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Phenological studies of selected savanna mosses of south-western Nigeria

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Abstract. It was established that there is little diversity of bryophytes in the derived savanna. Mosses were found in the sampling sites, whereas liverworts were rarely observed. The reproductive methods of four dominant sexually reproducing savanna mosses – *Archidium ohioense*, *Bryum coronatum*, *Fissidens minutifolius* and *Trachycarpidium tisserantii* were monitored over two consecutive rainy seasons. Protonemal and gametophyte production were noticed in the field in March/April, and capsule dehiscence and spore dispersal occurred in September/October. The sequential stages of development, starting with gametangial production and ending with the falling of the dehisced capsules, occurred within the rainy season. However, *A. ohioense* and *T. tisserantii* did not discharge their spores easily (cleistocarpous), unlike the stegocarpous species *B. coronatum* and *F. minutifolius*. Water availability and possibly high humidity may have contributed to growth. The short period between sex organ formation and dehiscence of capsule seen in these studies, compared with the longer period in some temperate mosses, may be an advantage for bryophytes in a savanna environment.
Key words. Bryophytes; phenology; savanna; climate; inselbergs; West Africa.

Bryophytes are abundant in many different types of plant communities, and have a substantial and distinctive influence on the functioning of ecosystems where they are abundant[1]. Bryophytes are usually morphologically small, though Martin[2] recorded an unusual example of a stem of *Polytrichum commune* Hedw. in New Zealand which attained a length of 150 cm under water. The plants are poikilohydric: they frequently desiccate completely when water is in short supply but rapidly resume growth and photosynthesis upon rehydration[3].

The biology of reproduction is one of the salient factors contributing to evolutionary conservatism in bryophytes[4]. Propagation of bryophytes occurs both sexually and asexually. Sexual reproduction accounts for a degree of genetic flexibility in the majority of moss species and in many liverworts[4]. Sexual reproduction is by oogamy, involving male and female organs: antheridia and archegonia respectively. Gametangial induction and development may be influenced by nutritional factors[5], photoperiods[6], moisture[7], phytohormones[8] and temperature[9].

About half of all bryophyte species are dioecious[3]. Monoecious species clearly run a high risk of inbreeding. An important aspect of the life history of bryophytes is the timing and regulation of the stages of the life cycle[10]. In sexually reproducing mosses, this cycle comprises several easily recognised stages: spore, protonema, buds, full-growth gametophyte, gametangia and sporophyte. Forman[11] suggested that phenological studies may be used to investigate the factors which permit the development of a given stage in a species. The nutritionally independent haploid gametophyte phase of annual bryophytes usually alternates with a less complex diploid sporophyte phase.

The occurrence of bryophytes in Africa is restricted mainly to cool substrates that provide enough moisture to support growth. Olarinmoye[12] reported that the humidity of the air is a major factor controlling the distribution of epiphyllous liverworts in Western Nigeria.

Derived savanna occupies about 8% of the total land area of Nigeria[13]. Typical derived savanna vegetation in Nigeria is found in the south-western part of the country[14]. This type of vegetation, mainly grassland, is formed as a result of human activities or disturbances[15]. Egunyomi[16] reported for the first time in Nigeria the occurrence of *Archidium ohioense* Schimp ex C. Müll. on the moist parts of inselbergs, beneath grasses that are burnt annually. The present work investigates the timing of the appearance of sexual developmental stages in *A. ohioense* and three other savanna mosses in south-western Nigeria, West Africa.

Material and methods

Studies were carried out on 2 inselbergs at the Obafemi Awolowo University campus in Ile-Ife, in south-western Nigeria, located within the latitudes 7°30′ and 7°34′ N and longitudes 4°30′ and 4°32′ E, near the northern boundary of the dry forest vegetation zone. The vegetation of Ile-Ife is lowland rainforest agricultural mosaic, with small patches of derived savanna on the inselbergs[17]. Fresh shoots of 4 dominant sexually-reproducing mosses: *Archidium ohioense* Schimp ex C. Müll., *Bryum coronatum* Schwaegr., *Fissidens minutifolius* Mitt. and *Trachycarpidium tisserantii* Dix. et P. Vard. were sampled from their natural populations in savanna vegetation parts of the inselbergs. (Hills I 410 m and II, 400 m alt.). Samples were collected every month for two periods of 7–9 months.

Table 1. Maturation stages of gametangia and sporophytes in mosses (see also Clarke and Greene[20])

Maturation Stage		Index
Gametangia		
Juvenile (J)		1
Immature (I)		2
Mature (M)		3
Dehisced (D)		4
Sporophyte		
Swollen venter	(SV)	1
Calyptra in perichaetium, early	(ECP)	2
Calyptra in perichaetium, late	(LCP)	3
Calyptra intact, early	(ECI)	4
Calyptra intact, late	(LCI)	5
Operculum intact, early	(EOI)	6
Operculum intact, late	(LOI)	7
Operculum fallen	(OF)	8
Empty and fresh	(EF)	9

Table 2. Maturation stages of sporophyte of *Archidium* and *Trachycarpidium*

Maturation Stage		Index
Sporophyte		
Swollen venter	(SV)	1
Immature capsule	(ICAP)	2
Mature capsule	(MCAP)	3

Developmental stages were observed and index ratings recorded, according to the methods of Greene[18] modified by Longton and Greene[19] and Clark and Greene[20] (table 1).

The developmental stages in table 1 were used in monitoring *Bryum coronatum* and *Fissidens minutifolius*. However, the authors modified the index for the sporophyte stage for *Archidium* and *Trachycarpidium* as shown in table 2.

Gametangial scores were determined using a dissecting microscope in 5 perichaetia/perigonia from 10 shoots and 60 sporophytes respectively. Maturity indices for individual specimens were averaged to give the monthly antheridial and archegonial indices. The mean index values were calculated using the formula of Longton and Green[21]:

$$\frac{\Sigma \text{ Index ratings X number of gametangia/sporophytes}}{\text{Total number of gametangia/sporophytes}}$$

The meteorological data for the Obafemi Awolowo University campus during the period of the investigations were supplied by the Meterological Unit, Faculty of Agriculture, O.A.U., Ile-Ife.

Results

In each of the four species sampled, between 950 and 1,200 perichaetia/perigonia were analysed and these showed a defined seasonal cycle of gametangial develop-

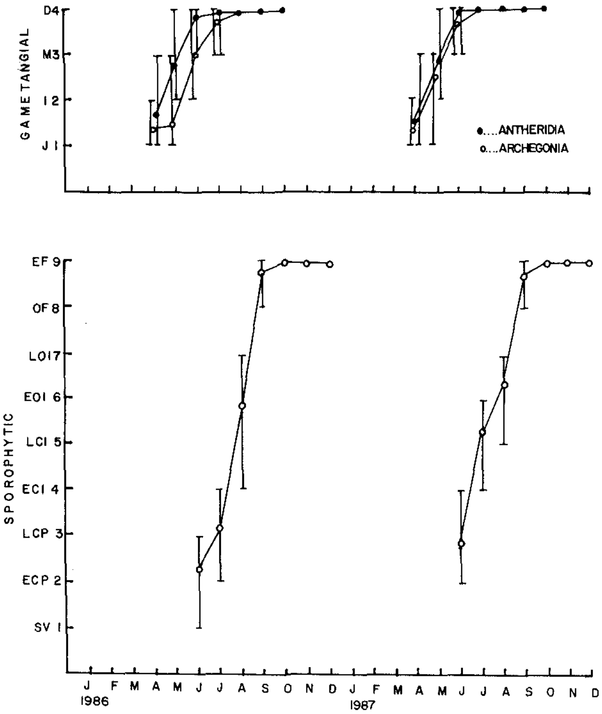

Figure 1. Indices of maturity for *Bryum coronatum*; gametangial development (above) and sporophytic (below). Vertical bars represent the range of stages present.

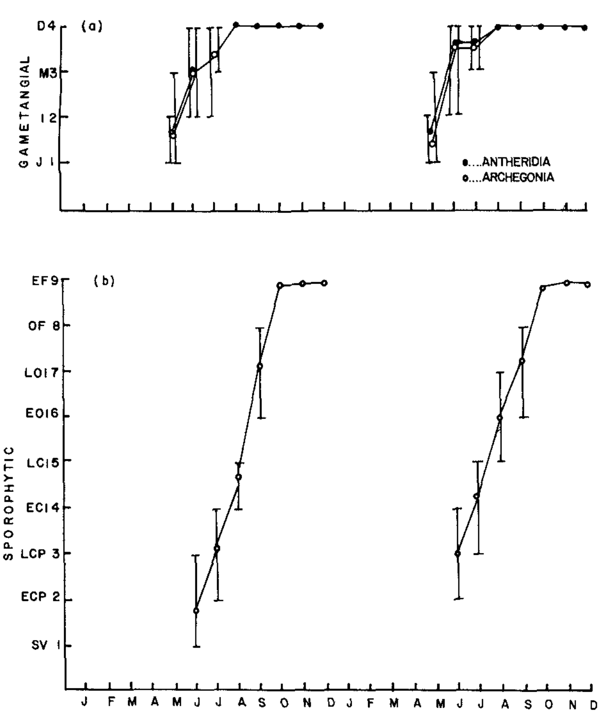

Figure 2. Indices of maturity for *Fissidens minutifolius*; gametangial development (above) and sporophytic (below). Vertical bars represent the range of stages present.

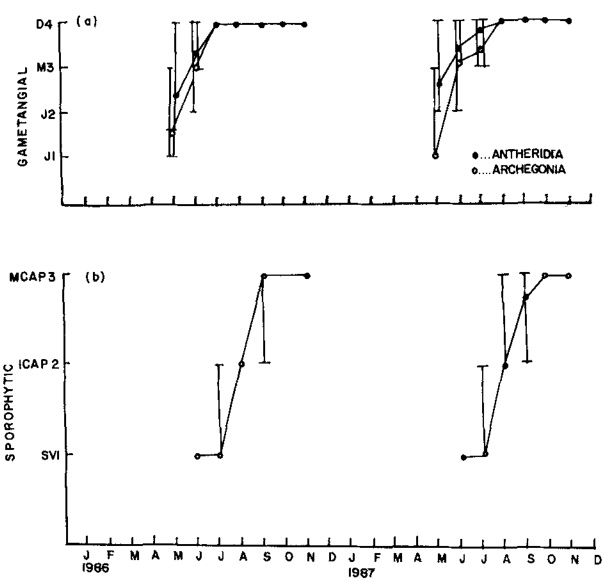

Figure 3. Indices of maturity for *Archidium ohioense*; gametangial development (above) and sporophytic (below). Vertical bars represent the range of stages present.

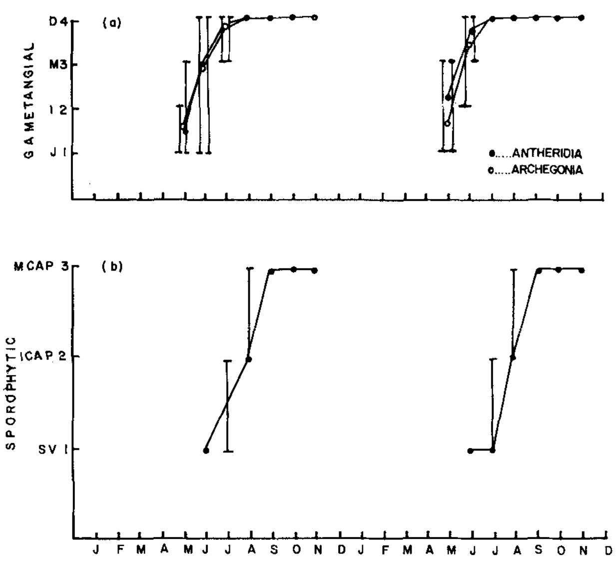

Figure 4. Indices of maturity for *Trachycarpidium tisserantii*; gametangial development (above) and sporophytic (below). Vertical bars represent the range of stages present.

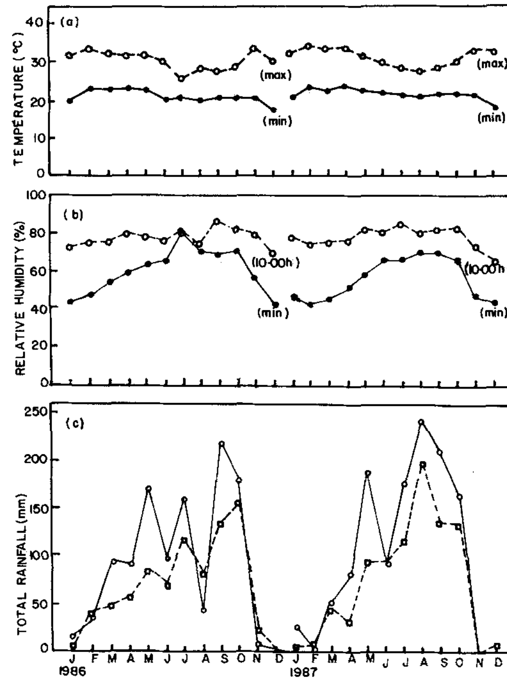

Figure 5. Meterological data of Ile-Ife. *a* Maximum and minimum temperatures; *b* 10.00 h (at 10.00 am) and minimum relative humidity; *c* 0 total rainfall, □ number of rainy days.

ment. The juvenile gametangia were first encountered at the beginning of the rainy season: in April in *Bryum* and *Fissidens minutifolius* (figs 1 and 2), and in May in *Archidium* and *Trachycarpidium* (figs 3 and 4). Both sex organs were formed in the same month, with the antheridia developing a little earlier than the archegonia. The findings of Egunyomi[22] and Odu[23] on mosses of tropical rain-forests conform with this observation. The majority of the gametangia reached the dehisced stage in May/June for *Bryum* (fig. 1), June for *F. minutifolius* (fig. 2), May/June for *Archidium* (fig. 3) and June for *Trachycarpidium* (fig. 4).

The exact time of fertilization is not known. However, mature sex organs usually occur between May and June. Sporophyte development commenced in all species early in June when swollen venters were seen. Rapid development was observed as the rainy season progressed, and capsule maturation occurred in September in *Bryum* and *Fissidens* (viz. figs 1 and 2). The stegocarpous capsule dehiscence and discharge occurred in September/October.

Identical sporophyte developments occur in *Archidium* and *Trachycarpidium* (both have cleistocarpous capsules). The distinct stages were monitored from June (figs 3 and 4) until July/August, when capsules were formed. As there were no opercula, the OF stage (table 1) was never reached[24]. Undehisced capsules from the previous growing season were usually present on old shoots of *Archidium* and *Trachycarpidium*. A rapid succession of developmental stages coincided with the rainy season, high humidity and favourable temperature (fig. 5).

Discussion

The observed period between gametangial initiation and spore dispersal was 4–5 months in *Bryum* and *Fissidens*. The phenological cycle is completed within the rainy season. In contrast, it takes 15–20 months after gametangial initiation for the stage of spore dispersal to be reached in matured capsules of the temperate moss *Pleurozium schreberi* (Brid.). Mitt.[19], and 24 months in the bipolar moss *Polytrichum alpestre* Hoppe[25]. Water availability seemed to influence the phenological cycle, as also observed by Longton[4], in whose study the cycle was completed within 9 months.

In four tropical mosses: *Racopilum africanum* Mitt., *Fissidens glauculus* C. Müll., *Thuidium gratum* Jaeg., and *Stereophyllum* sp., gametangial initiation, fertilization and sporophyte development also occurred during the rainy season[23], while capsule dehiscence and spore dispersal occurred in the dry season to complete the reproductive cycle within a 12-month period.

Among the four species observed in our study, there appeared to be phenological strategies in the dioecious species, *Bryum* and *F. minutifolius* and the monoecious species, *Archidium* and *Trachycarpidium*. Empty and fresh capsules were observed in *Bryum* and *F. minutifolius* in October, while in *Archidium* and *Trachycarpidium* mature undehisced capsules were observed in September. The cleistocarpous nature of the latter two mosses makes spore dispersal a bit difficult.

Bryophytes show a preference for cool, moist climatic conditions, and there is a greater diversity of species in temperate climates than in the tropics. However, some tropical mosses have shown special adaptations to high temperatures[26], with gemmae and resistant tubers which provide a very reliable means of surviving drought[27,28]. Makinde[24] reported that apart from the sexual reproductive methods encountered in the mosses studied, regeneration occurred largely by vegetative methods. The dispersal of spores at maturity is aided by wind (*Stegocarpous* mosses) while vegetative propagules are presumably dispersed through water washing and animals (reptiles and rodents).

The very short life cycle recorded in these savanna mosses, and their high capability for vegetative reproduction, may be a strategy for circumventing the harsh conditions of the savanna vegetation which is periodically disturbed by fire.

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