Bothalia 14, 3 & 4: 647–651 (1983)

Annual habit and apomixis as drought adaptations in *Selaginella tenerrima*

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ABSTRACT

Selaginella tenerrima A. Braun ex Kuhn, widely distributed in the savanna-woodland and savanna zones of tropical Africa, is strictly annual. Dormant megaspores survive the yearly drought. Apomixis has been confirmed through laboratory cultures. Microsporangia are usually absent or very few, and the sporophyte chromosome number is triploid: 2n = 30.

RÉSUMÉ

LE CARACTÈRE ANNUEL ET L'APOMIXIE DE SELAGINELLA TENERRIMA: *FACTEURS D'ADAPTATION À LA SÉCHERESSE*

Selaginella tenerrima *A. Braun ex Kuhn, largement répandue dans la savane boisée et les zones de savanes de l'Afrique tropicale, est strictement annuelle. Des mégaspores dormantes survivent aux sécheresses annuelles. L'apoximie a été confirmée par des cultures en laboratoire. Les microsporanges sont habituellement absents ou très limités et le nombre de chromosomes sporophytes est triploïde: 2n = 30.*

INTRODUCTION

The annual habit is very common in the angiosperms, especially those living under a seasonally dry climate. Such plants survive the rainless part of the year as dormant seeds, emerge during the rains, grow very rapidly, produce large quantities of seeds, and die away at the beginning of the next dry season. Similar life cycles (with the spores as drought surviving organs) are extremely rare in the pteridophytes, from among which only a few dwarfish selaginellas are unquestionably annuals. Until recently, very little was known about their biology.

Apomixis in the pteridophytes renders the reproduction independent of liquid water and considerably shortens the critical gametophytic phase. It has, therefore, often been regarded as an adaptation to xeric environments (Tryon, A. F., 1968; Klekowski, 1969). It is very rare within the genus *Selaginella*, and has up to the present been reported for only a few species, e.g. *S. rubricaulis* R. Sim and *S. spinulosa* A. Braun [= *S. selaginoides* (L.) Link] (Bruchmann, 1912), *S. anocardia* A. Braun (Goebel, 1915) and one race of *S. rupestris* (L.) Spring (Lyon, 1904; Tryon R. M., 1971). In all apomictic selaginellas microsporangia are very few or completely absent (Bower, 1935; Tryon R. M., 1955, 1971).

S. tenerrima A. Braun ex Kuhn from tropical Africa, combines both these remarkable features of annual habit and apomixis. A report on the seasonal pattern and reproductive biology of this species seems, therefore, to be of interest for students of pteridophyte ecology and evolution.

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GEOGRAPHICAL DISTRIBUTION AND HABITAT REQUIREMENTS

S. tenerrima occurs in western, central and southern tropical Africa, from Guinea and Mali through Nigeria, Cameroon, the Central African Republic, Congo (Brazzaville) and Gabon to Angola, Zambia and Mozambique (Alston, 1957, 1959; Kornaś, 1979; Kuhn, 1868; Schelpe, 1970, 1977; Schelpe & Diniz, 1979; Tardieu-Blot, 1964a, 1964b). It certainly is much more widespread than indicated on our map (Fig. 1), but is very easily overlooked, because of its small size and moss-like appearance. It seems to be more common in the seasonally dry areas of the savanna-woodland and savanna zones, although a few stations in the rain forest zone (in S. Nigeria and Gabon) have also been recorded. It usually occurs in bare soil, forming small tufts, often associated with tiny bryophytes (e.g. *Fissidens* spp.), in rock crevices, under overhangs, around the bases of boulders in holes in the soil, and in other similar microhabitats, where it enjoys an increased humidity and some kind of protection from the competition of larger vascular plants.

PHENOLOGY AND LIFE-FORM

The seasonal pattern of growth and sporulation of *S. tenerrima* has been followed in two areas, one situated south of the equator, in Zambia, and the other north of the equator, in N.E. Nigeria and N. Cameroon. In both of them, young sporophytes emerged from the megaspores near the end of the rainy season: in April–June in Zambia and in September–November in Nigeria and Cameroon (Fig. 2). Germination of megaspores was apparently stimulated by the increase in soil moisture; laboratory experiments conducted in Poland have demonstrated, that the fresh megaspores from N. E. Nigeria were able to germinate in January and

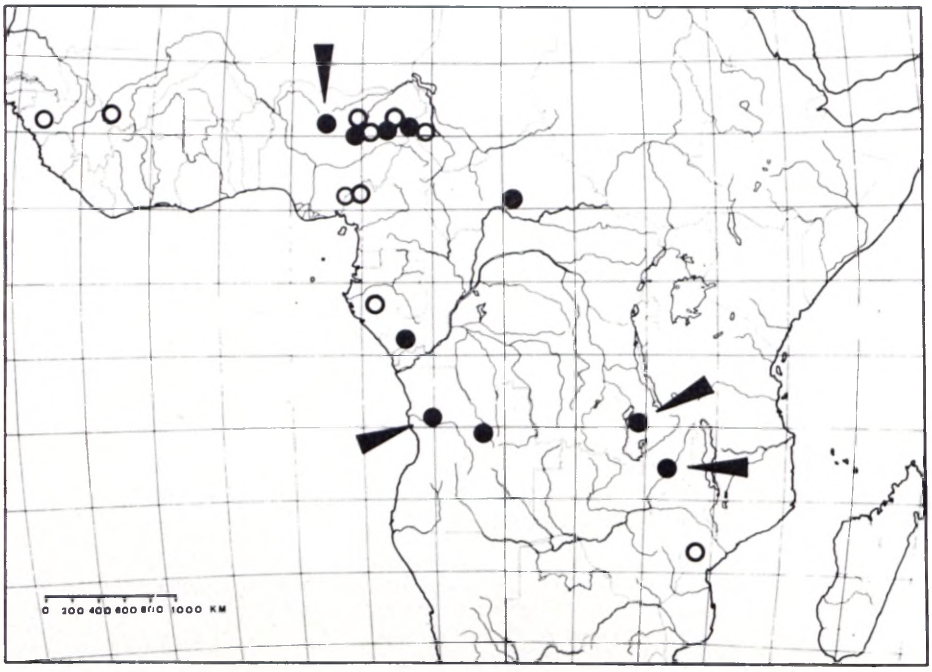

FIG. 1.—Distribution of *Selaginella tenerrima*. Solid circles show stations from which herbarium specimens have been revised, open circles represent records from literature. Stations from which microsporangia are known, are indicated by arrows.

February, therefore possibly lacking an inherent dormancy period. Sporophytes developed very fast under natural conditions and set strobili in a few weeks. In more humid habitats, they attained a height of up to 6 cm, but in the drier ones they remained dwarfish and often unbranched, forming a single strobilus at the apex of a stem of only 0,5 cm tall (Fig. 3).

The life duration of the sporophytes was extremely short. Soon after the end of the rains, they turned yellow and died. Megaspores were shed in such quantities that they were easily detectable on the soil surface near the tufts.

S. tenerrima is strictly annual: no perennating vegetative organs have ever been detected, and most of the mature sporophytes retained the empty wall of the megaspore at their base (Fig. 3).

REPRODUCTIVE BIOLOGY

All available living and herbarium material of *S. tenerrima* has been checked for the presence of strobili and the two types of sporangia (see Appendix). Practically every individual plant studied, even the smallest one, bore strobili, the number of which ranged from 1 to 40. Most of the sporophytes contained only megasporangia; in 5 samples (including the type collection from Angola — *Welwitsch* 45, BM, K) very few microsporangia were also seen (usually no more than 1–3 in c. 100 strobili inspected). The normal number of megaspores per sporangium was four, and their output in all populations was enormous — a feature which is similar to the very high production of seeds in annual angiosperms.

CULTURE EXPERIMENTS AND CHROMOSOME NUMBER

The populations of *S. tenerrima* studied in the field persisted from year to year even in the absence of microspores and microgametophytes. Apomixis is the only explanation of this situation. We were able to confirm this mode of reproduction in laboratory

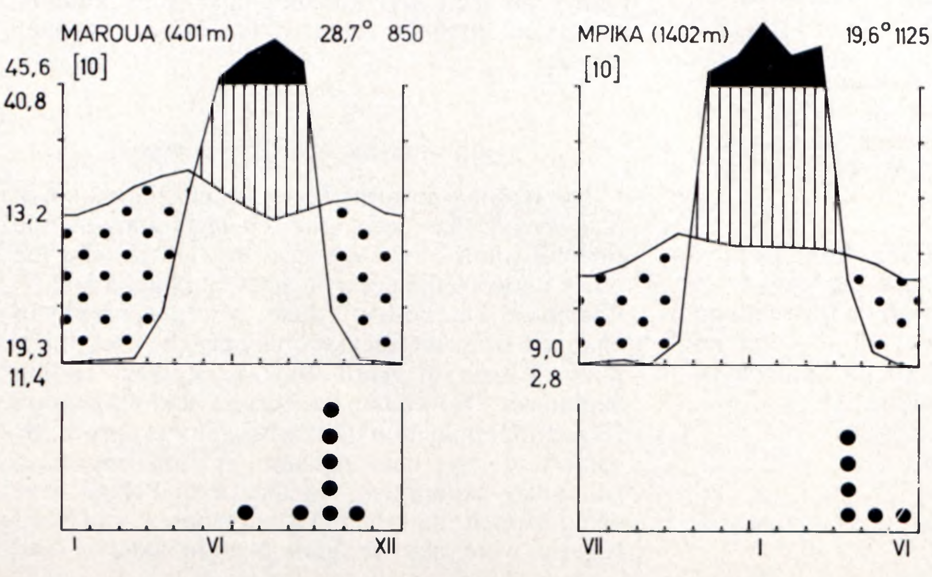

FIG. 2.—Above: climate diagram of stations in N. Cameroon (Maroua) and Zambia (Mpika) near which *Selaginella tenerrima* occurs. Drawn after Walter & Lieth (1960). Below: phenology of *S. tenerrima* in N.E. Nigeria and N. Cameroon (left) and in Zambia (right). Roman numerals designate the months; each dot shows one herbarium collection.

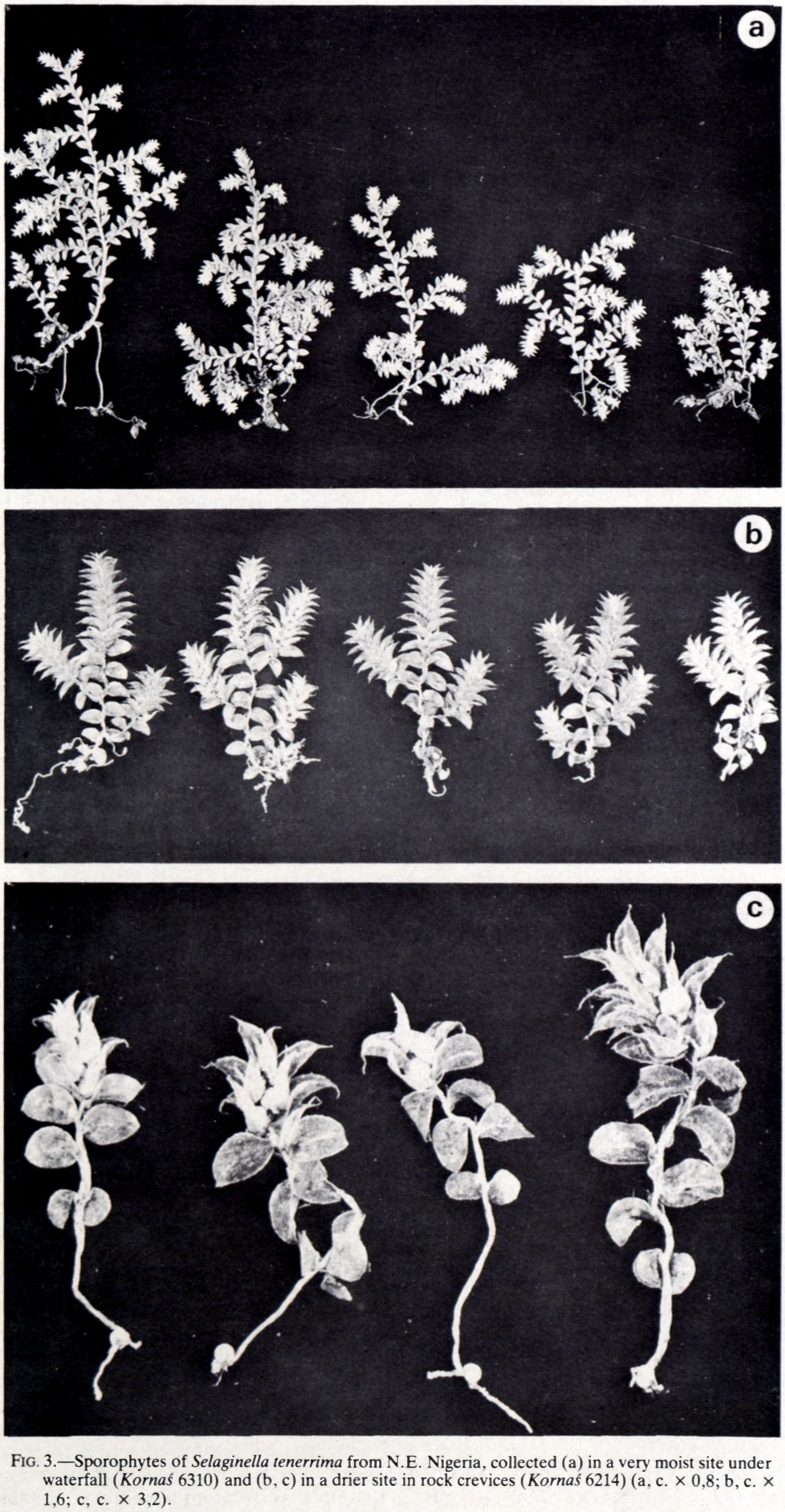

FIG. 3.—Sporophytes of *Selaginella tenerrima* from N.E. Nigeria, collected (a) in a very moist site under waterfall (*Kornaś* 6310) and (b, c) in a drier site in rock crevices (*Kornaś* 6214) (a, c. × 0,8; b, c. × 1,6; c, c. × 3,2).

cultures, where sporelings of up to six leaves were obtained from megaspores from three samples collected in N.E. Nigeria (*Kornaś* 6214, 6245, 6261 — see Appendix).

Megaspores are furnished with a trilete scar marking the commissures along which they dehisce. After a few weeks of watering, a germinating megaspore opened along the scar, expressing the prothallium with three tufts of rhizoids, which were twice as long as the diameter of the megaspore (Fig. 4). Such a quick germination is characteristic of tropical selaginellas as opposed to those of the temperate zones in which the dormant condition may last for many months or even for years (Bruchmann, 1912; Hofmeister, 1867). The prothallia of *S. tenerrima* never turned green, even on their tops. Several archegonia were formed on the upper surface of the prothallium. The short neck of each archegonium consisted of four rows of cells and was two cells high. Sporelings which grew in a permanent layer of water (1−2 mm) developed rhizoids which were visible up to the stage of two cotyledons, whereas sporelings growing in drier conditions were without rhizoids and had shorter hypocotyls (Figs 4 & 5).

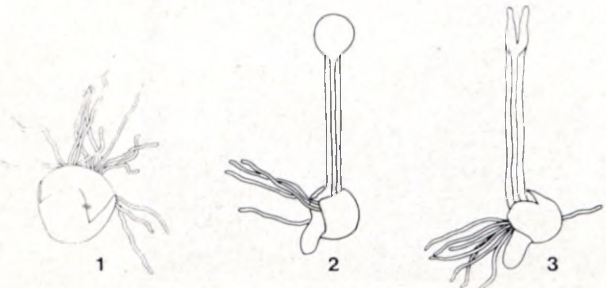

FIG. 4.—*Selaginella tenerrima* (*Kornaś* 6214). 1, dehiscent megaspore showing exposed prothallial tissue with rhizoids (c. × 15); 2 & 3, young sporelings (c. × 10).

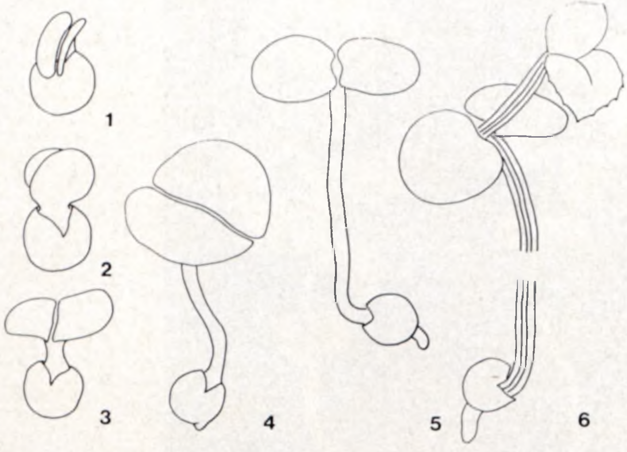

FIG. 5.—*Selaginella tenerrima* (*Kornaś* 6214). 1−6, young sporelings (c. × 10).

Chromosome counts were made from root-tips and shoot apices of the sporelings. Material was fixed in Navashin's fixative diluted with an equal part of distilled water. Microtome sections 10 μm thick were stained with Newton's gentian violet. Chromosomes are small and have approximately the same length within the somatic plate (c. 0,7 μm). The chromosome number is 2n = 30 (Fig. 6).

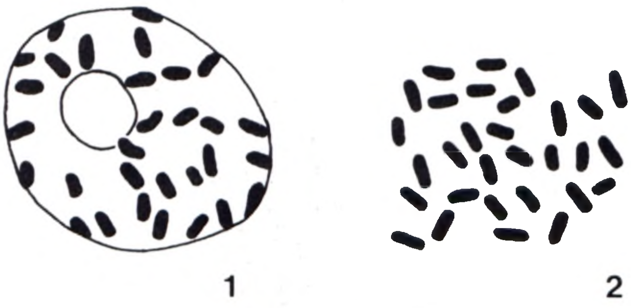

FIG. 6.—*Selaginella tenerrima* (*Kornaś* 6214). 2n = 30. 1, root tip prometaphase; 2, root-tip metaphase (c. × 4000).

The chromosome numbers in the genus *Selaginella* have been established for only c. 80 species out of the c. 700 known (Löve *et al.*, 1977). The basic numbers are x = 7, 8, 9 and 10. Therefore the investigated species *S. tenerrima* proved to be triploid. Unfortunately the mode of reproduction of the remaining triploid species (*S. bluuensis* v.A.v.R. from North Borneo, *S. biformis* A. Braun ex Kuhn and *S. vogelii* Spring from the Kew collection — Jermy *et al.*, 1967), is not known at present. Of the apomictic species, the chromosome numbers are known for *S. rupestris* (L.) Spring and *S. selaginoides* (L.) Link; they have both proved to be diploid with 2n = 18 (Löve *et al.*, 1977).

DISCUSSION

Annual selaginellas are currently known only from the tropic subtropic and south temperate regions of the Old World. Besides *S. tenerrima*, two other species have been reported to represent this life-form, namely *S. gracillima* (Kunze) Alston (= *S. preissiana* Spring) from Australia and *S. pygmaea* (Kaulf.) Alston [= *S. pumila* (Schlechtend.) Spring] from South Africa (Hieronymus, 1902; Velenovsky, 1905). In both species, empty megaspores are usually found attached to the base of mature sporophytes. Possibly a few other dwarfish selaginellas, closely resembling those listed above, have a similar life cycle, e.g. *S. ciliaris* (Retz.) Spring from S.E. Asia, N. Australia and W. Pacific, or *S. perpusilla* Baker from Africa and Madagascar. In *S. ciliaris*, apomixis seems to occur, as indicated by the lack of microsporangia (Alston, 1951; Hieronymus, 1902). Little is known about the habitat requirements of these tiny plants, but most probably they are similar to those of *S. tenerrima*. On the other hand, the annual selaginellas are included in various infrageneric taxa (*S. pygmaea* and *S. gracillima* in the subgenus *Homeophyllum*, *S. tenerrima* in the subgenus *Heterophyllum* — Hieronymus, 1902) and therefore their striking similarities may result rather from a convergent evolution, stimulated by the water stress in seasonally dry climates, than from a real phylogenetic affinity.

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APPENDIX: HERBARIUM SPECIMENS STUDIED

All specimens with megasporangia; micr. = microsporangia present.

NIGERIA.— Kaduna State: Samaru near Zaria, *Harris* et al. 7168 (KRA, micr.). Plateau State: Naraguta F. R., *Lawlor & Hall* FHI 46545 (K). Borno State: Gubi near Biu, *Kornaś* 6310 (KRA). Borno State: Takaskara Hills, *Kornaś* 6214 (KRA). Borno State: Ngoshe, *Kornaś* 6304 (KRA). Gongola State: Wuro Dawa, *Kornaś* 6261 (KRA). Gongola State: near Uba, *Kornaś* 6245 (KRA).

CAMEROON.—Koza, 20 km au N. de Mokolo, *Biholong* 120 (P).

CENTRAL AFRICAN REPUBLIC.—Rég. Bambari, Moroubas, *Tisserant* 2788 (P).

CONGO (BRAZZAVILLE).—Entre Sibité et Loudima, N. N. (P).

ANGOLA.—Distr. Golungo Alto, Serra do Alto Queta, *Welwitsch* 45 (BM; K, type collection; micr.). Lunda: Xá Sengue, *Exell & Mendonça* 402 (BM).

ZAMBIA.—Mporokoso Distr.: Lumangwe Falls, *Kornaś* 3748 (KRA, micr.), 3751 (KRA, micr.). Mpika Distr.: near Kapiri Kaswela, *Kornaś* 4024 (KRA, micr.).