

How does reproductive strategy influence demography? A case study in the tropical, unisexual epiphyllous moss *Crossomitrium patrisiae*¹

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PREMISE OF THE STUDY: Leaf-inhabiting organisms offer an experimentally tractable model system within which to investigate the influence of alternative reproductive strategies on plant metapopulation dynamics. We conducted a field study to determine whether (1) threshold colony sizes exist for the onset of sexual and asexual expression, and (2) alternative reproductive strategies differentially influence within-patch dynamics of the tropical pleurocarpous moss *Crossomitrium patrisiae*.

METHODS: The growth, reproduction, and fate of 2101 colonies of *C. patrisiae* were followed over 2 years to investigate threshold size and age for sporophyte and brood branch formation and their influence on within-patch growth rates and longevity.

KEY RESULTS: Asexual expression rather than sexual onset was limited by a minimal colony size. Age was uncoupled with threshold sizes. Colonies bearing brood branches survived nearly twice as long as sterile and solely sporophytic colonies. However, no effect of reproductive strategies on colony growth rates was found.

CONCLUSIONS: This study is among the few attempts to correlate life history strategies with demographic parameters of terrestrial plants. Specifically, we provide evidence for differential influence of reproductive strategies on metapopulation survivorship.

KEY WORDS bryophyte; demography; epiphyll; Hookeriaceae; metapopulation; rainforest; reproductive strategy; tropics

Reproduction is fundamental for the maintenance of plant populations and can be accomplished through a variety of sexual or asexual means (Maynard Smith, 1978). Bryophytes (mosses, hornworts, and liverworts) harbor the greatest diversity of reproductive strategies among land plants (Wyatt and Anderson, 1984). Nearly all bryophytes are capable of clonal propagation in various forms (Stark et al., 2004). Sexual reproduction is less frequent in unisexual bryophytes when compared with cosexual because fertilization depends on water-mediated dispersal of motile sperm thus imposing strong spatial constraints (Shaw, 2000; Vanderpoorten and Goffinet, 2009). When fertilization is accomplished in bryophytes, the production of the sporophyte is traditionally considered more expensive than production of asexual propagules (Rydgren et al., 1998;

Stark et al., 2001; Ehrlén et al., 2000; Pohjamo and Laaka-Lindberg, 2003, 2004; Hassel et al., 2005; Zartman et al., 2015).

Reproduction is particularly important for organisms living on spatially isolated and ephemeral substrates as is the case for the rich leaf-inhabiting (epiphyll) community typical of tropical forests around the world (Coley et al., 1993; Anthony et al., 2002; Gilbert et al., 2007), which is mainly represented by bryophytes and lichens (Gradstein, 1997; Lücking, 2008; Vorholt, 2012). The exceptionally fast generation times and sensitivity of epiphylls to microclimatic conditions make them ideal model systems for empirically testing metapopulation hypotheses (Zartman and Nascimento, 2006; Alvarenga et al., 2009; Sonnleitner et al., 2009; Johansson et al., 2012; Oliveira and ter Steege, 2015; Zartman et al., 2015). For example, the impacts of seasonal variation on plant metapopulation stability can be quantified in tractable time periods, potentially anticipating the consequences of changing climate patterns on plant demography (Coley et al., 1993; Marino and Salazar Allen, 1993; Sonnleitner et al., 2009; Zartman et al., 2015). However, few studies have disentangled how reproductive strategies interact with the local metapopulation dynamics of plant taxa.

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Seed and spore-producing plants growing on ephemeral substrates such as epiphytes and epiphylls are generally cosexual (Longton and Schuster, 1983; van Dulmen, 2001). Such a pattern is exemplified in bryophytes because their frequency of sporophyte expression has been positively associated with cosexuality (Maciel-Silva and Pôrto, 2014), and the close proximity between male and female gametangia ensures autogametophytic selfing despite suboptimal microclimates (Zartman et al., 2015). The vast majority of epiphyllous bryophytes are cosexual liverworts (Schuster, 1988; Gradstein, 1997). However, as an exception, the only obligatorily epiphyllous moss genus *Crossomitrium* Müll.Hal. (Hookeriaceae) is unisexual (Allen, 1990) and, contradicting expectations for the unisexual condition, *Crossomitrium patrisiae* (Brid.) Müll.Hal. has one of the highest fertilization rates ever recorded for a unisexual bryophyte (Alvarenga et al., 2013). Such an extraordinary divergence in life history calls for a thorough investigation of the demographic mechanisms that contribute to the success of this species in such an extreme habitat. The sharply different sizes of sexual and asexual propagules, that is, spores (20 μm) and brood bodies (up to 0.5 mm in length) of *C. patrisiae*, point to obviously different dispersal potentials. Large asexual propagules are expected to contribute to local-scale growth and maintenance (Söderström and During, 2005), and because asexual propagules are produced typically earlier than spores (Maciel-Silva and Pôrto, 2014), they may act as a “safety net” for short-term population maintenance (Söderström and During, 2005).

The current study represents, to our knowledge, the first attempt to disentangle the effect of reproductive strategies on the demography of a uniquely unisexual epiphyllous moss. We conducted demographic censuses over 2 years to test two predictions: (1) postzygotic expression (sporophyte emergence) occurs at older ages and/or larger colony sizes than asexual (brood branch) expression, and (2) faster colony growth rates and higher longevity are more likely associated with asexual (brood branch) expression rather than postzygotic (sporophyte) expression.

MATERIALS AND METHODS

Focal species—*Crossomitrium patrisiae* (Hookeriaceae) is a unisexual pleurocarpic moss widely distributed and endemic to the neotropics (Buck, 1998) growing on leaves in the understory and subcanopy of humid forests. Gametophytes of *C. patrisiae* are bigger (4–10 cm long, 2–4 mm wide) (Buck, 1998) (Fig. 1A, B) than other epiphyllous bryophytes, which are mostly liverworts of the family Lejeuneaceae (Gradstein, 1997). Gametophytes cover small portions of the available space, $\sim 10\%$ (± 0.05 SD) of leaf surface (Alvarenga et al., 2013). The sporophyte setae reach 4–12 mm (Fig. 1C), and mean spore size is 20 μm . Asexual propagules are found mainly on specialized brood branches tightly adnate to the substrate and easily distinguished by orbicular, closely imbricate leaves, giving the

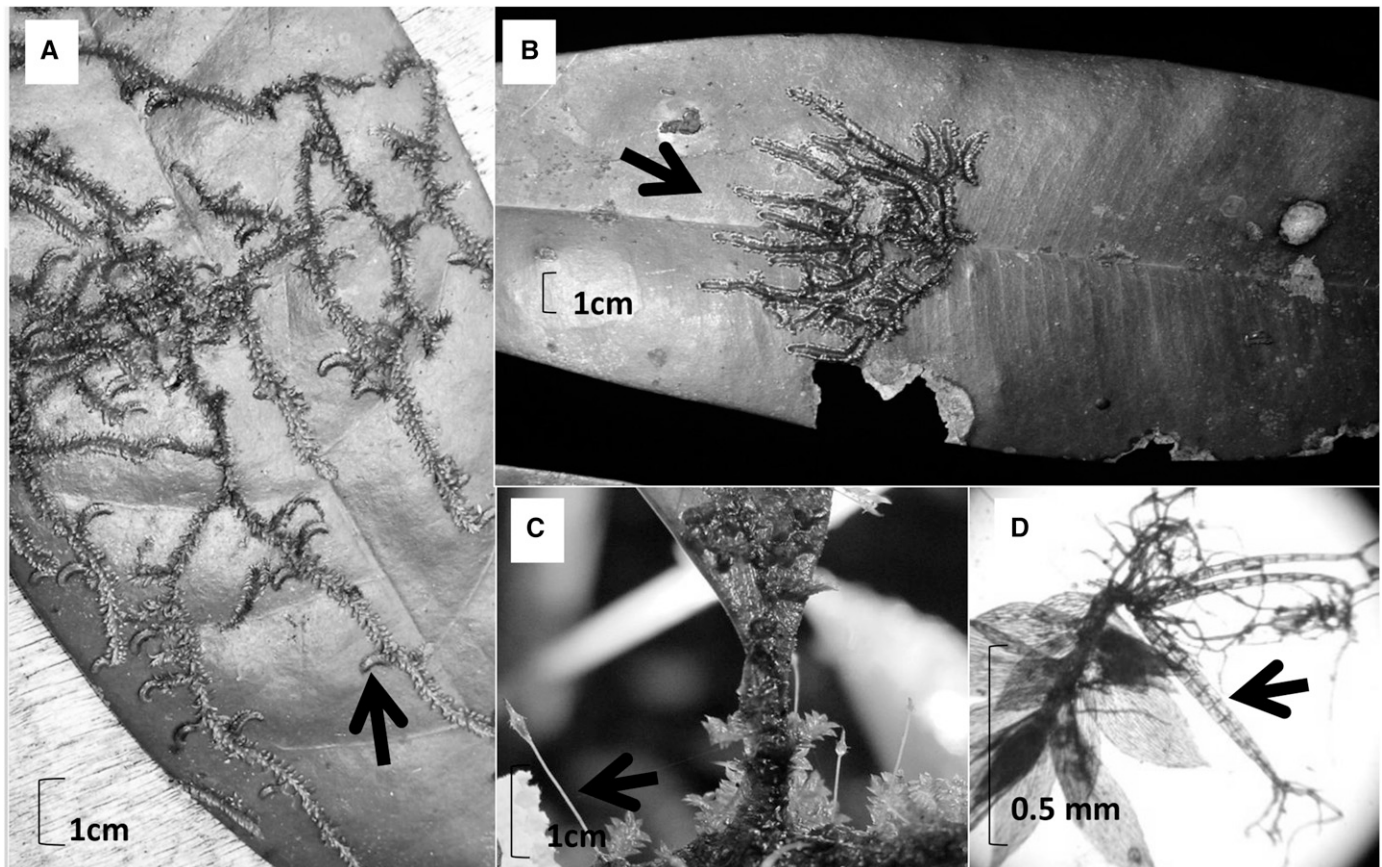


FIGURE 1 *Crossomitrium patrisiae* in the studied area. Arrows indicate (A) brood branches; (B) individual of *C. patrisiae* at the age of 6 months in a size usually found in the studied area; (C) sporophytes; (D) asexual brood body complex under compound microscope growing a gametophyte in early stages of development.

branches a julaceous aspect (Fig. 1A). Each brood body is part of a complex consisting of a rhizoidal initial, a multicellular stalk, and many smooth, reddish-brown, multicellular brood bodies identical in form to the fringe hairs of calyptras, measuring up to 0.5 mm (Fig. 1D).

Study area—Samples of *C. patrisiae* were collected in a Brazilian Atlantic rainforest fragment (2,700 ha) of the Ecological Station Murici, northeast of Brazil (9°11'05"–9°16'48"S and 35°45'20"–35°55'12"W) (Velooso et al., 1991). The area is between 100 and 650 m a.s.l. and has a warm and humid tropical climate. Annual mean of the highest temperatures is 31°C, the mean lowest temperature is 20°C, and the annual mean rainfall is 1165 mm (data provided by Meteorological and Climatic Research Center of Embrapa Agricultural Information). The dry season occurs between August through February, and the rainy season occurs between March through July. The total precipitation of 307 mm in 2008 and 710 mm in 2009 were below average.

Data collection—Ninety-six small shrubs (hereafter referred to as phorophytes) with at least one leaf colonized by *C. patrisiae* were randomly selected for study (each phorophyte occupies an area of approximately 1 m²). We refer here to all individuals of *C. patrisiae* colonizing a single host leaf as a colony. *Crossomitrium patrisiae* grows over leaves and twigs (Buck, 1998) but in the current study, *C. patrisiae* individuals were restricted to leaf surfaces. Phorophytes on which the focal species was recorded included representatives of the families Nyctaginaceae, Ochnaceae, Rubiaceae, Sapindaceae, Sapotaceae, Violaceae, and Vitaceae. Epiphyllous bryophyte communities occur on a great variety of phorophyte species of different families and are usually considered host nonspecific (Pócs, 1982; Sonnleitner et al., 2009). All colonized leaves were numbered in January 2008 ($n = 689$) with plastic tags and checked at 3-month intervals until January 2010. In each visit, colonies were revisited and photographed with a Nikon Coolpix 5400 digital camera and evaluated for the presence of brood branches and sporophytes. In the total area inspected of 96 m², 2101 leaves were colonized by *C. patrisiae* during the study.

Colony dynamics—(1) *Sexual and asexual initiation*—Sexual and asexual initiation refer to the first observation of sporophytes (postzygotic reproductive structures) and brood branches, respectively. All colonies marked on the first census were excluded from the analyses that included age of reproductive initiation due to the impossibility of determining their precise age. Age estimates of the remaining 1412 colonies were based on the maximum time elapsed between the censuses in which the colony was present. For example, colonies present in only one census were aged as 3 mo old, colonies present in two subsequent censuses were aged 6 mo old, and so forth. Reproductive initiation is based on the moment of first observation of sporophytes and/or brood branches. Size at reproductive initiation was quantified as cover area (cm²) using the software Image J (Ferreira and Rasband, 2012). Singular individuals of *C. patrisiae* can be easily traced, and thus, we counted the number of *C. patrisiae* individuals for all colonized leaves for estimates of growth rates.

(2) *Growth rates*—Relative growth rate (RGR) was calculated for each colony as $RGR = (S_t/S_0)/\Delta t$, where S_0 corresponds to the initial colony size, S_t corresponds to the colony size at time t , and $\Delta t = 3$

mo. Growth rates in number of individuals and covered area were correlated (results not shown), and thus the first measure was used in statistical analyses due to larger n . Geometric means of all growth intervals were used in statistical analyses.

(3) *Life length*—Among the 1412 colonies with known age, 397 suffered mortality due to leaf fall (herein referred to as deterministic extinction), 340 suffered mortality on intact leaves (herein referred to as stochastic extinction), and 675 survived the study. Because leaf fall is unlikely to be influenced by the reproductive strategies of the focal species, deterministic extinctions were not included in the analyses of life length. Thus, life length herein refers to the age of the colony at the moment of its disappearance on persisting leaves (stochastic extinction).

Reproductive strategies—Evidence from experimental studies of fine-scale metapopulation dynamics of epiphylls indicates that patch extinction and colonization are disproportionately affected by within- as compared to among-phorophyte variation of neighborhood patch density of epiphyll conspecifics (Zartman et al., 2012). Bryophyte spore dispersal has repeatedly been demonstrated to be strongly leptokurtic with the vast majority (ca. 90%) of spores falling within a 2-m radius of the colony source (Stoneburner et al., 1992; Roads and Longton, 2006), but there is an aerial spore bank. Thus, to minimize interference of fine-scale dispersal from neighboring phorophytes, we removed all conspecific colonies from neighboring phorophytes (≤ 10 m radius) at the beginning of the study. Focal colonies were considered to be under potential influence of asexual recruitment (e.g., gemmae effects) when at least one individual per leaf produced brood branches.

To analyze the influence of sexual and asexual strategies on longevity and growth rates, each colony was classified into one of the following reproductive states: (1) presence of both brood branches within the colony and sporophytes within the colony or in other colonies of the same phorophyte; (2) presence of brood branches and absence of sporophytes; (3) absence of brood branches and presence of sporophytes; (4) absence of brood branches and sporophytes. These categories were used in statistical tests.

Statistical analyses—We used generalized linear models (GLM) with binomial error distribution and logit link function to investigate whether nonexpressive colonies were significantly smaller and younger than sexually and asexually active colonies, thus indicating a threshold size (cover area) and age. Reproductive activity (expressing vs. nonexpressing) was the binary dependent variable (Crawley, 2007). To take seasonality into account in the analysis of threshold size, cohort (moment of colony establishment) was included as a cofactor. Interactions among reproductive state and cohort were also tested and removed from the model when deemed nonsignificant. We carried out a two-way ANOVA to compare the average size between the two reproductive modes (sexual and asexual) and between cohorts. Data were log-transformed when necessary.

The effects of reproductive state (presence of brood branches and/or sporophytes) and cohort on colony growth rates and life length were evaluated through generalized linear models with Poisson error distribution and log link function. All statistical analyses were performed in the software R version 2.10.1.1 (R Development Core Team, 2007).

RESULTS

Prediction 1: Postzygotic investment (sporophyte emergence) occurs at older ages and/or larger colony sizes than asexual (brood body) expression—Among the 1412 colonies with known age, 117 (8.3%) produced brood branches and 23 (1.6%) produced sporophytes. Half of the colonies that produced sporophytes had previously produced brood branches, and sexual reproduction was not observed in the same colony in consecutive years. Threshold size for reproductive initiation was constant throughout censuses (Table 1) and significant for asexual expression (minimum size: 0.32 cm², mean size: 2.79 ± 0.73 cm²; GLM coefficient: 0.56, $P < 0.0001$), but not for sporophyte production (minimum size: 0.80 cm², mean size: 3.52 ± 1.57 cm²; GLM coefficient: 7.00, $P > 0.05$). Cohort also had a significant effect on asexual threshold size; colonies from January 2009 showed significantly smaller threshold sizes for asexual initiation than colonies from April 2008 (GLM coefficient: -2.58, $P < 0.05$). Interaction between reproductive activity and cohort was not significant. In turn, age was not detected as a significant predictor for any reproductive strategy. Reproductively active colonies were not significantly older than nonreproductive ones (sexual reproduction, GLM coefficient: -0.01, $P > 0.05$; asexual reproduction, GLM coefficient: -0.005, $P > 0.05$). Nearly 50% of colonies produced brood branches before the minimal detectable age (3 mo), and sporophyte production peaked in the rainiest months. Average size of asexually expressive colonies was significantly smaller than the sexually expressive (ANOVA, $F_{1,37} = 7.04$, $P < 0.05$) regardless cohort (ANOVA, $F_{5,37} = 2.14$, $P > 0.05$).

TABLE 1. Mean (±1 SD) number of individuals, covered area, and age of colonies of *Crossomitrium patrisiae* initiating sexual (production of sporophytes) and asexual (production of brood branches) reproduction and nonreproductive colonies in each census.

Census	Reproductive type initiated		
	Asexual	Sexual	Nonreproductive
No of individuals			
Apr 08	5.00 ($n = 2$)	—	2.85 ± 2.39 ($n = 25$)
Jul 08	5.00 ($n = 2$)	5 ± 2.76 ($n = 6$)	2.99 ± 3.14 ($n = 149$)
Oct 08	4.03 ± 4.54 ($n = 38$)	7.00 ($n = 2$)	2.39 ± 2.01 ($n = 340$)
Jan 09	2.00 ± 1.79 ($n = 10$)	2.00 ($n = 1$)	2.45 ± 2.51 ($n = 463$)
Apr 09	3.24 ± 2.35 ($n = 25$)	2.00 ($n = 1$)	2.42 ± 2.37 ($n = 582$)
Jul 09	3.63 ± 4.33 ($n = 16$)	7.25 ± 6.37 ($n = 13$)	2.48 ± 3.00 ($n = 961$)
Oct 09	3.15 ± 2.50 ($n = 20$)	—	2.59 ± 3.13 ($n = 610$)
Jan 10	1.40 ± 0.55 ($n = 4$)	—	2.36 ± 3.10 ($n = 602$)
Covered area (cm ²)			
Apr 08	4.15	—	1.21 ± 1.20
Jul 08	2.2	4.41 ± 1.31	1.43 ± 1.68
Oct 08	3.31 ± 1.60	5.04	0.74 ± 1.03
Jan 09	2.66 ± 2.54	1.01	1.04 ± 1.87
Apr 09	2.24 ± 1.75	3.10	0.90 ± 1.63
Jul 09	3.34 ± 2.44	4.03 ± 1.38	1.43 ± 1.89
Oct 09	2.29 ± 1.60	—	1.74 ± 2.11
Jan 10	2.15 ± 2.40	—	1.83 ± 0.87
Age (months)			
Apr 08	3.00	—	3.00
Jul 08	3.00	4 ± 1.22	3.20 ± 0.75
Oct 08	4.62 ± 1.95	3.00	4.03 ± 1.53
Jan 09	5.73 ± 3.41	3.00	5.48 ± 2.31
Apr 09	8.40 ± 3.24	6.00	6.78 ± 3.19
Jul 09	9.38 ± 4.08	10.5 ± 4.52	6.79 ± 4.08
Oct 09	12.45 ± 4.27	—	9.32 ± 4.84
Jan 10	12.75 ± 2.87	—	9.88 ± 5.70

Prediction 2: Faster colony growth rates and higher longevity are more likely associated with asexual (brood branch) expression rather than postzygotic (sporophyte) expression—

Reproductive state did not affect growth rates but significantly affected colony life length. Colonies bearing only brood branches lived as long as colonies bearing brood branches and under effect of sporophytes (GLM coefficient: -0.15, $P < 0.0001$), and longer than colonies under effect of sporophytes only (GLM coefficient: -0.51, $P < 0.0001$) and nonreproductive colonies (GLM coefficient: -0.46, $P < 0.0001$) (Fig. 2). The model also showed that colonies from July 2008 and October 2008 lived longer than colonies from April 2008 (July 2008 vs. April 2008: GLM coefficient: 0.39, $P < 0.0001$; October 2008 vs. April 2008: GLM coefficient: 0.46, $P < 0.0001$), which in turn lived longer than colonies from July 2009 (GLM coefficient: -0.24, $P < 0.05$) and October 2009 (GLM coefficient: -0.48, $P < 0.05$). Interaction between reproductive state and cohort was not significant.

DISCUSSION

This 2-year demographic survey shows that colonies of *C. patrisiae* initiate asexual reproduction after reaching a minimal threshold size and that this size is adjusted probably by environmental signals because some cohorts had significantly different thresholds. On the other hand, sexual reproduction depends on water availability, because a threshold size was not observed for sporophyte production and this was concentrated in the rainiest months. Although the average size of sporophytic colonies was significantly greater than

that of asexual colonies, regardless of cohort, the lack of threshold size for sexual initiation indicates that some very small colonies produce sporophytes during the rainy season, when resource acquisition is apparently facilitated. If production of asexual branches is stimulated by signals related to less favorable environmental conditions, it is reasonable that a threshold gametophyte size exists for starting this investment.

Contrary to expectation, critical size for reproductive expression was uncoupled with age in *C. patrisiae*. Factors other than time, which influence fine-scale variation in habitat patch quality, must explain the differential growth rates that retard or accelerate biomass increase and reproductive onset in same-age colonies. Indeed, these findings diverge from those reported from the epiphyllous liverwort *Radula flaccida* Gott. where sporophyte emergence occurs at a significantly larger colony sizes than that of asexual expression (Zartman et al., 2015). In this sense, *Crossomitrium patrisiae* has apparently adopted precocious sexual initiation in relation to other studied epiphylls, perhaps contributing to its high sexual output.

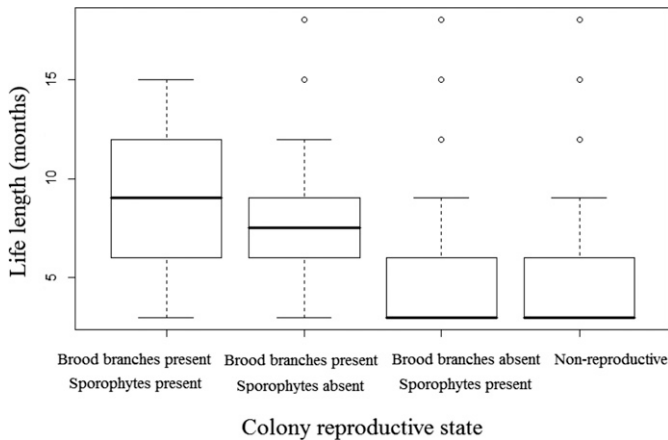


FIGURE 2 Colony life length of *Crossomitrium patrisiae* according to the different reproductive states (from left to right: $n = 28$; $n = 20$; $n = 117$; $n = 175$). Presence of sporophytes include sporophytes produced within the focal colony or in other colonies of the same phorophyte. Boxes represent standard deviations and bars represent $\pm 95\%$ confidence interval. Points are outliers.

Average sizes of sexual and asexual colonies of *C. patrisiae* range from 1–5 cm² (Table 1). In turn, sexually and asexually expressing colonies of *R. flaccida* were >20 cm² (Zartman et al., 2015), and threshold colony size at which sporophyte production was greater than that of asexual expression was 43 cm² (Zartman et al., 2015).

In comparison with epiphytic bryophytes of temperate regions, *C. patrisiae* initiates reproductive strategies at relatively smaller threshold sizes. For example, average colony sizes for first sex expression in female and male colonies were 68 cm² and 8.3 cm², respectively, for the facultative epiphytic liverwort *Ptilidium pulcherrimum* (G. Web.) Hampe, corresponding to approximately 9 yr of growth (Jonsson and Söderström, 1988). Likewise, colony sizes for the epiphytic moss *Neckera pennata* Hedw. ranged between 12–79 cm² at first reproduction, corresponding to 20–30 yr (Wiklund and Rydin, 2004), and the hepatic *Frullania dilatata* (L.) Dum averaged 18 cm² (Löbel and Rydin, 2009). In some epiphytes such as *Radula complanata* (L.) Dumort and *Orthotrichum speciosum* Nees, colony sizes for first sex expression are likewise quite small: 1.45 cm² and 0.26 cm², respectively (Löbel and Rydin, 2009), but these patches may encompass a greater number of plants grown through longer times than colonies of *C. patrisiae* of equivalent sizes. Thus, the extremely low minimal requirements for sexual and asexual reproductive initiation demonstrated herein for *C. patrisiae* suggest an extreme adaptation to its unpredictable and ephemeral substrate doubly imposed by its obligate outcrossing system of fertilization.

As predicted, colonies bearing brood branches in *C. patrisiae* lived longer than nonreproductive ones and longer than those solely under the influence of sporophytes. Contrary to our expectation, however, positive effects of reproductive strategies on growth rates were unapparent. Löbel and Rydin (2009) found similar results for some species in temperate forests, in which no effects of reproductive strategies (sexual vs. asexual) on growth rates were observed, but these were affected by life-history strategy (colonists, short-lived shuttle, long-lived shuttle, perennial stayers) instead. In the case of *C. patrisiae*, the costs of reproduction, such as reduced growth rates of individuals, may counteract possible positive effects of propagules in the size increase of the colony. Furthermore, field

observations and experimental pilot tests in laboratory suggest that gemmae may be either carried by water drops or left attached in the substrate after removal of gametophytes due to mechanical disturbance. The loss of individuals through stochastic disturbances can be compensated by production of new individuals from gemmae. Thus, the positive contribution of asexual propagules of *C. patrisiae* may not translate into higher growth rates if the addition of new individuals mostly compensates for the loss of those removed through stochastic disturbance. The significant effect of cohort in the analyses of life length may have been associated with such disturbance patterns related to precipitation dynamics. Colonies established at the beginning of the rainy season (April 2008) could be more disturbed than those established in the end of the rainy season (July 2008 and October 2008), and the colonies established in 2009 could have been affected by stronger disturbance resulting from higher precipitation in this year.

Asexual reproduction in bryophytes is considered central to local population expansion and maintenance because it may provide a competitive advantage (Kimmerer, 1994), mediate survival under hardships (Duckett and Renzaglia, 1993; Laaka-Lindberg and Heino, 2001), ensure relatively long-distance colonization events as in the case of smaller gemmae (Pohjamo et al., 2006), and even promote assurance of successful sexual reproduction by extending the life length of genotypes (Kimmerer, 1991; McLetchie and Puterbaugh, 2000; Cronberg et al., 2006). The results of the current study suggest support for the last of these cited benefits as half of the sexually reproductive colonies had, before sporophyte emergence, produced brood branches. However, fine-scale microclimatic and environmental data in the sites where reproductive colonies grow are necessary to disentangle how reproductive strategies and overall favorable environmental conditions affect life length.

Differences in life history strategies reflect adaptations for survival under stress imposed by the environment. Bryophytes adapted to transient, unstable, and unpredictable environments typically have high growth rates and early investment in easily dispersed and numerous offspring and require high quality resources and have low competitive ability (During, 1992). Stable environments favor species with the opposite traits. *Crossomitrium patrisiae* has been classified as “colonist-ephemeral” (Wu et al., 1987), one of the r-strategies among bryophytes. This species grows abundantly and profusely in the studied area. More than 2000 leaves were colonized by *C. patrisiae* in an area of approximately 96 m². Long-distance dispersion occurs mainly through spores that are abundantly produced during the rainy season. Moreover, on an individual basis, *C. patrisiae* presents one of the highest rates of sexual expression (76% of examined shoots) and fertilization (89% of cosexual populations, 40% of total female and 73% of female shoots occurring in cosexual colonies) ever recorded for a bryophyte with unisexual individuals (Alvarenga et al., 2013). The earlier use of gemmae in the life cycle certainly contributes to mating success.

Reproductive strategies play an important role in metapopulation (Johansson et al., 2012) and metacommunity (Löbel et al., 2009) dynamics and also in the genetic (Hock et al., 2009) structure of bryophyte populations. However, relatively few studies have attempted to quantify the demographic parameters that trigger shifts between sexual and asexual expression (McLetchie and Puterbaugh, 2000; Zartman et al., 2015). Furthermore, although it is known that reproduction entails costs to bryophytes (Convey and Lewis Smith, 1993; González-Mancebo and During, 1997; Stark et al., 2000; Bisang et al., 2006), few studies have quantified the minimal level of resources

required for reproductive initiation in these plants (Jonsson and Söderström, 1988; Rydgren and Okland, 2002; Hassel et al., 2005; Löbel and Rydin, 2009; Zartman et al., 2015). Here we have shown indications of differential resource limitations for sexual and asexual reproduction and their respective contribution to local colony dynamics of *C. patrisiae*. Future important lines of research should include the plasticity of reproductive behavior of epiphylls under predicted with the global climate change (sensu Ruete et al., 2012) to estimate the survival thresholds of these crucial components of tropical rainforests.

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