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Tuber production and fire-resistance in *Lycopodium carolinianum* L. in Zambia

JAN KORNAŚ

Institute of Botany, Jagiellonian University of Kraków

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Abstract

The seasonal periodicity of *Lycopodium carolinianum* L. var. *tuberosum* (Welw. et A. Braun ex Kuhn) Nessel in a dambo grassland in the Central Province of Zambia is described. Cauline tubers were formed on the apices of the creeping stems at the end of each growing season. Because of the downward curving of their initials the tubers became buried c. 1 cm underground. They were often the only parts of the plant which survived the grass fires occurring each year in the dry season. Hence, *L. carolinianum* var. *tuberosum* is a facultative geophyte in which the original, most probably xerophytic, adaptations became an effective means of protection against fire.

INTRODUCTION

Lycopods very seldom produce subterranean tubers as perennating organs. The best known case of this type is that of the monotypic Australian genus *Phylloglossum* Kunze (Pritzel 1902, Sampson 1916, Osborn 1919, Bower 1935, Eames 1936, Chadefaud and Emberger 1960), in which there is a strong seasonal periodicity: roots, leaf rosettes, strobili and young tubers are produced in the rainy season, but only the tubers underground survive the subsequent spell of drought. *Phylloglossum* grows in poor sandy soils, in shallow depressions wet during the rains and completely drying out in the rainless months. The tubers are regarded as an adaptation for surviving the critical periods of drought. Thus *Phylloglossum* is an example of a true geophyte, as yet the only one known among the Lycopods.

However, tubers are not confined to this genus, but occur also in *Lycopodium*, where they are believed to be also a xerophytic adaptation (Holloway 1916, 1917). The taxon usually referred to in this context

is the African *Lycopodium carolinianum* L. var. *tuberosum* (Welw. et A. Braun ex Kuhn) Nessel (=*L. tuberosum* Welw. et A. Braun ex Kuhn). Field data collected in Zambia reveal an interesting periodicity of tuber production (as suggested by Ballard 1950 upon inspection of herbarium specimens) and the importance of these organs for increasing the resistance of the plant to fire.

A site with a large population of *Lycopodium carolinianum* var. *tuberosum* was inspected several times during the year 1972—1973. It was located in the Central Province of Zambia, on the Great East Road (the Lusaka — Chipata highway) between Unda-Unda and Rufunsa, c. 128 km E of Lusaka, 15°21′S, 29°41′E, and 1180 m of altitude. The plants were growing in a grassland dominated by *Cyperaceae*, in a flat depression ("dambo") crossed by a small rivulet and surrounded by a savanna woodland ("miombo"). The soil in the depression was black and peaty, lying over poor sand; it was permanently waterlogged in the rainy season, but became dry as dust in the rainless half of the year. The following species have been collected in the vicinity of *Lycopodium: Rhynchospora rugosa* (Vahl) Gale (*Cyper.*) [1], *Mariscus deciduus* (Boeck) C. B. Cl. (*Cyper.*)[1], *Acriulus greigiifolius* (Ridl.) C. B. Cl. (*Cyper.*) [1], *Fuirena umbellata* Rottb. (*Cyper.*) [1] *Xyris* sp. (*Xyrid.*), various orchis (*Satyrium breve* Rolfe [1], *Disa* sp., *Eulophia* sp. div., and others), *Drosera affinis* Welw. ex Oliv. (*Droser.*), *Thelypteris confluens* (Thunb.) Mort. (*Thelypt.*), etc. Such habitats are typical of *L. carolinianum* in Zambia.

Lycopodium plants were not noticed in the observation plot at the end of the dry season in September. The first young shoots could be detected soon after the beginning of the rains, in mid-December. Each of them arose from a white underground tuber, c. 0.5—1.5 (2.5) cm long and c. 0.3—0.5 cm thick, produced in the previous year (Figs. 1, 2 B). Some few weeks later, at the beginning of February, the plants had already formed young strobili (Fig. 3). The tubers were completely shrunken and indistinguishable. The strobili matured and shed spores near the end of January. Simultaneously the very first initials of new tubers could be seen at the apices of the creeping stems (Figs. 2 A, 4). The tubers were obviously cauline in their nature (cf. Legros 1955, Alston 1959); this was also shown by the presence of reduced leaves on their surface (Figs. 1, 2). Information on the occurrence of root-tubers in *L. carolinianum* var. *tuberosum* (Engler 1908, Nessel 1939, Tardieu-Blot and Alston 1957, Tardieu-Blot 1964) are most probably based on misinterpretation of these organs.

The production of tubers in Zambian plants of *L. carolinianum* was connected with a periodical change in orientation of the stem apex, which grew plagiotropically during the vegetative season, but became positively geotropic when forming tuber initials (Fig. 4). Consequently the tubers

[1] Identified by the taxonomists of the Royal Botanic Gardens, Kew

Fig. 1. *Lycopodium carolinianum* var. *tuberosum* — tubers producing young shoots of the current season. Note presence of reduced leaves on surfaces of tubers. 16 September 1972. *J. Kornaś* Pl. Afr. 2866 (KRA)

were buried c. 1 cm or more under the soil surface. After a period of dormancy the growing apex reversed to negative geotropism and young shoots reappeared above the ground. These changes in the direction of

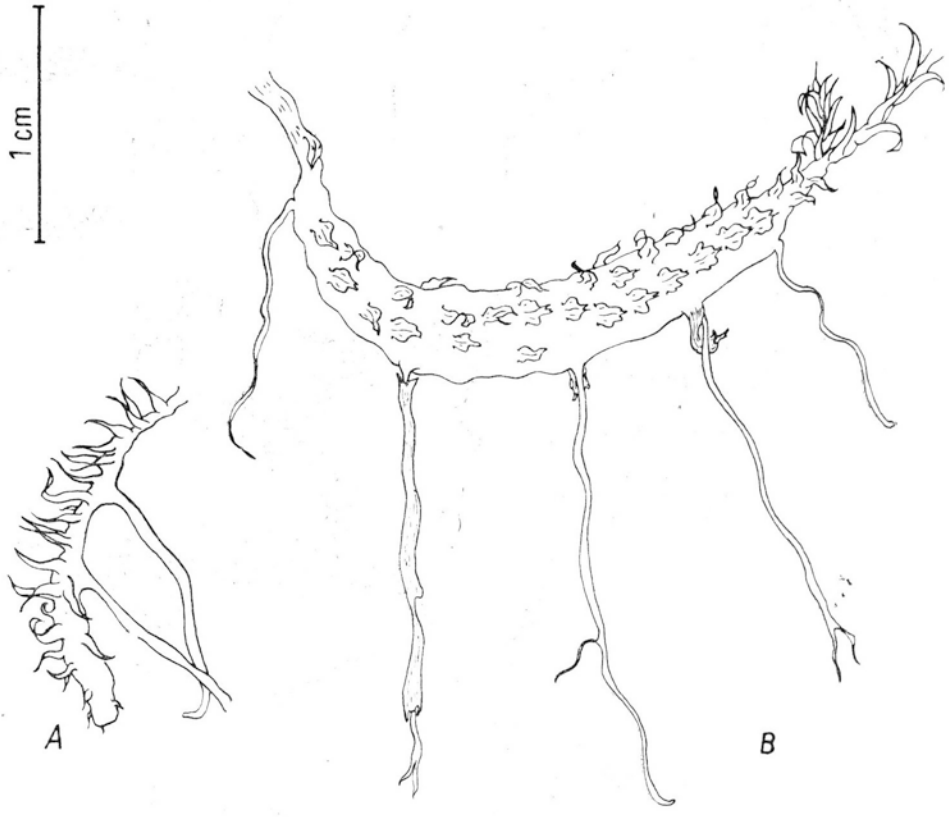

Fig. 2. *Lycopodium carolinianum* var. *tuberosum*. A — tuber initial. 14 January 1972. *J. Kornaś* Pl. Afr. 0852 (KRA). B — tuber with reduced leaves on its surface. 16 September 1972. *J. Kornaś* Pl. Afr. 2866 (KRA)

stem growth were sometimes visible in plants which had retained their older parts and showed U-shaped bends at the end of each annual segment (Fig. 5).

The seasonal periodicity found in the population of *L. carolinianum* var. *tuberosum* under observation closely resembles that of the related European species, *L. inundatum* L., studied by Velenovský (1892, 1905). There is, however, one essential difference, since the perennating buds of *L. inundatum*, formed each autumn on the stem apices, are situated just above the ground level. Hence *L. inundatum* represents the life-form of a hemicryptophyte, while *L. carolinianum* var. *tuberosum* may be either a hemicryptophyte (when the previous year's shoot persists through the dry season), or a geophyte (when only the tubers survive).

The site of *L. carolinianum* var. *tuberosum* near Rufunsa was burned each year in the dry season (which is normal in most of the grassland areas in Zambia). The grass fires were rather light and swept fast over

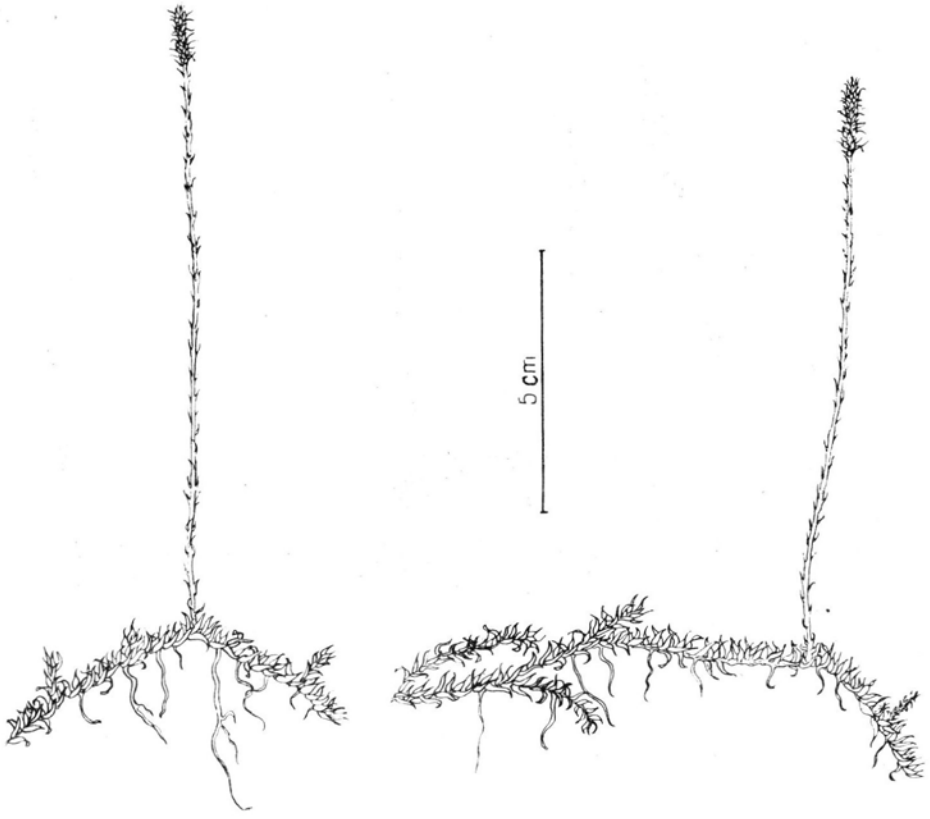

Fig. 3. *Lycopodium carolinianum* var. *tuberosum* — current season's shoots with young strobili. Tuber formation not yet visible. 2 January 1972. *J. Kornaś* Pl. Afr. 0778 (KRA)

the ground. They were, however, hot enough to kill or seriously damage many of the above-ground shoots of *Lycopodium*. The tubers survived undamaged, certainly because they were effectively protected by the thin cover of soil. Thus in *L. carolinianum* var. *tuberosum* the tubers — which seem to have been originally a kind of xerophytic adaptation — proved also to play an essential part in protecting the plant against fire. This observation is most probably the first of its kind for Lycopods. A similar origin of adaptations to annual burning in phanerogams of the savanna and savanna woodland zones in Africa and elsewhere has already been

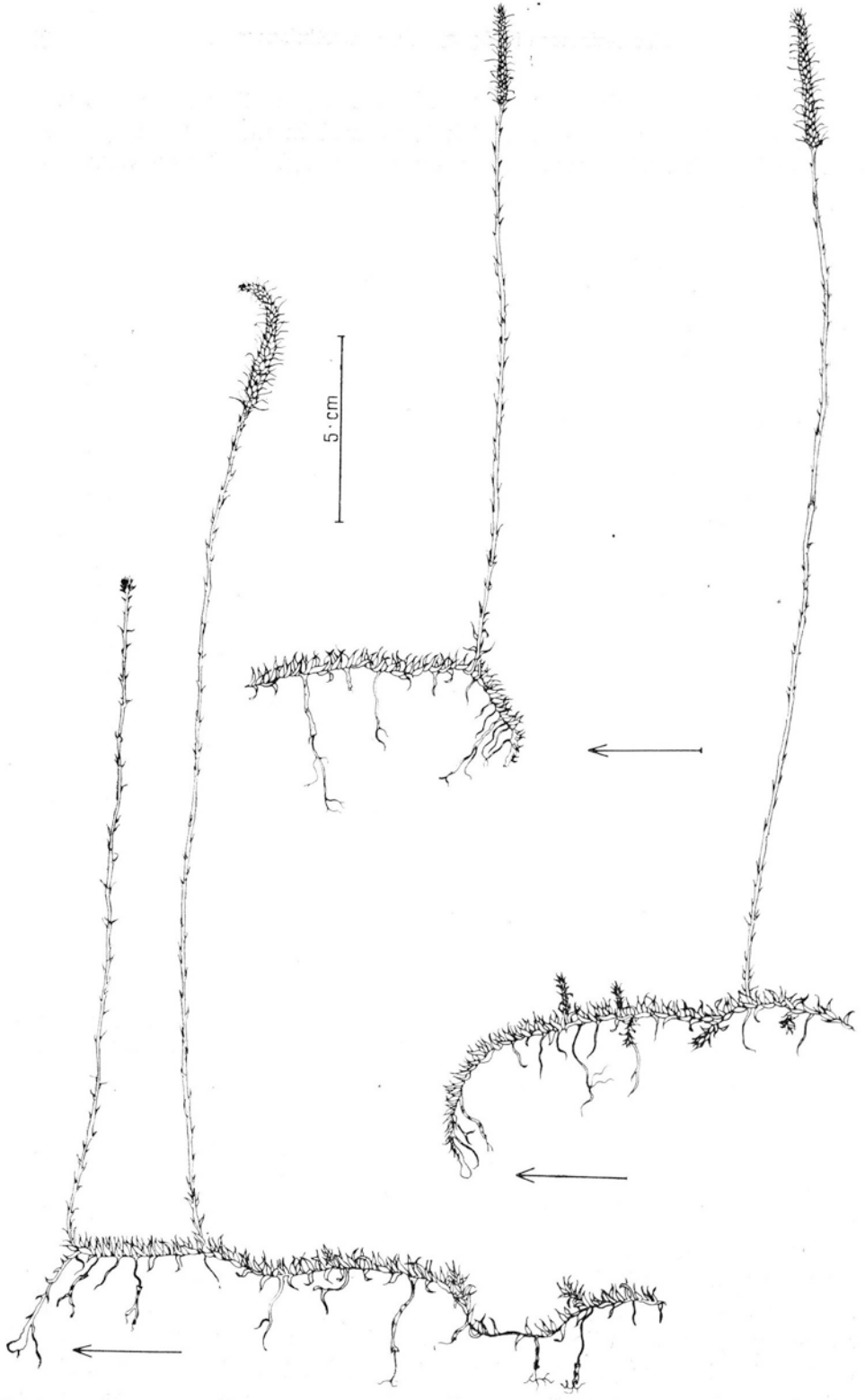

Fig. 4. *Lycopodium carolinianum* var. *tuberosum* — plants with mature strobili and tuber initials on the stem apices (indicated by arrows). 14 January 1972. *J. Kornaś* Pl. Afr. 0853 (KRA)

Fig. 5. *Lycopodium carolinianum* var. *tuberosum* — old shoots showing U-shaped bends at the end of the previous season's segments (indicated by arrows). 14 January 1972. *J. Kornaś* Pl. Afr. 0853 (KAR)

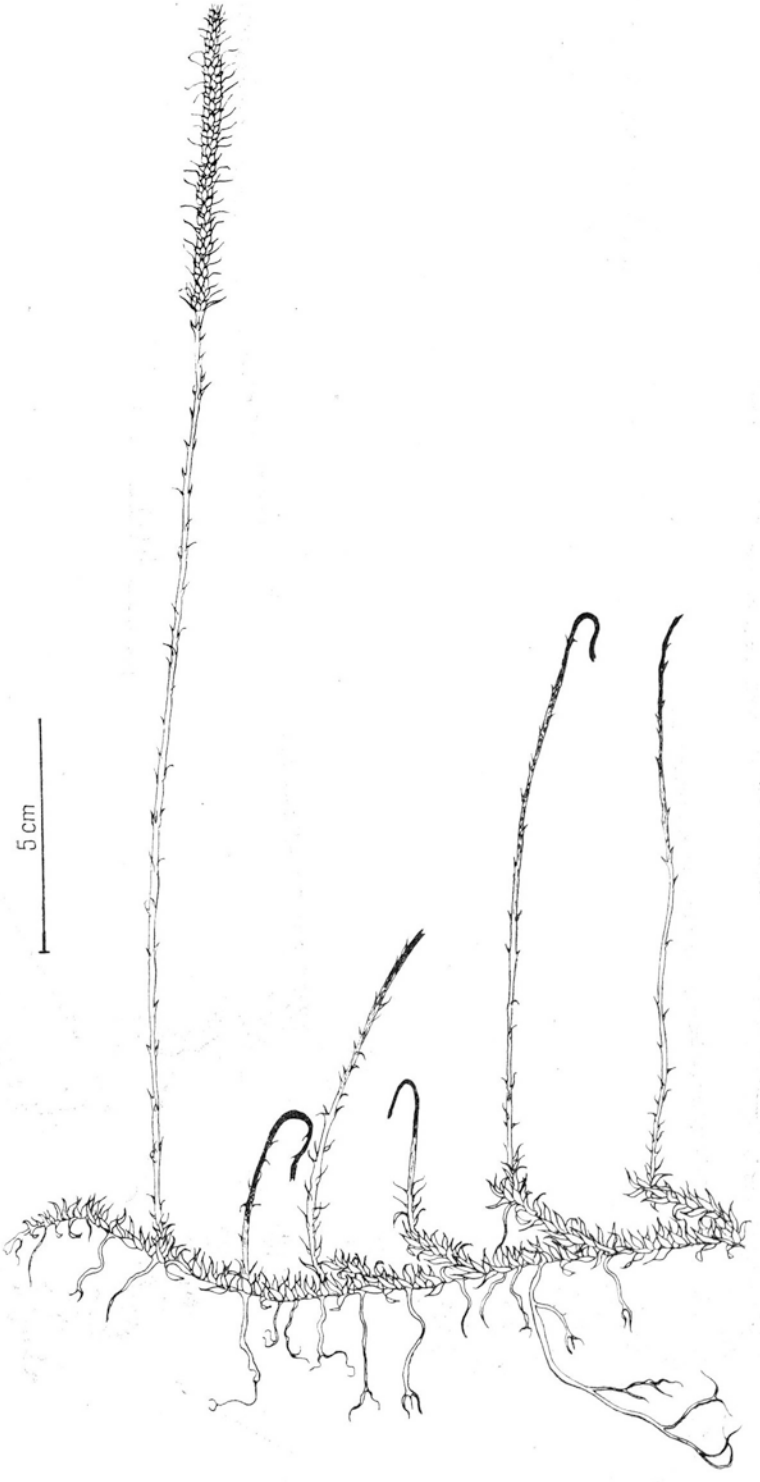

Fig. 6. ***Lycopodium carolinianum*** var. ***tuberosum*** — old shoot which survived grass fire in the pevious dry season. Note fire scars on the peduncles of the previous year. 14 January 1972. *J. Kornaś* Pl. Afr. 0853 (KRA)

assumed by various authors (cf. e.g. Cole 1974, Exell and Stace 1972, Eiten 1972, Medwecka-Kornaś — unpublished data).

In some individuals of *Lycopodium carolinianum* var. *tuberosum* only the erect peduncles and old strobili were burnt. This course of events is clearly visible from fire scars on living stems more than one year old (Fig. 6).

The field data collected in other Zambian localities of *L. carolinianum* are unfortunately not sufficient for any generalization on the life history of this species. Its seasonal periodicity seems to be rather flexible and very much influenced by the soil-water conditions: in permanently wet places the plants are probably able to grow actively even in the driest time of the year (herbarium specimens from Zambia collected in every month except November have been seen by the present author). Some geographical differences possibly also exist between the plants growing in higher rainfall areas in the North and those occurring in the much drier regions in the centre of the country. Further observations are needed to get a more complete picture of the life-history of *L. carolinianum* var. *tuberosum* under various environmental conditions.

L. carolinianum sensu lato is widely but very interruptedly distributed in America (eastern North America, the West Indies, Central America, and eastern South America), tropical Africa and South Africa, the islands of the Indian Ocean, Australia, and possibly also New Zealand (Fernald 1950, Tardieu-Blot and Alston 1957, Schelpe 1970). Several infraspecific (or even specific) taxa, which badly need further critical study, have been described within this complex. In southern tropical Africa 3 varieties occur: var. *grandifolium* Spring., var. *affine* (Bory) Schelpe, and var. *tuberosum* (Welw. et A. Braun ex Kuhn) Nessel, none of them identical with the American type variety var. *carolinianum* (Schelpe 1970). Var. *grandifolium* is a very strange-looking and easily distinguishable form, possibly of pathological origin. It has been seen by the present author in Zambia solely on bare peat in especially wet places. The only difference between the two other African "varieties" is the lack of tubers in var. *affine*. This character does not seem to be reliable, since the tuberless specimens may be simply those collected in the middle of the growing season, when tubers are normally indistinguishable (Ballard 1950). Careful re-examination of *L. carolinianum* in various parts of its African range seems to be necessary before the mutual relationship of its varieties can be definitively established.

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REFERENCES

Alston A. H. G., 1959. The ferns and fern-allies of West Tropical Africa. Crown Agents for Oversea Governments and Administrations, London, pp. 89.

Ballard F., 1950. *Lycopodium carolinianum* in Tropical Africa. Amer. Fern J. 40: 74—83.

Bower F. O., 1935. Primitive land plants also known as *Archegoniatae*. Macmillan and Co., London, pp. XIV+658. Reprinted 1967, Hafner Publ. Co., New York and London.

Chadefaud M., Emberger L., 1960. Traité de Botanique (Systématique), Tome II, Les végétaux vasculaires, Fasc. I. Masson et Cie., Paris, pp. XII+755.

Cole N. H. A., 1974. Climate, life form and species distribution on the Loma montane grassland, Sierra Leone. J. Linn. Soc., Bot. 69: 197—210.

Eames A. J., 1936. Morphology of vascular plants, Lower groups (*Psilophytales* to *Filicales*). McGraw — Hill Book Co., New York and London, pp. 433.

Eiten G., 1972. The cerrado vegetation of Brasil. Bot. Rev. 38 (2): 201—341.

Engler A., 1908. Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete, II Bd., Charakterpflanzen Afrikas (insbesondere des tropischen), 1. Die Pteridophyten, Gymnospermen und monokotylen Angiospermen. [In:] Engler E., Drude O. (red.), Die Vegetation der Erde 2. W. Engelmann, Leipzig, pp. XI+460.

Exell A. W., Stace C. A., 1972. Patterns of distribution in the *Combretaceae*. [In:] Valentine D. H. (Ed.), Taxonomy, Phytogeography and Evolution. Academic Press, London—New York, pp. 307—323.

Fernald M. L., 1950. Gray's Manual of Botany, 8th edition. American Book Co., New York etc., pp. LXIV+1632.

Holloway J. E., 1916. Studies in New Zealand species of the genus *Lycopodium*, Part 1. Trans. Proc. New Zealand Inst. 48: 253—303.

Holloway J. E., 1917. Studies in New Zealand species of the genus *Lycopodium*, Part. 2. Trans. Proc. New Zealand Inst. 49: 80—93.

Legros N. G., 1955. Quelques notes sur l'anatomie et la morhpologie de *Lycopodium carolinianum* L. var. *tuberosum* (A. Br. et Welw.) Nessel Recueil Trav. Lab. Bot. Fac. Sci. Univ. Montpellier, Sér. Bot. 7: 49—55.

Nessel H., 1939. Die Bärlappgewächse (*Lycopodiaceae*), Eine beschreibende Zusammenstellung mit besonderer Berücksichtigung ihrer Varietäten und Formen. G. Fischer Verl., Jena, pp. VIII+404.

Osborn T. G. B., 1919. Some observations on the tuber of *Phylloglossum*. Ann. Bot. (London) 33: 485—516.

Pritzel E., 1902. *Lycopodiales, Lycopodiaceae*. [In:] Engler A., Prantl. K. (red.), Die natürlichen Pflanzenfamilien, I Teil, Abt. 4, W. Engelmann, Leipzig, pp. 563—606.

Sampson K., 1916. The morphology of *Phylloglossum*. Ann. Bot. (London) 30: 315—331.

Schelpe E. A. C. L. E., 1970. Flora Zambesiaca, *Pteridophyta*. Crown Agents for Oversea Governments and Administrations, London, pp. 254.

Tardieu-Blot M. L., 1964. Pteridophytes. [In:] Aubréville A. (ed.), Flore du Gabon, no. 8. Mus. Natl. Hist. Nat., Paris, pp. 228.

Tardieu-Blot M. L., Alston A. H. G., 1957. Les Ptéridophytes d'Afrique intertropicale francaise (fin). Mém. Inst. Franç. Afrique Noire 50: 7—49.

Velenovský J., 1892. O morfologii os cévnatých tajnosnubných, Über die Morphologie der Achsen der Gefässcryptogamen. Rozpr. České Akad. Věd, Tř. 2, Vědy Mat. Přir. 1 (40): 813—832.

Velenovský J., 1905. Vergleichende Morphologie der Pflanzen, I Teil. Fr. Řivnač, Prag, pp. 279.

Walton J., Alston A. G. H., 1938. *Lycopodiinae*. [In:] Verdorn F. (ed.), Manual of Pteridology. M. Nijhoff, The Hague, pp. 500—506.

Author's address:
Prof. Dr. Jan Kornaś,
Institute of Botany, Jagiellonian Uniwersity;
ul. Lubicz 46; 31-512 Kraków 2, Poland

Powstawanie bulwek i odporność na ogień u *Lycopodium carolinianum* L. w Zambii

Streszczenie

Przedstawiono sezonową rytmikę rozwoju widłaka *Lycopodium carolinianum* L. var. *tuberosum* (Welw. et A. Braun ex Kuhn) Nessel w zbiorowisku roślin turzycowatych w okresowo podtapianym zagłębieniu ("dambo") w Zambii. Bulwki łodygowe tworzą się corocznie pod koniec sezonu wegetacji na końcach pełzających pędów. Wskutek przegięcia się rosnącego wierzchołka łodygi w dół dostają się one na głębokość około 1 cm pod powierzchnię gleby. Bulwki są zwykle jedynymi organami widłaka, które przeżywają pożar roślinności powtarzający się co roku w porze suchej. *L. carolinianum* var. *tuberosum* jest więc przykładem fakultatywnego geofita, u którego przystosowania, pierwotnie — jak się zdaje — natury kserofitycznej, zabezpieczają obecnie roślinę przed zabójczym działaniem ognia.