



ABSTRACT

Bryophytes are non-vascular plants capable of colonizing nearly all conceivable habitats and their occurrence varies with ecological zone. Despite the widespread distribution of bryophytes, little is known about the effect of climate on their distribution and

THE IMPACTS OF CLIMATE ON SPECIES DISTRIBUTION AND REPRODUCTION IN BRYOPHYTES

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INTRODUCTION

Bryophytes are green land plants which grow in a variety of habitats especially in moist places on soil, rocks, trunks and branches of trees and fallen log. The bryophyte communities are known for the fact that their species composition and richness is strongly influenced by external factors, especially water, light and temperature (Magdefrau, 1982) which makes them efficient bio-indicators (Frahm and Gradstein, 1991). While the bryophytes lack some of the adaptations to dry environments found in the vascular plants and are only able to grow and reproduce in wet environments, some bryophytes are able to survive in habitats with relatively little or no rainfall. Bryophytes are more sensitive to environmental alternations than vascular plants due to the absence of roots, a well developed vascular system and cuticle (Herben, 1987).



reproduction. The study investigated the impacts of climatic factors on species distribution and reproduction in bryophytes. The distribution of bryophytes were monitored in their natural populations across the study areas where their samples were carefully removed from their underlying substrata and each sample was kept in an envelope, labeled and brought to the laboratory for observations, identification and reproductive studies. The results showed a total of 22 species of mosses and liverworts widely distributed on various habitats. The bryophytes reproduced sexually, asexually and vegetatively with maturation cycles of the mosses studied began earlier than liverworts in response to early rain during the period of study. The findings of this study suggest that the climate of the sites in the present study cannot be considered harmful for bryophytes but rather has temperature and water availability that relatively favour the growth and reproduction of bryophytes.

Keywords: *Mosses, liverworts, maturity indices, rainfall distribution.*

Contrary to most vascular plants, bryophytes regulate water uptake mainly by capillarity and since they are usually small, their survival may be more restricted by the frequency rather by the volume of rainfall. The ecological distribution of bryophytes is influenced by macro climatic factors (rainfall and temperature) (Porley and Hodgetts, 2005) and micro environment features of shade (light intensity), habitat humidity and temperature (Pentecost, 1998) which makes them efficient bio-indicators (Frahm and Gradstein, 1991). Climate is the most important ecological factor that determines the bryophyte types, basic characters and the distribution areas of the bryophytes. The common effects of the climatic factors such as temperature,



humidity, rain and light have important role in formation of the bryophyte vegetation of a place (Pocs, 2004). Precipitation and temperature (climate) have a strong effect on species richness, since sexual reproduction and photosynthesis in bryophytes are highly dependent on water availability and optimal growth occurs with suitable temperatures (Ogunbiyi, 2021).

The bryophyte flora comprises many different and individually adapted species, in contrast to the wide ecological range shown by the vascular plants. Bryophytes are non-vascular plants capable of colonizing nearly all conceivable habitats and their occurrence varies with ecological zone. The guinea savanna ecological zone of Kwara State harbors a low diversity of bryophytes and great diversification of microhabitats (Ogunbiyi, 2020). The non-occurrence of many bryophytes in the guinea savanna ecological zone of Nigeria has been attributed to the climatic features and flora composition of the area (Ogunbiyi, 2003). The very few ones that grow in the savanna are exposed more to the harsh scourge of sunshine, temperature and inadequate rainfall distribution.

Despite the widespread distribution of bryophytes, little is known about the impacts of climate on their distribution and reproduction throughout the world and information concerning research results is very scanty. The reasons for this are the difficulties researchers often have with bryophyte identification, the limited amount of the same species available for analyses due to their inconspicuous position in the ecosystem. The aim of this study was to evaluate the impacts of climatic factors on species distribution and reproduction in bryophytes. The objectives of this study were to: (a) study the occurrence of bryophytes in different locations in the study area; (b) determine the effect of rain distribution on species diversity; and (c)



evaluate the effect of light and substrate characteristics on species distribution and reproduction.

MATERIALS AND METHODS

Study area

The study was conducted in eleven Local Government Areas of Kwara State, namely Ekiti, Ifelodun, Ilorin East, Ilorin South, Ilorin West, Irepodun, Isin, Offa, Oke-Ero, Oyun and Pategi. The study area falls within the middle belt zone of Nigeria making it a geographical transition between the southern forest zone and the northern savanna. The study area experiences high temperature all over the year round due to its latitudinal location within the tropics. The area records a minimum and maximum temperature of 28°C and 37°C, respectively with the highest air temperature usually in March while the minimum during the peak of the rainy season (Figure 1).

Sampling design and study of bryophytic species

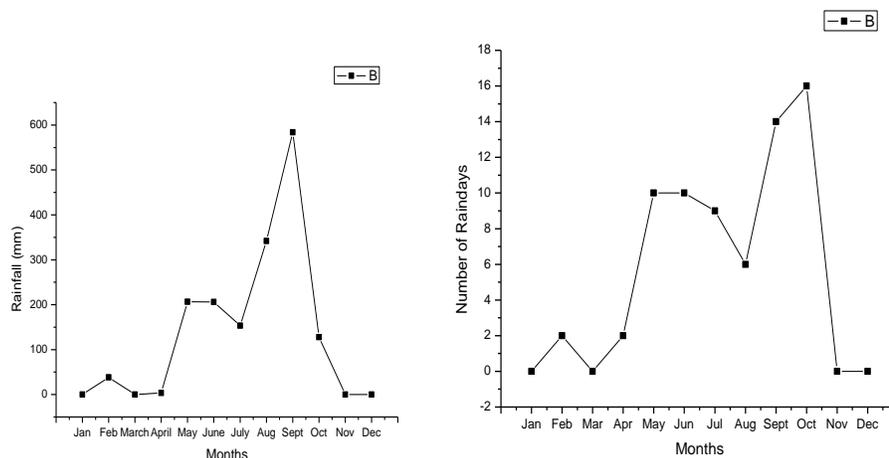
The distribution of bryophytes were monitored in their natural populations across the study area where their samples were carefully removed from their underlying substrata and each sample was kept in an envelope, labeled and brought to the laboratory for observations, identification and reproductive studies. Stereomicroscope was used to assess the sex expression of each gametophyte.

The results collected were subjected to statistical analysis. Climatic data showing monthly total rainfall, number of raindays, relative humidity and temperature of the areas during the period of study were obtained from the weather station of the Nigeria Meteorological Agency (Nimet), Ilorin International Airport, Kwara State.



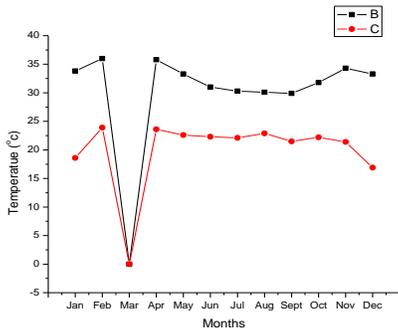
RESULTS

A complete inventory of the study area revealed a total of 22 species of liverworts (6) and mosses (16) distributed on different substrates such as tree barks, soil including termitaria, concrete, rock and rotten logs or decaying wood (Table 1). A close observation of the substrates showed that young and fresh moss and liverwort shoots only appeared on the substrates after the commencement of rain in each year except those that were under shade or received continuous supply of moisture. The mosses and liverworts showed periodicity in growth, related to the rainy and dry seasons (Figures 1 and 2). The results showed that most species were recorded under shade environment compared with others found in open space and exposed landscapes where light was abundantly received (Table 1). The common species in most areas were *Hyophila involuta*, *Barbula indica*, *Fissidens planifrons*, *F. grandifolius* and *Cyathodium cavernarum* which had the highest number of species and occurred on virtually all substrates especially in a cool and shady places where more moisture was available and devoid of extreme light intensity.

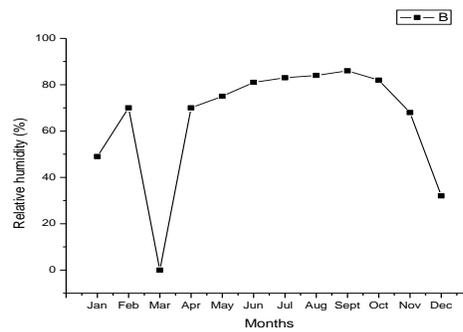


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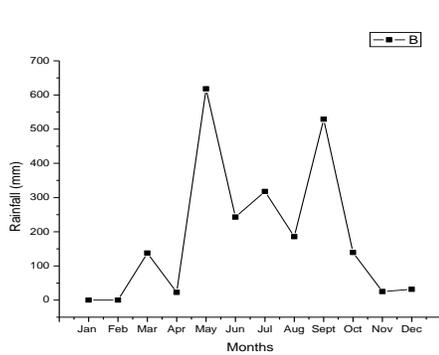


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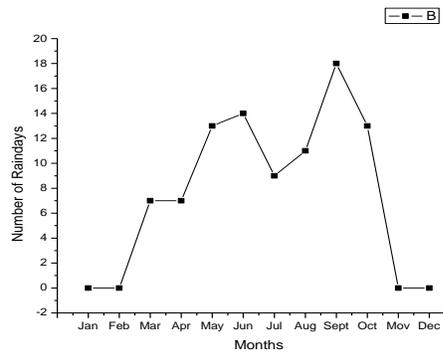


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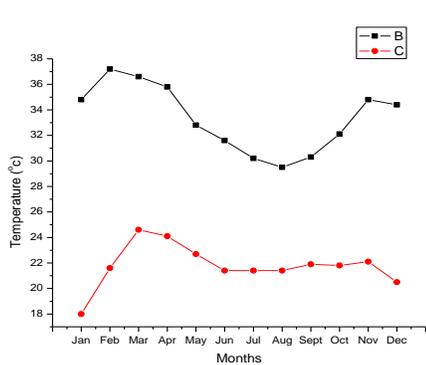
Figure 1: 2015 Climatic data of Kwara State: (a) Total rainfall, (b) Number of rain days, (c) Temperature (B: maximum; C: minimum) and (d) Relative humidity.



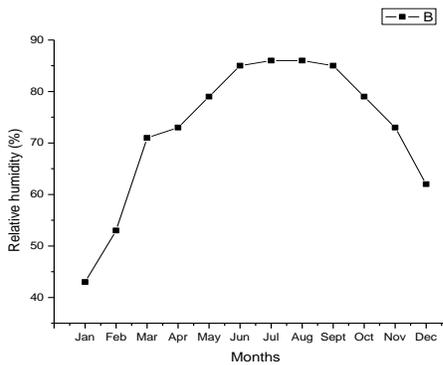
a)



(b)



(c)



(d)

Figure 2: 2016 Climatic data of Kwara State: (a) Total rainfall, (b) Number of rain days, (c) Temperature and (d) Relative humidity.



Table 1: Bryophyte species and their natural habitats

Species	Habitat	Substrate	Light
<i>Archilejeunea abbreviata</i>	Epiphytic	Tree bark	Open space and shade
<i>Cyathodium cavernarum</i>	Terrestrial	Rock, soil, sandcrete material	Shade
<i>Mastigolejeunea nigra</i>	Epiphytic	Tree bark	Shade
<i>Lejeunea sp</i>	Epiphytic	Tree bark and rotten log	Open space/shade
<i>Archilejeunea africana</i>	Epiphytic	Tree bark	Shade
<i>Riccia nigrella</i>	Terrestrial	Soil	Open space/shade
<i>Hyophila involuta</i>	Terrestrial	Rock, sandcrete material, soil, rotten log	Open space/shade
<i>Barbula indica</i>	Terrestrial	Sandcrete material, soil	Open space
<i>Fissidens planifrons</i>	Terrestrial	Soil, rock	Shade/open space
<i>Philonotis hastata</i>	Terrestrial	Rock, soil	Shade/open space
<i>Pelekium gratum</i>	Terrestrial/epiphytic	Rock, soil, palm tree	Shade/open space



<i>Stereophyllum macrocarpum</i>	Epiphytic	Tree bark (palm tree)	Shade
<i>Fissidens grandifolius</i>	Terrestrial	Soil, rock	Shade
<i>Racopilum africanum</i>	Terrestrial/epiphytic	Soil, palm tree	Shade
<i>Heterophyllum bulbiferum</i>	Terrestrial/epiphytic	Soil, tree bark	Shade
<i>Calymperes afzelii</i>	Epiphytic	Palm tree	Shade
<i>Brachymerium acuminatum</i>	Epiphytic	Rotten log	Open space
<i>Erythrodontium barteri</i>	Epiphytic	Tree bark	Shade
<i>Calymperes proligerum</i>	Epiphytic	Palm tree	Shade
<i>Brachymerium leptophyllum</i>	Terrestrial	Sandcrete material	Open space
<i>Bryum coronatum</i>	Terrestrial	Sandcrete material, soil	Open space
<i>Erpodium coronatum</i>	Epiphytic	Tree bark	Shade

The results of the reproductive strategies showed that bryophytes reproduced in three different ways: sexual, asexual and vegetative reproduction. Of the three types of reproduction, sexual reproduction was the most frequent type of reproduction found in the selected species (Table 2). The monthly maturity indices of gametangia and sporophytes of bryophytes recorded during the period of study are shown in Table 3. The results showed that the maturation cycles of the



mosses studied began earlier than liverworts in response to early rain during the period of study.

Table 2: Comparative morphology and reproductive strategies of the selected bryophyte species

Species	Habit/habitat	Reproductive type	Breeding system	Sporophytes	Vegetative reproduction	No. of sporophyte
<i>Barbula indica</i>	Acrocarpous, terricolous	Sexual and asexual	Dioicous	Stegocarpous	Present	Polysporous
<i>Fissidens planifrons</i>	Acrocarpous, terricolous	Sexual and asexual	Monoicous	Stegocarpous	Present	Polysporous
<i>Calymperes proligerum</i>	Acrocarpous, terricolous	Asexual	Monoicous	Stegocarpous	Present	Monosporous
<i>Hyophila involuta</i>	Acrocarpous, terricolous	Sexual and asexual	Dioicous	Stegocarpous	Absent	Monosporous
<i>Fissidens grandifolius</i>	Acrocarpous, terricolous	Sexual	Dioicous	Stegocarpous	Absent	Monosporous
<i>Erpodium coronatum</i>	Acrocarpous, terricolous	Sexual	Dioicous	Stegocarpous	Absent	Polysporous
<i>Pelekium gratum</i>	Pleurocarpous, orticolous, rupicolous	Sexual	Monoicous	Stegocarpous	Absent	Monosporous



<i>Bryum coronatum</i>	Acrocarpous, terricolous	Sexual and asexual	Dioicous	Stegocar-pous	Present	Monosetous
<i>Stereophyllum macrocarpum</i>	Acrocarpous, terricolous	Sexual and asexual	Dioicous	Stegocar-pous	Present	Polysetous
<i>Brachymerium acuminatum</i>	Acrocarpous, terricolous	Sexual	Dioicous	-	Absent	Absent
<i>Philonotis hastata</i>	Acrocarpous, rupicolous	Asexual	Monoicous	-	Present	Absent
<i>Archilejeunea africana</i>	Pleurocarpous, corticolous	Sexual/vegetative	Monoicous	-	Absent	Absent

Gametangial initiation and development, fertilization of archegonia and sporophyte development occurred mostly during the period of moisture availability and wet months (March-October). Abundant gametangia initiation and maturation were recorded in most of the moss species within 3 months of the substrate colonization and growth. The pattern of gametangia initiation was essentially the same, with the antheridia being formed earlier than archegonia in some species while in others both antheridia and archegonia formed concurrently.

The appearances of young antheridia in the juvenile and immature stages were first noticed in March or April in *Barbula indica*, *Fissidens planifrons* and *Fissidens glandifolius* in some of the habitats sampled soon after the beginning of the rainy season of each year (Table 3).



Archegonia appeared concurrently with the antheridia in May in *Archilejeunea africana*, *Calymperes afzelii* and *Pelekium gratum* (Table 3), otherwise young archegonia were first seen 2-3 months after the development of antheridia in other species.

Microscopic studies revealed that rapid development of sporophyte started immediately after fertilization in all the mosses. The results showed that the first appearance of the sporophyte was between March and September. The sporophytes in the swollen venter (SV) stage were first recorded in *Fissidens planifrons* and *Barbula indica* immediately after fertilization between March and May. Sporophyte development started in April in *Barbula indica* while it was produced one month after gametangia initiation in May in *Fissidens* sp, *Pelekium gratum* and *Stereophyllum macrocarpum* (Table 3).

Clear seasonality in gametangial and sporophytic development was confirmed, with only minor variation among species/ sites or years. The gametangial initiation and developmental stages coincided with the rainy season and high humidity and active spore dispersal occurred in early dry season (December) depending on the species. The availability of water over the year varies markedly and moisture decisively influenced the phenology of these species. The results showed that bryophyte phenology was found to be related to microclimate as was shown by the difference in maturation cycles in the study period. The results further showed that sex organs were initiated shortly after the commencement of rainy season for the year, and the development of sex organs occurred during the rainy period when the relative humidity was high and the mean temperature was relatively high (Figures 2 and 3) .

Spore dispersal occurred during the dry season which is characterized by little or no rainfall, lower relative humidity and high mean temperature. The results showed that the climatic and environmental



factors played a major role in the initiation and development of gametangia from various habitats and they also influenced sporophyte development and dispersal of matured spores in all the habitats. Growth and initiation of gametangia occurred at the onset of rainy season, while fertilization and sporophyte development also occurred during the rainy season. Spore dispersal occurred majorly during the dry season and when landed on suitable substrata, the reproductive cycle continues during the subsequent rainy season after germination.

DISCUSSION

The occurrence of few numbers of bryophytes (mosses and liverworts) on various ecological substrates in the study areas can be attributed to a series of ecological factors including climate (rainfall, temperature and relative humidity), nutrients and habitat factors. This is in agreement with the findings of other researchers (Proctor, 1984; Eldridge and Tozer, 1997; Batista *et al.*, 2018) who reported that rainfall (moisture) and nutrient availability are the primary determinant in distribution of bryophytes and lichens. The desiccation-tolerant species of dry sunny places face the additional constraint that they quickly dry out in sunshine and, for most of the time the sun is shining, they will be dry and metabolically inactive. The high occurrence of mosses and liverworts under shade than in exposed landscapes shows that bryophytes are shade loving plants. This result is in agreement with the report of Asthana (2006) who reported that bryophytes are shade loving land plants capable of growing in moist substrates.

The greater abundance of mosses than liverworts in many sites may be related to more members of this group having specialized morphological, anatomical and physiological traits of desiccation tolerance (Goffinet *et al.*, 2009; Proctor and Tuba, 2002; Proctor *et al.*,



2007), which can survive successfully in extreme environments. The absence of many species particularly hornworts may not be unconnected with the inadaptability of this group to the prevalent climatic and environmental conditions of the area. These results are in agreement with the findings of Cleavitt (2002), who reported that ecological distribution of bryophytes is considered to be affected by the degree of their physiological tolerance to particular range of environmental conditions. The distribution of bryophytes in a habitat is a true reflection of moisture content and the nutrient composition of the substrates where each species is found.

The apparently low species observed in the present study is an indication of the peculiar feature of climate of the study areas where intense sunshine, high temperature, low humidity, low rainfall distribution and strong winds among other factors, limit the growth and development of many plant species and dictate the occurrence of the more tolerant species, and this may be why hornworts are absent from this area. The higher species diversity in temperate region where there is constant availability of precipitation and consequent high humidity, low temperature than in the tropics justifies this observation (Fatoba, 2001). The fact that diversity of bryophytes is relatively low is not surprising, since extreme ecological and climatic conditions reduce the species number world over. The occurrence of mosses in high numbers is in consonance with what is obtainable elsewhere particularly from polar to tropical regions which illustrates their high adaptability to different environmental conditions. The availability of water and light during the growing season are the main factor limiting growth, photosynthesis, distribution and development of moss communities in temperate as well as in tropical regions (Barrett, 2013; Fatoba, 1997; Olarinmoye, 1974). The occurrence of bryophytes that fluctuates greatly between seasons of the year clearly shows the



bryophyte dependency on moisture status of the substrate. This result agrees with the findings of Proctor (1984) who opined that the ecological distribution of many bryophytes is highly sensitive to factors that affect plant water status.

Although bryophytes are widely distributed on several substrates as reported in this study, different types of bryophytes have their ranges of climatic and environmental conditions within which they can best grow and successfully reproduce (Song *et al.*, 2015). Bryophyte species are naturally and globally well equipped to grow at low temperature. The high temperature prevalent in Kwara State, Nigeria (tropical Africa) might be responsible for low diversity of bryophytes. The report of Tuba (1987) that metabolic activities are normally carried out at relatively low temperature and low light intensity in poikilohydric plants justify the low abundance of bryophytes in Kwara State. However, bryophytes have evolved and persisted in their own different environments and thrived under a wide range of climatic and environmental conditions. Their relatively low optimal temperature for growth might be closely related to their reduction and non persistence, even non dominance in certain environments, like guinea savanna, where they have been displaced by dominant vascular plants. The mosses and liverworts reported in this study tend to respond differently to habitat and climatic conditions of the environment, with liverworts preferring more sheltered and moist conditions. Similar results were recorded in forests where liverworts were mostly found on humid substrates that supply sufficient moisture and nutrients (Clausen, 1964; Johnson-Groh, 1987; Wood, 2007). The small size and the absence of roots are indications that most bryophytes react in a different way to environmental stress such as short periods of drought, in that they cannot draw water reserves in the substrate even for a short period. The apparently higher climatic sensitivity of



liverworts compared to mosses could be attributed to their lower desiccation tolerance (Wood, 2007), especially observable in leafy liverworts due to their life form traits (During, 1992). This is manifested by the high sensitivity of the group to anthropogenic factors (Patino *et al.*, 2010). It is probably due to this that mosses can be found in a comparatively wider range of landscapes, including grasslands and artificial substrates (Vanderpoorten and Goffinet, 2009) while liverworts seem to be more dependent on sheltered habitats like forests as compared with other open and exposed landscapes thereby limiting their occurrences in different habitats.

The appearance of bryophytes on their respective substrates which coincides with the commencement of rainy season or period of moisture availability underscores the importance of moisture in bryophyte distribution. It is assumed that water availability is of major importance during the colonization of substrates by bryophytes. The occurrence of bryophytes mostly in humid area especially along drainages and the river course shows that they need water for survival. This observation is in agreement with the findings of Ogunbiyi (2003) who reported that bryophytes grow mostly in humid area along drainages and the river course and tree drooping in Kwara State.

The reproductive cycle of the bryophyte species is influenced by the environment due to the climatic seasonality present in Kwara State, as they have adopted wider varieties of reproductive strategies than seed-producing plants. The climatic factors especially rainfall contribute to the success of the sexual reproductive cycle in bryophytes as it favours the self-fertilisation and the formation of the sporophytes, as well as provide moisture to the development of the asexual diaspores. Climatic data obtained for this study suggest that the months with heaviest rainfall (increasing moisture) are important for triggering different stages in the life cycle of bryophytes, such as



reproductive branches and gametangia, and fertilisation. Thus, gametangial maturation, fertilisation, and the majority of sporophyte maturation occur during the rainy months. These results are consistent with the findings of other researchers (Milne, 2001; Oliveira and Porto, 2001; Glime, 2007 and Maciel-Silva and Valio, 2011) who reported that environmental factors such as precipitation may impact on the sexual expression of some species. Similarly, spore dispersal is best achieved during the dry season. Thus, climatic factors are the main factors influencing the spread of bryophyte species in Kwara state.

The luxuriant gametangia initiation recorded mostly during the moist conditions suggest that all bryophytes require good substrate moisture for reproduction. The strategies help to prevent these reproductive structures from exposure to harsh environmental conditions during the developmental stages. The distribution of rainfall over a larger number of days results into a regular supply of water with attendance high atmospheric humidity for longer period, the features that guarantee successful reproduction in all the species. The combination of the length of the growing season and the distribution of precipitation during the year undoubtedly influences the timing of the various life cycle events in the selected bryophytes. The most moist substrates supported high numbers of gametangia compared with the dry substrates, demonstrating the importance of moisture availability for the success of gametangia formation. This result is consistent with the findings of other researchers who confirmed the importance of the rainy season for fertilization in bryophytes (Egunyomi, 1979; Fatoba, 1998; Oliveira and Porto, 2002). It is abundantly clear that the initiation of sexual reproduction (except in the case of species under continuous supply of moisture) only



occurs at the onset of rainy season and that the sporophyte maturation, i.e dehiscence only occurs after the rainy season.

The observable occurrence of mosses and liverworts at temperatures up to 37°C in this study suggests that all the species may be naturally adapted to high temperatures. This temperature requirement coincides with the maturation and dispersal of spores in the dry season, favouring the establishment of new shoots. The ecological niches of these bryophytes support this observation. As temperature is one of the most important environmental factors controlling activities of plants and probably the best predictor of bryophyte growth and reproduction (Greene and Clayton-Greene, 1977), the high temperature tolerance for species distribution in all the affected moss and liverwort species shows that the growth of bryophyte shoots may not be entirely restricted to low temperatures as is universally believed.

In spite of the fact that reproductive performance of bryophytes cannot be divulged from abiotic factors like light, humidity and temperature, endogenous rhythms are considered as necessary factors affecting reproduction in bryophytes. The short life cycle and the ease with which bryophytes disperse their spores enable them to react quickly to climatic change. The short life cycle recorded in these savanna bryophytes and their high capacity for vegetative reproduction, may be a strategy for circumventing the suboptimal conditions of the savanna vegetation which is periodically disturbed by fire and other anthropogenic activities.

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