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How tropical moss sporophytes respond to seasonality: examples from a semi-deciduous ecosystem in Brazil

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Abstract – We report on the phenology of the sporophytes of *Octoblepharum albidum* Hedw. (Calymperaceae), a moss growing in a seasonal ecosystem between the semi-deciduous Atlantic Forest and neotropical savanna areas of Brazil. We examined 100 sporophyte-bearing plants in ten different populations every two weeks between March/2014 and April/2015. This is the first analysis of phenological data of bryophytes using a circular presentation to interpret cyclical phenomena. Sporophyte development events in *O. albidum* were clearly seasonal, with the frequencies of all phenophases being related principally to rainfall. The three early stages of sporophyte development (immature to post-meiotic sporangium) occurred predominantly during the dry season, contrasting with sporangia dehiscence, which occurred mainly during the rainy season. Our findings contribute to a better understanding of the reproductive biology of bryophytes in tropical ecosystems, particularly those in seasonal habitats. We also highlight the consequences of misinterpreting some of the phenophases in mosses, and how revised concepts of these phases improved phenological interpretations.

Bryophyte / Cerrado / Atlantic Forest / *Octoblepharum albidum* / phenology

INTRODUCTION

Phenological studies examine repetitive growth and reproductive events in plants and animals and their climatic associations (Stark, 2002; Morellato *et al*., 2010) with the objective of better understanding the effects of abiotic variables on plant growth and reproduction (Cardoso *et al*., 2012; Landi *et al*., 2014; Ramos *et al*., 2014), investigating evolutionary questions (Staggemeier *et al*., 2010; Davies *et al*., 2013; Chang-Yang *et al*., 2013; Holanda *et al*., 2015; Sigrist & Sazima, 2015), managing economically important species (Baldauf *et al*., 2014), and evaluating possible consequences of climate changes on species and ecosystem activities (Walther *et al*., 2002; Cleland *et al*., 2007).

Many phenological studies of bryophytes have focused on species from temperate habitats (Arnell, 1905; Greene, 1960; Hancock & Brassard, 1974; Miles *et al*., 1989; Rincon & Grime, 1989; Longton, 1990; Ayukawal *et al*., 2002; Sundberg, 2002; Laaka-Lindberg, 2005; Glime, 2013a and other references therein), with more limited examinations of taxa from tropical areas (Odu, 1982; Makinde & Odu, 1994;

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Fatoba, 1998; Milne, 2001; Oliveira & Pôrto, 2001; Pôrto & Oliveira, 2002; Maciel-Silva *et al.*, 2011; Zartman, 2015). Bryophyte species inhabiting very humid tropical forests (e.g., the Atlantic Rain Forest in southeastern Brazil and the Amazonian Forest) are able to produce new gametangia throughout the year, although with slight variations in the values of some phenophases, and with fertilization and sporophyte production being reported as continuous (Maciel-Silva *et al.*, 2011; Zartman *et al.*, 2015). In extremely seasonal ecosystems (e.g., seasonally dry forests in the semiarid region of Brazil, known as "*Caatinga*"), however, bryophytes respond strongly to rainfall variations, producing only gametangia or only sporophytes during distinct seasons (Nunes *et al.*, 2015). Intermediate patterns, with accentuated production of mature gametangia in the rainy season and late sporangia in the dry season, have been observed in savanna areas in Nigeria and in the Atlantic Rain Forest in northeastern Brazil (Egunyomi, 1979; Fatoba, 1998; Oliveira & Pôrto, 2001; Pôrto & Oliveira, 2002).

The life cycle of bryophytes is dominated by the gametophytic phase, a unique trait among extant land plants (Goffinet & Buck, 2012). The moss sporophyte begins to develop after fertilization: in most mosses the seta elongates, elevating the sporangium; the sporangium expands as spores are formed; and the sporangium subsequently loses water, dehisces, and releases its spores (Greene, 1960; Oliveira *et al.*, 2014). The sporophyte remains attached to the maternal gametophyte during its entire growth (Schofield, 1985). Gametophytes and sporophytes tend to respond differently to different abiotic variables, with sporophytes generally being more sensitive to desiccation and high temperatures than gametophytes (McLetchie & Stark, 2006; Stark *et al.*, 2007).

The phenology of the moss *Octoblepharum albidum* Hedw. (Calymperaceae) was investigated in northeastern Brazil and Nigeria (Egunyomi, 1979; Pôrto & Oliveira, 2002), and sporophyte development was found to be influenced by the local rainfall regime: sexual reproduction and hence sporophyte development is initiated in the wet season, and is completed after seven months, with spores being released in the dry season. No study has, however, examined the actual influences of climatic variables on each phenophase of the sporophyte of this species.

The Atlantic Forest extends to the interior of Brazil, where it transitions to dryer savanna vegetation (*Cerrado*) at elevations above 600 m. Unlike the southeastern coastal rain forests that experience essentially no dry season, the inland Atlantic Forest sites are subjected to a relatively severe dry season and are semi-deciduous (Morellato & Haddad, 2000). The ecosystem selected for the present study (transitional vegetation between semi-deciduous Atlantic Forest and savanna) experiences two very distinct seasons, and therefore provided a natural laboratory for testing the effects of climatic seasonality on bryophyte phenology.

Our goal was to study the sporophyte phenology of a moss in a seasonal Brazilian ecosystem located between semi-deciduous Atlantic Forest and savanna areas, and to relate the frequencies of sporophyte phenophases to climatic variables. The study area is characterized by a significant seasonality (ca. 25 times more rain during the rainy season than during the dry season; for details, refer to the "study site" section). Based on the hypothesis that sporophyte development in tropical bryophytes responds directly to the degree of seasonality (Egunyomi, 1979; Pôrto & Oliveira, 2002; Maciel-Silva *et al.*, 2011; Zartman *et al.*, 2015; Nunes *et al.*, 2015), we expected the sporophyte phenophases of *Octoblepharum albidum* growing in a transition area between semi-deciduous Atlantic forest and savanna to be strongly synchronized with the local climate (principally rainfall) and to see seasonal responses of the sporophytes, with increased numbers of young sporophytes during the rainiest months and increases in late phenophases (i.e., open sporangia dispersing spores) during the driest months. Since other climatic variables have been suggested as being important to sporophyte development in bryophytes (Chopra & Bhatla, 1981; Hohe *et al*., 2002; Laaka-Lindberg, 2005), we also investigated the relationships of relative humidity, temperature, and solar irradiance to sporophyte phenophases.

MATERIALS & METHODS

Study site and species

The study site was located in an ecological station on the campus of the Federal University of Minas Gerais, Belo Horizonte, Brazil (Estação Ecológica da UFMG; *c*. 114 ha; 19°52’39’’S x 43°58’18’’W, *c*. 840 m a.s.l.). The vegetation there is composed of semi-deciduous Atlantic Forest and “*Cerrado*” (neotropical savanna). The mean annual temperature between 1980 and 2014 was 21.8°C, and the total mean annual rainfall was 2042 mm. The rainy season (September to April) is characterized by a total average rainfall of 1510 mm, with the heaviest rains occurring between December and February. The dry season (May to August) has a total average rainfall of 61 mm (Inmet, www.inmet.gov.br; Jardim & Monteiro, 2014). Average temperature varies from a minimum of 16°C in the dry season to 28°C during the rainy season. Short-term droughts (locally known as “*veranico*”) may occur during the rainy season (Engel & Martins, 2005).

Octoblepharum albidum is a pantropical, epiphytic, autoicous moss (male and female gametangia occurring on different branches on the same gametophyte). This species is widespread in Brazil, occurring in Atlantic and Amazonian forests, seasonally dry forests (*Caatinga*), and savanna (*Cerrado*) (Peralta, 2015). It is classified as a generalist species, occurring at the edges, as well as in the interior, of forests (Costa, 1999; Gradstein *et al*., 2001; Silva & Pôrto, 2009). As this species is widespread in the tropics and occurs in different ecosystems, it provides a suitable model for studying the phenologies of tropical mosses and their responses to environmental factors (Egunyomi, 1979; Pôrto & Oliveira, 2002; Zhang *et al*., 2003; Maciel da Silva *et al*., 2009; Maciel-Silva *et al*., 2013).

Field sampling

We selected ten populations of *Octoblepharum albidum,* spaced at least 2 m from one another, along a one km transect. The populations considered in this study were growing as colonies on tree trunks (from ground level to breast height).

We examined ten sporophyte-bearing plants per population at each site visit. Observations were carried out every two weeks between March, 2014 to April, 2015 (except between 15 Dec 2014 and 19 Jan 2015), totaling 26 observational events. As our main goal was to describe the phenological status of sporophytes in each population, we observed and classified the first ten sporophytes encountered in each population, thus including new developing sporophytes. A hand lens (10x magnification) was used to inspect and classify the phenophases of the sporophytes. We adopted the systems of Greene (1960), Stark (2002), and Pôrto & Oliveira (2002), with some modifications (Oliveira *et al*., 2014; Table 1).

Table 1. Phenological phases of sporophytes (based on Greene, 1960; Stark, 2002; Pôrto & Oliveira, 2002; Oliveira *et al*., 2014)

Phenophase	*Main traits*
Phenophase 1	Immature sporangium with calyptra still in perichaetium
Phenophase 2	Immature sporangium (before meiosis) with calyptra intact and extended seta
Phenophase 3	Enlarged sporangium (after meiosis) with calyptra intact and extended seta
Phenophase 4	Enlarged sporangium without calyptra, operculum intact
Phenophase 5	Sporangium with operculum fallen, but still containing spores
Phenophase 6	Sporangium with operculum fallen, with no spores
Abortive	Sporophyte apex brown or shriveled

The calyptra is composed of maternal gametophytic tissue protecting the sporophyte apex and immature sporangium during its development; if this organ is damaged, sporophytes will abort or show decreased fitness (Budke *et al*., 2013). Accordingly, we classified sporophytes as aborted if their apices had turned brown or shriveled. Species identity was confirmed in the laboratory (Allen, 1991); vouchers (Maciel-Silva 255, 259, 271, 275, 281, 282, 286 and 296) were deposited in the BHCB Herbarium (UFMG).

Climatic variables

Climatic data were obtained from an automated meteorological station installed near the study site (Inmet, automatic station A52). Data were collected every minute and made available on an hourly basis (www.inmet.gov.br/sonabra/maps/pg_automaticas.php). We used the total daily values of rainfall (mm) and irradiance ($kj.m^{-2}$), as well as mean daily temperature (T° in °C) and relative humidity values (RH as %).

Data analysis

As phenological data are generally presented as year-round observations without start or end dates (Zar, 1999; Staggemeier *et al*., 2010), the use of circular statistics is more convenient than linear presentations (Morellato *et al*., 2010). The year of our study has therefore been represented as a circle of 360 degrees, with the origin, by convention, being January 1 (0° or 360°) and the days of the year being converted to angles (Staggemeier *et al*., 2010); we then calculated the mean and median angles, the lengths of the mean vectors (r), and the circular standard deviation (Csd) (Zar, 1999; Morellato *et al*., 2010). To test for the presence of seasonality in sporophyte development in *O. albidum*, we analyzed the distributions of the mean angles of all of the phenophases, using the Rayleigh test, Z (Morellato *et al*., 2010). When the mean angles were significant (meaning the data had a mean direction; $P < 0.05$), we calculated the mean date from the conversion of the mean angle. The mean date indicates the time of year with the greatest intensity of a given phenophase; similarly, the median angle represents the center of phenophase duration; and the mean vector (r) represents the concentration of that phenological activity (r varies from 0 to 1, with high values indicating aggregated phenological activity) (Morellato *et al*., 2010). All circular analyses were conducted using “circular” package software (Agostinelli & Lund, 2013) for R 3.2.0 (2015).

We used the total daily values of rainfall and irradiance, mean daily temperature values (T°), and the relative humidity of the air in the 15 days prior to each phenological sampling in our analyses, and Spearman correlations were performed among the climatic variables. As the following variables were found to be correlated: rainfall and relative humidity (r = 0.73), T° and irradiance (r = 0.69), and relative humidity and irradiance (r = 0.55), these predictors were used to construct different models. We then applied the three multiple regression models to each phenophase: *model 1* – rainfall and irradiance; *model 2* – rainfall and T°; *model 3* – RH and T°. Multiple regressions, using all three models, were performed for all phenophases. Phenophase frequencies were previously transformed to log (x + 1) and climatic data were standardized (mean = 0 and sd = 1) to obtain comparable Beta values. Analyses were conducted using Statistica 8.0 software (Statsoft).

RESULTS

Temperatures remained stable during the study period (mean of 21.5°C), but the rainfall between March, 2014 and April, 2015 (1613 mm) was lower than the previous 30-year average, with an effective dry season from May to November in 2014, and short-term drought within the rainy season during January, 2015 (Fig. 1). Irradiance varied from ca. 15,400 (June – August) to 25,600 kj.m^{-2} (October – January), and RH from 40% (September – October) to 78% (February – April).

Sporophyte development showed a seasonal pattern in the moss *Octoblepharum albidum*, with all phenophases having significant mean angles (Table 2). Phenophases 6 (late-opening sporangia), 1, 2 (young sporangia), and 3 (sporangia after sporogenesis with calyptra) had mean dates of occurrence in the dry season (May to July), while phenophases 4 (closed sporangia with no calyptra) and 5 (early-opening sporangia) were concentrated in the rainy season (October-January; Figs 2-3). Additionally, the peaks of occurrence of phenophases 3 and 5 were accentuated (r ≈ 0.50) (Table 2 and Fig. 3). Although the numbers of aborted sporophytes increased by 10% (Fig. 2) between January and February, 2015 (during the rainy season, with higher T° and irradiance levels; Fig. 1), no statistically significant seasonal pattern was identified (Fig. 3 and Table 2). Aborted sporophytes were found from phenophases 1 to 4. Although the phenophases of sporophyte production by *O. albidum* were concentrated in certain periods of the year, we also observed a few young sporophytes developing during the entire study period, with no interruptions.

Table 2. Results of the circular statistical analyses of the sporophyte phenophases of *Octoblepharum albidum* in a semi-deciduous ecosystem (Brazil). Rayleigh tests used to evaluate the significance of the mean angles or mean dates (not shown when values were not significant – n.s.).

Parameters	*Phen 1*	*Phen 2*	*Phen 3*	*Phen 4*	*Phen 5*	*Phen 6*	*Abortive*
Mean date	19/Jul	16/Jul	31/May	22/Oct	23/Jan	15/May	–
Mean angle (ā) ± Csd	197° ± 85°	194° ± 81°	149° ± 66°	295° ± 94°	23° ± 67°	133° ± 80°	38° ± 115°
Mean length of vector (r)	0.33	0.37	0.51	0.26	0.50	0.37	0.13
Median value	203°	183°	155°	300°	33°	124°	33°
Rayleigh test (Z)	0.329	0.371	0.512	0.258	0.505	0.373	0.133
Rayleigh test (P)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	n.s.

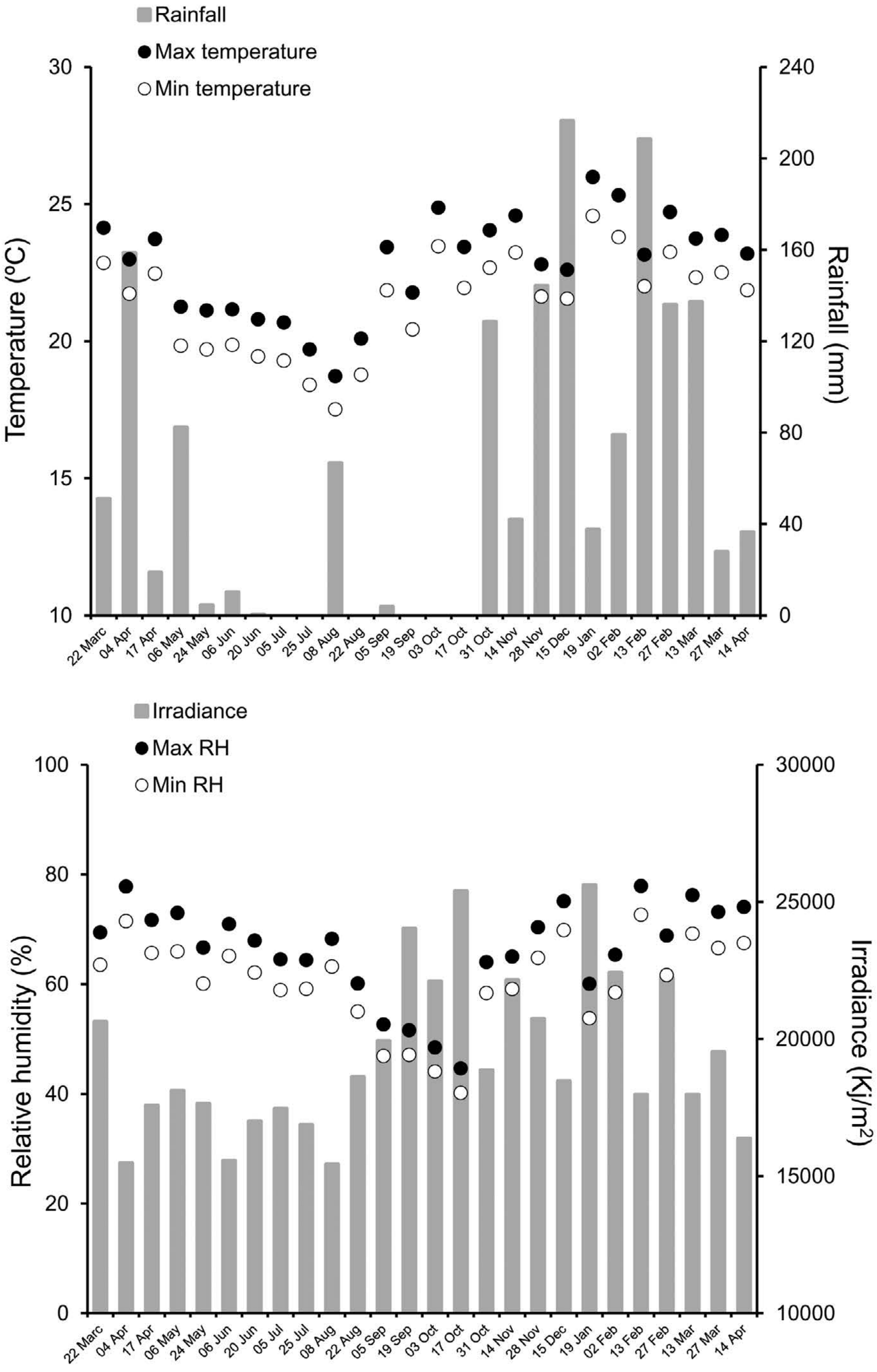

Fig 1. Daily climatic data in a semi-deciduous ecosystem, Belo Horizonte, Brazil, from March/2014 to April/2015. Total rainfall (mm) and irradiance (kj.m^{-2}); mean, maximum, and minimal air temperatures (°C) and relative humidity (%) values (automated station A52, www.inmet.gov.br).

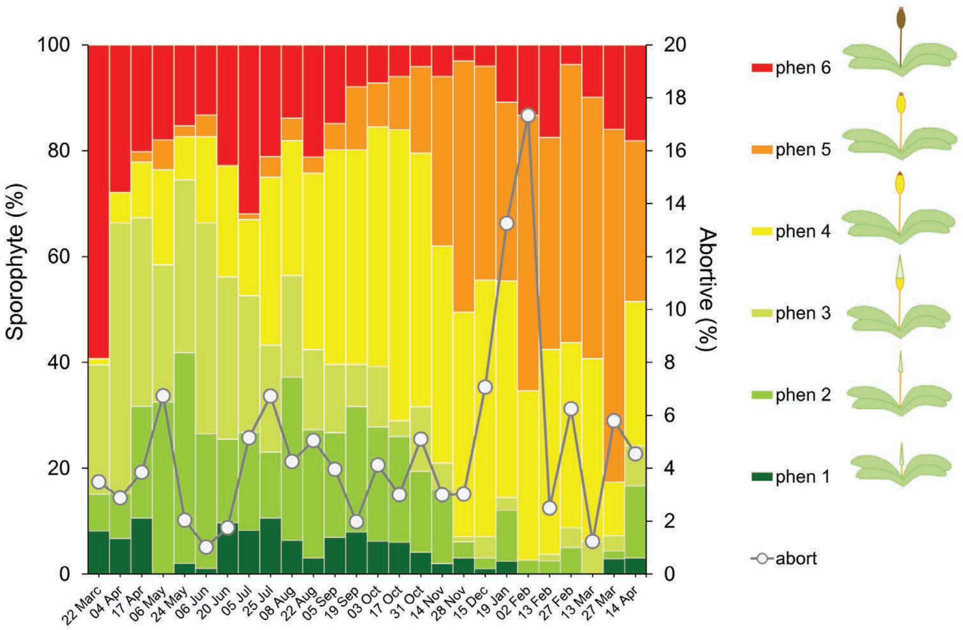

Fig 2. Percentages of sporophytes of *Octoblepharum albidum* in different phenophases as well as abortive stages, in a semideciduous ecosystem (Belo Horizonte, Brazil), from March/2014 to April/2015.

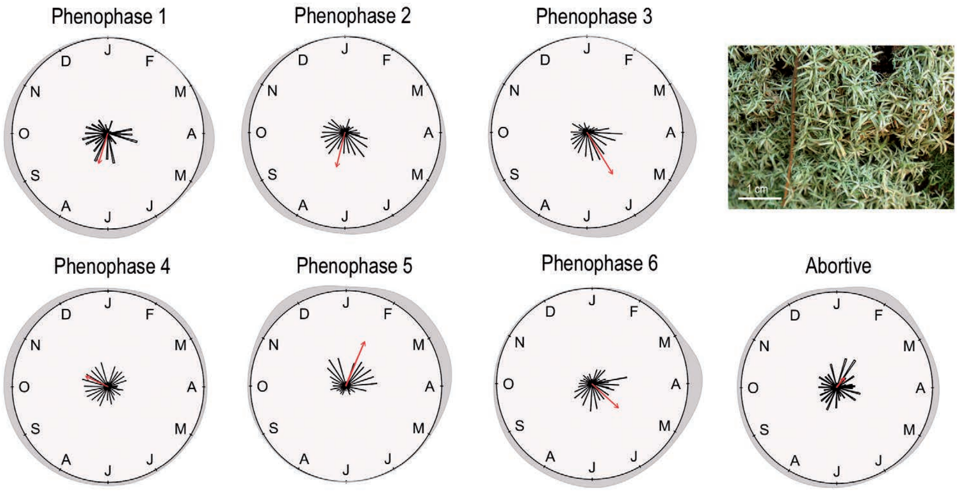

Fig 3. Frequencies of the different phenophases as well as abortive stages of the sporophytes of *Octoblepharum albidum* from March/2014 to April/2015. Red arrows indicate the mean dates of phenophase occurrences; vector lengths indicate concentration near that date. General view of moss plants, with sporophytes on the right.

Table 3. Summary of the three multiple regression models developed based on climatic variables and the frequencies of the sporophyte phenophases of *Octoblepharum albidum* in a semi-deciduous ecosystem (Brazil)

Response variables	*Regression summary*			*Standardized regression coefficient (Beta)*	
	R^2	$F_{(3,22)}$	P	*Predictor 1*	*Predictor 2*
Model 1 (Rainfall and irradiance)					
Phen 1	0.32	5.38	0.0100	– 0.565**	– 0.150$^{\text{n.s.}}$
Phen 2	0.45	9.40	0.0010	– 0.669***	– 0.198$^{\text{n.s.}}$
Phen 3	0.57	15.15	< 0.0001	– 0.472**	– 0.657***
Phen 4			n.s.		
Phen 5	0.44	9.23	0.0010	0.508**	0.509**
Phen 6	0.42	8.55	0.0020	– 0.459**	– 0.532**
Abortive			n.s.		
Model 2 (Rainfall and temperature)					
Phen 1	0.33	5.57	0.0100	– 0.499**	– 0.178$^{\text{n.s.}}$
Phen 2	0.52	12.48	0.0002	– 0.553**	– 0.342*
Phen 3	0.37	6.91	0.0040	– 0.253$^{\text{n.s.}}$	– 0.496**
Phen 4			n.s.		
Phen 5	0.35	6.29	0.0070	0.329$^{\text{n.s.}}$	0.417*
Phen 6	0.24	3.74	0.0400	– 0.303$^{\text{n.s.}}$	– 0.321$^{\text{n.s.}}$
Abortive			n.s.		
Model 3 (Relative humidity and temperature)					
Phen 1	0.29	4.72	0.0190	– 0.445*	– 0.346$^{\text{n.s.}}$
Phen 2	0.51	12.18	0.0002	– 0.531**	– 0.532**
Phen 3	0.31	5.29	0.0100	0.001$^{\text{n.s.}}$	– 0.561**
Phen 4			n.s.		
Phen 5	0.26	4.08	0.0300	0.098$^{\text{n.s.}}$	0.511**
Phen 6			n.s.		
Abortive			n.s.		

** Indicates P-values < 0.05, ** <0.01 and *** < 0.001; n.s. regression values not significant.*

Model 1 was found to better explain the relationships between the climatic variables and the phenophases, although the other two models also contributed to these relationships (Table 3). Models 1 and 2 were both relevant for phenophases 1 and 2, with the frequency of early sporophytes being negatively associated with rainfall values. Models 2 and 3 contributed to explaining the variations in phenophase 2, with this phenophase decreasing with increasing rainfall, relative humidity, and mean temperatures. Phenophase 3 decreased with increasing rainfall and irradiance levels (model 1), and with increasing mean temperatures (models 2 and 3). Phenophase 4 may not be influenced by any climatic variable in our study, although a slight negative relationship with relative humidity was detected (model 3). Phenophase 5 was positively, and phenophase 6 negatively, related to the predictors of model 1 (rainfall and irradiance); additionally, phenophase 5 was negatively related to mean temperatures in models 2 and 3. The frequency of aborted sporophytes was not related to climatic variables in our study.

DISCUSSION

Sporophyte development of the moss *Octoblepharum albidum* was seasonal in the semi-deciduous ecosystem studied here, with the three early stages (immature to post-meiotic sporangia) being present mostly from March to November, 2014 (predominantly the dry season, during the study period). Closed sporangia were observed mostly from July, 2014 to March, 2015 (the end of the dry season and during the rainy season), early-opening sporangia were mostly observed from November, 2014 to April, 2015 (rainy season), and late-opening sporangia mostly from February to October (the end of the rainy season and during the dry season). Principally rainfall, as well as mean T°, irradiance, and RH to some degree, were related to the frequencies of the six phenophases. Our hypotheses were therefore partially supported, as the numbers of both young (phenophases 1 & 2) and late (phen. 6) sporophytes increased with decreasing rainfall. Mature sporangia were overrepresented during the rainy season, with the values of phenophase 5 being positively related to increasing rainfall and irradiance levels.

Egunyomi (1979) reported that *Octoblepharum albidum* (in Nigeria) produced sporophytes during the rainy season and that its spores were dispersed during the dry season. Similarly, Pôrto & Oliveira (2002) observed in a lowland tropical rain forest in Brazil, that sporophyte development in this species begins at the end of the rainy season, with many sporangia opening during the dry season. However, as the authors of both studies considered only a single phenophase corresponding to both early and late-opening sporangia (i.e., one phenophase corresponding to phenophases 5 and 6 in our study) as marking the period of spore liberation, their interpretation of the precise timing of spore dispersal was overestimated. We suggest the fertilization events (not directly measured here) occur mostly during the rainiest months (November to March), but a few fertilized archegonia are also eventually recorded in other months, as observed by Pôrto & Oliveira (2002). Sporophytes develop predominantly during the dry season, and then spores begin to be dispersed with the first rainfall, and spore release was completed by the beginning of the dry season. As such, cohorts of spores would be germinating during the rainy season up to the end of the rains. Although spores depend on water for germination, they can germinate even under conditions of low moisture availability (Maciel da Silva *et al*., 2009), and the protonemata or young leafy gametophytes can apparently tolerate periods of desiccation and survive through the dry season (Proctor *et al*., 2007). Finally, phenophase 6, representing late-opening sporangia emptied of their spore contents, coincides largely with the dry season, when the majority of spores have already been dispersed.

In a classical study of tropical African mosses, Odu (1982) concluded that spore dispersal occurred predominantly during the dry season in *Racopilum africanum* Mitt., *Thuidium gratum* (P. Beauv.) A. Jaeger, and *Fissidens glauculus* Müll. Hal. ex Dusén in humid environments in Nigeria. Fatoba (1998) identified the same pattern for *Bryum coronatum* Schwägr. and *Hyophila involuta* (Hook.) A. Jaeger in similar habitats, although the phenophase used by these authors as a proxy for spore dispersal was “empty and fresh sporangium”, that is, the period after the actual dispersal phase for most spores. The phenological stages of moss sporophytes generally follow Greene (1960), with some or no modifications (Stark, 2002). These studies assumed that the phenophase “operculum fallen” = recently open sporangium (containing > 1/2 spores), could be used as a proxy for spore dispersal.

The use of a spore maturity index, instead of a single phenophase, aids our understanding of the transition between "early and late-opening sporangia" phenophases and in estimating the true period of spore dispersal. Accordingly, *Racopilum africanum*, *Thuidium gratum*, and *Fissidens glaucus* disperse their spores mostly during the last months of the rainy season, leaving only empty sporangia in the dry season (Odu, 1982). Similarly, Makinde & Odu (1994) reported that the four dominant sexually reproducing mosses in a savanna habitat in Nigeria dispersed their spores at the end of the rainy season, and they were able to find protonemata and new gametophytes *in situ* at the beginning of the rainy period.

Seasonality is an important variable that can explain the variations observed in the vegetative and reproductive cycles of mosses (Glime, 2013a, b). In tropical habitats with slight seasonality (e.g., altitudinal and sea-level tropical rain forests in southeastern Brazil), bryophytes tend to produce gametangia and sporophytes more or less continuously throughout the entire year, although with peaks of gametangial maturation during the rainy season and spore dispersal at the end of the rainy season (Maciel-Silva *et al*., 2011). Seasonality was not found to influence the production of sporophytes in the liverwort *Radula flaccida* Lindenb. & Gottsche in the Amazonian Forest (Zartman *et al*., 2015); conversely the moss *Fabronia ciliaris* (Brid.) Brid. growing in a seasonally dry forest (e.g., *Caatinga* vegetation in Brazil) showed strong variations in gametangia (observed during the rainy season) and sporophyte production (during the dry season) that was likely influenced by the distinct seasonality of that environment (Nunes *et al.*, 2015). The vegetation in our study site was semi-deciduous, but with components of tropical rain forest and neotropical savanna, and the presence of accentuated dry and rainy seasons were found to determine the mean dates for the occurrence of key events in the sexual cycle of *O. albidum*.

Rainfall seems to be the main factor controlling gametangia formation, fertilization, and sporophyte development in tropical habitats (Egunyomi, 1979; Odu, 1982; Makinde & Odu, 1994; Fatoba, 1998; Oliveira & Pôrto, 2001; Oliveira & Pôrto, 2002; Maciel-Silva, 2011). We detected relevant contributions of rainfall in the present study, especially in terms of pre- to post-meiotic sporangia, with late-opening sporangia being underrepresented in the rainiest months. Increasing numbers of spore dispersing sporangia were observed in the rainiest months, as well as periods with elevated irradiance levels and mean temperatures – supporting the assumption that after fertilization (in the rainy season), sporophytes develop throughout the dry season, and then ultimately disperse their spores during the following rainy season.

Although no signs of seasonality or relationships with the climatic variables examined were observed with abortive sporophytes, an increase of approximately 10% in the numbers of aborted sporophytes was observed during the short drought period that occurred during the rainy season (January/2015) – suggesting that sporophytes are less tolerant of desiccation conditions combined with high temperature and irradiance levels (rainy season) than of desiccation at lower temperature and irradiance levels (dry season). Alternatively, many young sporophytes may not survive dehydration-rehydration cycles during the warm summer, as repair costs for damaged cells are much higher at elevated temperatures (Stark, 2001).

The present study was the first to analyze the phenological data of a bryophyte using a circular approach that is more appropriate for understanding cyclical phenomena. These findings contributed to our understanding of bryophyte biology in seasonal tropical ecosystems, their phenological patterns, and the roles of climatic variables in the sexual cycle of tropical mosses, and also illustrated the consequences of misinterpreting some of their phenophases. Additional comparative studies focusing on different ecosystems will still be needed, as well as investigations of microclimatic effects at the population level.

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