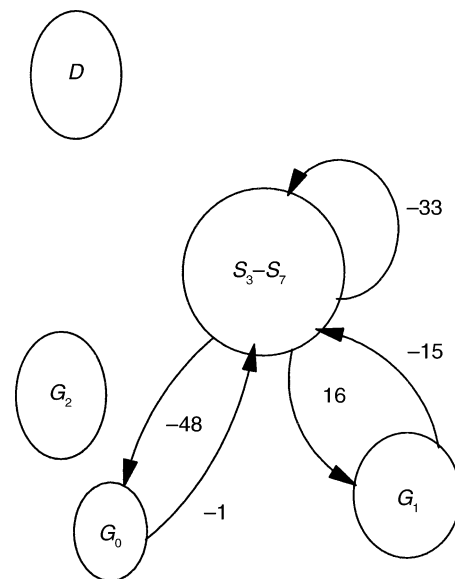

FIG. 3. Life-cycle graph showing the results of the life-table response experiment (LTRE) analysis for identifying the contribution of each life-stage transition to the difference in population growth rate $\Delta\lambda$ of -0.167 observed between the sporophyte and the reference subpopulation of *Hylocomium splendens*. Only life-stage transitions that contribute ≥ 0.001 to $\Delta\lambda$ (multiplied by 1000) are shown. The explained contributions here sum to -0.081 units, which is 49% of $\Delta\lambda$. The classification into life stages (D = diaspore bank; G = growing points; S = mature segments) is explained in Materials and methods: Construction of transition matrices.

RESULTS

Segment size distributions

Hylocomium splendens segments were significantly larger in the sporophyte subpopulation (SP) ($\log_2$ DM = 6.37 ± 0.66 [mean $\pm$ 1 SD]) than in the reference subpopulation (REF) ($\log_2$ DM = 5.88 ± 0.98) at the start of the transition period (*t* test of difference; t_{714} = 7.29, $P < 0.001$). Thus a larger proportion of the SP subpopulation had large segments than the REF subpopulation (Fig. 2). The size difference between subpopulations was probably not due to environmental variation, as REF and SP segments grew intermingled throughout the entire study area in all years.

Population growth rates

The population growth rates of the two subpopulations, REF without sporophytes and SP with sporophytes, were $\lambda_{REF} = 1.258$ and $\lambda_{SP} = 1.091$, respectively. These estimates corresponded closely to the means of 1000 bootstrap λ values for each subpopulation ($\lambda_{REF} = 1.257$ and $\lambda_{SP} = 1.091$). The 95% confidence intervals for the λ have ranges from 1.204 through 1.319 for REF and from 1.020 to 1.153 for SP. Population growth rates differed significantly between the two subpopulations ($P < 0.001$). In none of the 1000 bootstrap matrix pairs was $\lambda_{SP} > \lambda_{REF}$.

Elasticity analyses

Survival of mature segments (the S–S self-loop; cf. Fig. 1A) contributed 64% of the total elasticities in the REF subpopulation. Production of additional growing points by ramification (S–G_0) and the maturation of G_0 growing points (G_0–S) were the branching processes contributing most strongly to λ—13% and 14% of the total elasticity, respectively (Fig. 1A). The contributions from different transitions to λ differed little between the SP and the REF subpopulations. The most noticeable differences were observed for mature segment survival; in the SP subpopulation (Fig. 1B) the S–S self-loop contributed 73% and transitions S–G_0 and G_0–S only 8% each to the total elasticity. Regeneration made similar and low contributions to λ in both subpopulations.

Life-table response experiment (LTRE) analysis

The difference in population growth rate between the SP and the REF subpopulations was -0.167, of which the LTRE analysis accounted for 49% (-0.082 units). The lower λ of the SP subpopulation was ascribed mainly to the lower rate of multiple ramification; the S–G_0 transition that contributed -0.048 to the difference, and to the mature-segment survival that contributed -0.033 (Fig. 3). The negative contribution from mature-segment survival was a result of negative contributions (-0.042) from transitions among large segments (S_6 and S_7) and transitions from medium-sized segments (S_4 and S_5) to large segments (-0.013), while transitions from large segments to medium-sized segments gave positive contributions (0.023). Positive contributions to $\Delta\lambda$ were also provided by the initiation of G_1-regenerated growing points.

DISCUSSION

Our results demonstrate a significant long-term difference in population growth rate λ between sporophyte-producing *Hylocomium splendens* segments and female segments that do not carry sporophytes. The LTRE (life-table response experiment) analysis shows that sporophyte production reduces the frequency of multiple ramifications (S–G_0 transitions), brings about lower mature segment survival and inferior size development (S–S transitions), and causes inferior size development of G_1 growing points that develop into mature segments (G_0–S). Sporophyte production is associated with higher frequency of G_1-regenerated offspring (S–G_1), however, all these results are in agreement with short-term (one-year) costs of sexual reproduction for the same subpopulations (K. Rydgren and R. H. Økland, *unpublished manuscript*).

Our analyses are built on the assumption that spores, the sexual reproductive units, have zero fitness. Any successful establishment of new gametophytes from spores under natural conditions will reduce the difference in λ between segments that do or do not invest in sexual reproduction. The lack, so far, of observations of new *H. splendens* gametophytes establishing from spores under field conditions (Økland 1995, Jonsson and Esseen 1998, Rydgren et al. 1998a), and the absence of a soil-buried propagule bank in this species (Jonsson 1993, Rydgren and Hestmark 1997), suggest that sporophyte production has a negative effect on the population growth rate in established vegetation. There are, however, indications that *H. splendens* spores germinate in new, previously unoccupied substrates following land upheaval areas (N. Cronberg, *personal communication*). This raises the possibility that sexual reproduction is ecologically important in sites where soil is recurrently exposed following disturbance.

Recruitment mainly by asexual reproduction is a trait that *H. splendens* (Callaghan et al. 1978, Økland 1995, Rydgren et al. 1998b, 2001) shares with many other dioecious mosses (Longton 1992). The ubiquitous distribution (Persson and Viereck 1983) and high genetic variation (Cronberg et al. 1997) of *H. splendens* populations are apparently in contrast to the notion that rarity of dioecious bryophytes results from failure in sexual reproduction (Longton 1992). Alternatively, establishment of *H. splendens* from sexual spores may occur, at least intermittently (Cronberg et al. 1997; N. Cronberg, *personal communication*), contributing significantly and positively to the population growth rate.

The demographic costs of sexual reproduction, as estimated by comparing subpopulations of fertile and nonfertile females, represents the difference between populations with maximal and minimal investment in

sexual reproduction, respectively. Consequently, our study does not establish how large the fertile proportion of the population must be to create long-term demographic costs for the population as a whole. In natural forest-floor populations of *H. splendens*, where frequencies of sporophytic mature segments as low as 0.05% to 4.4% (of all segments) have been reported (Callaghan et al. 1978, Økland 1995, Rydgren and Økland 2001; N. Cronberg, *personal communication*), the demographic costs associated with sexual reproduction are likely to be very low. Even on cliff walls and boulders, from which sporophyte frequencies of 8% to 29% have been reported (Rydgren and Økland 2002*b*), sexual reproduction incurs costs that are likely to be small relative to the variation in population growth rate between years (Økland 1997) and between sites (R. H. Økland, *unpublished data*).

The large between-year variation in sporophyte production in *H. splendens* (Rydgren and Økland 2001, 2002*b*) shows that this species has a flexible allocation to sexual reproduction that, in addition to internal factors such as the resource status or size of individual segments (Økland 1995), also depends on external factors such as microclimate (e.g., radiation, temperature, and moisture). Furthermore, segments that carry sporophytes are generally large (cf. Fig. 2) and therefore tend to place themselves in favorable vertical positions in the bryophyte carpet (Rydgren and Økland 2002*b*; also see Økland 2000). *H. splendens* has mechanisms, at the levels of individual segments and the population, to ensure that investments in sexual reproduction are not made unless sufficient resources are available. Environmental variability may act as a long-term selective force for flexible allocation to sexual and asexual reproduction (Westley 1993).

In the forest floor, where *H. splendens* has high spore and sporeling mortality and low adult mortality (Økland 1995, 1997), continuation of the segment chain by clonal growth ("survival") is the main strategy for *H. splendens* persistence (Rydgren et al. 2001). In environments with low and relatively stable adult mortality and unpredictable and often large juvenile mortality, sexual reproduction will continuously be kept at a low level and have negligible effects on population fitness (Syrjänen and Lehtilä 1993).

It has been hypothesized that clonal plants may lose their capacity for sexual reproduction if recruitment mainly occurs through asexual reproduction (Klekowski 1988, Eckert et al. 1999). Populations of *H. splendens* (and probably many other plants as well) growing in the forest floor usually have low frequency of sporophytes, maintaining sexual reproduction at rates that incur negligible demographic costs. This accords with the view that the ecological roles of sexual spores and asexual diaspores are different, for vascular plants (Gardner and Mangel 1999) as well as for bryophytes (Mishler 1988, Kimmerer 1991). In *H. splendens*, asexual diaspores ensure population maintenance

in established vegetation and repopulation of small gaps created by disturbance (Jonsson and Esseen 1998, Rydgren et al. 1998*a*, *b*, 2001), while sexual spores may be spread over greater distances and play an important role in colonizing extensive, unoccupied substrates. Furthermore, sexual reproduction increases genetic variation. Most likely, the maintenance of sexual reproduction at low rates in a species' preferred habitats contributes to population fitness in a very long time perspective.

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