

Hapaxanthly and pleonanthly in African rattans (Palmae: Calamoideae)

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Abstract—Hapaxanthly, and its alternative state, pleonanthly, are terms that have long been used to differentiate the flowering behaviour in palms. Despite the fact that hapaxanthly and pleonanthly have recently been reviewed [1–3], there has persisted some confusion regarding the inflorescence structure and life form of the rattans of Africa. Recent field observations have provided further information with regard to the flowering behaviour of the African rattans and have confirmed the hapaxanthic nature of *Laccosperma* and the pleonanthic nature of *Eremospatha* and the sole representative of *Calamus* in Africa, *C. deërratus*. The genus *Oncocalamus*, long recorded as being hapaxanthic, is now known to be pleonanthic. Basic knowledge of the life form of economically valuable plants such as rattan is essential if rational decisions are to be made about their long-term management and sustainable utilisation.

Key words: Rattan; flowering; inflorescence behaviour.

INTRODUCTION: A DISCUSSION OF HAPAXANTHY AND PLEONANTHY

A number of taxa within the palm family produce what appears to be a terminal inflorescence [2], the production of which results in the death of the individual stem, or axis. This terminal inflorescence, however, is not 'terminal' as such but comprises numerous lateral inflorescences arising in the axils of, often markedly, reduced leaves on the upper portions of the stem [2, 4]. In palms, this has been widely termed hapaxanthly [1]. In pleonanthly, the opposite state to hapaxanthly, the lateral production of inflorescences occurs on the lower portions of the stem which then continue to grow vegetatively and reproduce over a relatively long period throughout its adult life [1, 2, 5]; pleonanthic palms are thus polycarpic [6].

Whilst there is little morphological difference between hapaxanthly and pleonanthly [1], the differences between the two flowering states are ultimately physiological [1, 4]. In hapaxanthic palms, the primary axis undergoes a vegetative phase,

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which may be up to 50 years in the genus *Corypha* [7], followed by a relatively short reproductive phase that results in the production of several to many axillary inflorescences. The true apex of the stem aborts and the stem then dies after flowering. In taxa with solitary stems, such as in all the species of *Corypha*, the whole plant dies after a reproductive event and is thus monocarpic. However, in multiple-stemmed palms such as some rattans, although individual axes can be hapaxanthic, the continued production of basal suckers ensures the survival of the individual as a whole [2]. Hence hapaxanthly, as used by most palm botanists, is not synonymous with monocarpy [2] (i.e. palms with hapaxanthic axes can be polycarpic).

In the majority of palms, the inflorescence units expand acropetally, i.e. in order of their age such that they develop and mature from the base to the apex [8]. However, in some palms, notably within the tribe Caryoteae (sub-family Arecoideae), the inflorescences develop and mature in the reverse fashion (basipetally) i.e. the younger inflorescences develop below the older (often fruiting) axes [1, 2]. Both acropetal and basipetal inflorescences are encountered in hapaxanthic palms, whilst in pleonanthic taxa, the inflorescences are always acropetal (*ibid.*).

The lack of morphological difference between hapaxanthly and pleonanthly has led to speculation that perhaps there is not such a clear distinction between the two flowering states. Indeed [9] suggests that there exists a continuum between hapaxanthly and pleonanthly in the genus *Metroxylon*, and there are species within that genus that may be described as somewhat intermediate between the two states. However, when clearly defined (e.g. [8]), hapaxanthly and pleonanthly can be consistently applied to usefully describe a distinct feature obvious to all. For this reason, the use of hapaxanthly and pleonanthly are maintained throughout this paper.

GEOGRAPHICAL DISTRIBUTION OF HAPAXANTHY

With the exception of the Central and South American *Raphia taedigera*, an otherwise African genus, hapaxanthly is limited to the Old World palms. In all, 16 genera of palms, the majority of them in the Calamoideae, are wholly or partly hapaxanthic. In addition, the majority of hapaxanthic palms are climbers. Within the African rattan genera, *Laccosperma* is hapaxanthic, whilst *Eremospatha*, *Oncocalamus* and *Calamus* are pleonanthic.

THE AFRICAN GENERA

Laccosperma

Laccosperma is clearly hapaxanthic and has long been recorded in the literature as such [1, 3, 5, 6, 10–23]. After flowering, although the flowering stem itself dies, the individual cluster continues to produce vegetative growth. From long-term field observations in the Campo Faunal Reserve in Cameroon, between 1995–2000, it



Figure 1. Lateral inflorescence of *Eremospatha cuspidata* (G. Mann and H. Wendl.) H. Wendl., near Fieembue (01.16N; 09.26E), Rio Muni, Equatorial Guinea (Sunderland no. 1909).



Figure 2. Lateral inflorescence of *Oncocalamus mannii* (H. Wendl.) H. Wendl., near Eteembue (01.16N; 09.26E), Rio Muni, Equatorial Guinea (Sunderland no. 1923).

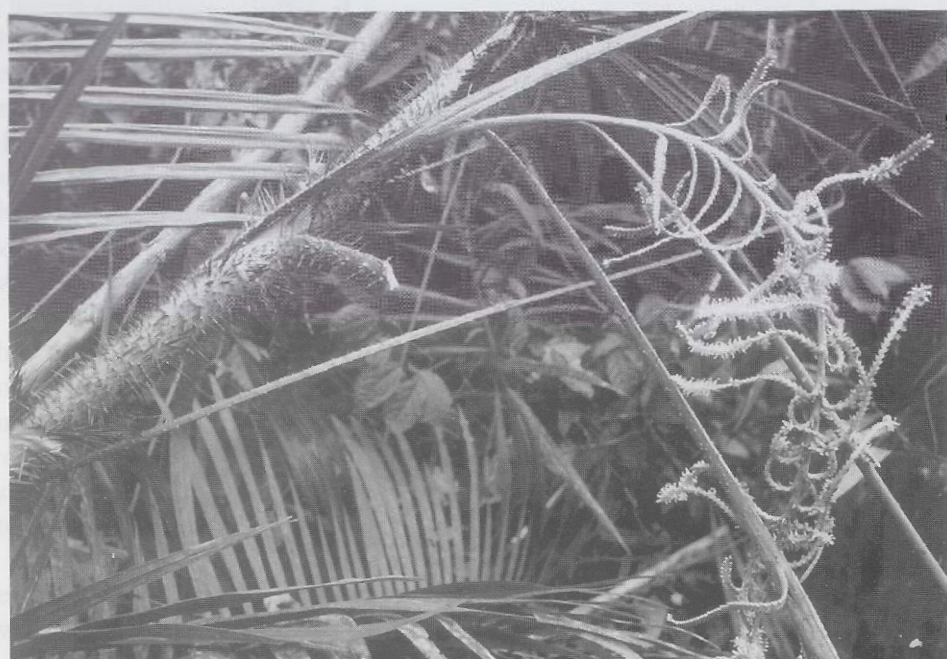


Figure 3. Lateral inflorescence of *Calamus deerratus* G. Mann and H. Wendl., Mungo River (04.08N; 09.31E), South West Province, Cameroon (Sunderland no. 1754).

Table 1.

Hapaxanthly in the Palmae (adapted from Uhl and Dransfield, 1987 [1])

Sub-Family	Genus	No. of spp.	No. of hapaxanthic spp.
Coryphoideae	<i>Corypha</i>	8	8
	<i>Nannorrhops</i>	1	1
Calamoideae	<i>Daemonorops</i>	116	1 (<i>D. calicarpa</i>)
	<i>Eleiodoxa</i>	1	1
	<i>Fugeissona</i>	6	6
	<i>Korthalsia</i>	26	26
	<i>Laccosperma</i>	5	5
	<i>Meuroxylon</i>	6	5
	<i>Myrialepis</i>	1	1
	<i>Plectocomia</i>	16	16
	<i>Plectocomiopsis</i>	5	5
	<i>Raphia</i>	28	28
	<i>Salacca</i>	15	1 (<i>S. secunda</i>)
Arecoideae	<i>Arenga</i>	22	17
	<i>Caryota</i>	12	12
	<i>Wallichia</i>	7	7



Figure 4. Hapaxanthic inflorescence of *Laccosperma acutiflorum* (Becc.) J. Dransf. near Mamfe (05.38N; 09.17E), South-West Province, Cameroon (Sunderland no. 1855).

appears that at least one stem from each cluster produces flowers and fruits each year (author, personal observation).

Eremospatha

Despite being noted as hapaxanthic by Tomlinson [2], all species of *Eremospatha* are pleoanthy and the inflorescences are produced laterally, some distance from the stem apex.

Oncocalamus

The inflorescence unit of *Oncocalamus* was first described as 'lateral' [10]. Subsequent descriptions of *Oncocalamus* also described the genus as pleoanthy [11, 14].

However, almost certainly due to the poor quality and incomplete nature of herbarium material, first Tomlinson [2], subsequently followed by several other palm workers, described *Oncocalamus* as being hapaxanthic [1, 3, 9, 16, 20, 21, 24, 25]. Recent field work and the collection of voucher specimens has clarified the morphological picture somewhat and has confirmed that all four species of *Oncocalamus* are indeed pleonanthic and possess long, pendulous inflorescences arising laterally some distance from the stem apex.

Calamus

C. deerratus produces long whip-like inflorescences and, in common with all other species of *Calamus*, is pleonanthic.

ECOLOGY AND EVOLUTION

Hapaxanthly was initially described as an ancestral condition in palms [17, 26]. However, Dransfield [19], Moore and Uhl [24], Uhl and Dransfield [1], and Tucker [3] consider it a derived condition. The fact that hapaxanthly occurs in unrelated genera, as well as the occurrence of both hapaxanthly and pleonanthly in the same genus (e.g. *Metroxylon*, *Daemonorops* and *Salacca*), also suggests that hapaxanthly arises independently and does not commonly imply a common or close ancestor. This has also been proven cladistically by Baker *et al.* [27].

In ecological terms, Dransfield [6] speculates that the hapaxanthic habit has been developed for the colonisation of temporary habitats such as light gaps in forest and he suggests that:

... hapaxanthly is an adaptation allowing greater possibilities of colonising open habitats by the presentation of a large quantity of fruit at one moment'.

In Africa, however, all three of the endemic rattan genera (one being hapaxanthic and two of which are pleonanthic) have representative species that colonise forest gaps. In addition, the two forest-dwelling species of the hapaxanthic genus, *Laccosperma*, *L. laeve* and *L. opacum* occur in deep shade in the lower to mid-canopy. Hence colonisation might not be the only advantage of hapaxanthly in particular and the adaptive significance of hapaxanthly and pleonanthly might be related to other ecological aspects, such as fruit size and the influence of dispersal agents. This is especially relevant given that Dransfield [6] did not state that pleonanthic palms do not colonise gaps (Baker, personal communication).

From recent field observations, it appears that one obvious advantage of presenting ripe fruit in such a conspicuous manner as with the nature of hapaxanthic inflorescences, is that they attract dispersal agents. In the Rio Muni region of Equatorial Guinea, canopy-feeding hornbills (in particular the black and white

hornbill, *Ceratogymna atrata*) have been seen by me feeding from the striking hapaxanthic inflorescence units of *Laccosperma acutiflorum* emerging abruptly from the canopy. Consequently, very little fruit fall is observed beneath the inflorescence due to the high levels of avian feeding of this type [28]. Conversely, in *Eremospatha* and *Oncocalamus*, the ripe fruits are more commonly consumed by primates (Gartlan, personal communication; author, personal observation). Being pleonanthic, the inflorescence units of these taxa are more commonly produced beneath the vegetative structure of the individual plant where primates are able to climb and feed with relative ease. Hence, the fruits are not immediately available to hornbills or other canopy feeders. This observation is also supported by variation in fruit size. The fruits of the hapaxanthic *Laccosperma* (except for the forest dwelling *L. opacum*) tend to be small (8–12 mm in diameter) and more amenable to avian feeders. However, the fruits of the pleonanthic *Oncocalamus* and *Eremospatha* are relatively large and robust (usually up to 15 mm in diameter; to between 12–15 mm wide and up to 25 mm long, respectively) and are more likely to be better dealt with by primates. Interestingly, in the absence of primate dispersers in some forest areas due to over-hunting, there is almost 100% fruit fall among the large-fruited pleonanthic species; seedlings are often encountered near to the mother plant and there is very little evidence of dispersal of any kind.

SUMMARY

Although, in morphological terms, hapaxanthly and pleonanthly are essentially indistinct, the physiological variation in their manifestation means that they remain useful features in the description of the habit and life form of palms. These terms, when suitably defined, are unambiguous and describe an easily recognised state used for distinguishing many palm species. The clarification of the flowering behaviour of the African rattans in this paper provides useful baseline information that will hopefully contribute to their future management, particularly in intensive silvicultural systems. Knowledge of the life form, reproductive nature and the ecological significance of any commercially valuable species, such as rattan, is essential if coherent management strategies are to be developed and implemented to ensure their sustainable utilisation.

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REFERENCES

1. N. Uhl and J. Dransfield, *Genera palmarum*. Allen Press, Kansas (1987).
2. P. B. Tomlinson, *The Structural Biology of Palms*. Oxford University Press, Oxford (1990).
3. R. Tucker, Hapaxanthly: dying in order to succeed, *Mooreana* 1, 15–24 (1991).
4. W. J. Baker, J. Dransfield, M. M. Harley and A. Bruneau, Morphology and cladistic analysis of sub-family Calamoideae (Palmae), in: *Evolution, Variation and Classification of Palms. Memoirs of the New York Botanical Garden*, A. Henderson and F. Borchsenius (Eds), Vol. 83, pp. 307–324 (1999).
5. P. Tuley, The inflorescence of Nigerian Lepidocaryoid palms, *Principes* 9, 93–98 (1965).
6. J. Dransfield, The growth of rainforest palms, in: *Tropical Trees as Living Systems*, P. B. Tomlinson and M. Zimmerman (Eds), pp. 247–268. Cambridge University Press, Cambridge UK (1978).
7. J. Fisher, R. Sanders and N. Hammer, The flowering and fruiting of *Corypha umbraculifera* in Miami, Florida, *Principes* 31, 68–77 (1987).
8. J. Dransfield and J. Mogeia, The flowering of *Arenga* (Palmae: Caryotoideae), *Bot. J. Linn. Soc.* 88, 1–10 (1984).
9. W. C. McClatchey, Phylogenetic analysis of morphological characters of *Metroxylon* section *Coelococcus* (Palmae) and resulting implications for studies of other Calamoideae genera, in: *Evolution, Variation and Classification of Palms. Memoirs of the New York Botanical Garden*, A. Henderson and F. Borchsenius (Eds), Vol. 83, pp. 285–306 (1999).
10. G. Mann and H. A. Wendland, On the palms of western tropical Africa, *Phil. Trans. Linn. Soc.* 24, 421–439 (1864).
11. Wright (1902).
12. N. H. Ridley, Branching in palms, *Ann. Bot.* 21, 417–422 (1907).
13. O. Beccari, Contributo alla conoscenza delle 'Lepidocaryeae' africane, *Webbia* 3, 247–294 (1910).
14. J. Hutchinson, *Families of Flowering Plants. II Monocotyledons*. Macmillan, London (1934).
15. C. Ginies, Structure de la feuille d'un palmier-liane: l'*Ancistrophyllum secundiflorum*, *Bulletin de l'IFAN* 12 (3), 730–742 (1960).
16. P. B. Tomlinson, Palms of Africa, *Principes* 6, 96–103 (1962).
17. E. J. H. Corner, *The Natural History of Palms*. Wiedenfeld and Nicolson, London (1966).
18. H. E. Moore, Wednesdays in Africa, *Principes* 15, 111–119 (1971).
19. J. Dransfield, Terminal flowering in *Daemonorops*, *Principes* 20, 29–32 (1976).
20. J. Dransfield, The ecology and natural history of rattans, in: *A Guide to the Cultivation of Rattan*, R. W. M. Wan, J. Dransfield and N. Manokaran (Eds), pp. 27–34. Forest Research Institute, Forest Record No. 35, Kuala Lumpur, Malaysia (1992).
21. P. Tuley, in: *The Palms of Africa*, pp. 34–84. Trendline Press, UK (1995).
22. T. C. H. Sunderland, The Rattans of Rio Muni, Equatorial Guinea: utilisation, biology and distribution. A report for the European Union Project No. 6 ACP-EG-020, Proyecto Conservacion y Utilizacion Racional de los Ecosistemas Forestales de Guinea Ecuatorial (CUREF) (1998).
23. T. C. H. Sunderland, New research on African rattans: an important non-wood forest product from the forests of Central Africa, in: *The Non-wood Forest Products of Central Africa: Current Research Issues and Prospects for Conservation and Development*, T. C. H. Sunderland,

- L. E. Clark and P. Vantomme (Eds), pp. 87–98. Food and Agriculture Organisation, Rome (1999).
24. H. A. Moore and N. Uhl, Major trends in the evolution of palms, *Bot. Rev.* **48**, 1–69 (1982).
25. J. Dransfield and N. Manokaran (Eds), *PlantResources of SE Asia — Rattans*. PROSEA, Indonesia (1994).
26. R. Holtum, Growth habits of monocotyledons — variations on a theme, *Phytomorphology* **5**, 399–413 (1955).
27. W. J. Baker, J. Dransfield and T. Hedderson, Phylogeny, character evolution and a new classification of the Calamoid palms, *Syst. Bot.* **25** (2), 297–322 (2000).
28. K. D. Whitney, M. K. Fogiel, A. M. Lamperti, K. M. Holbrook, D. M. Stauffer, B. D. Hardesty, V. T. Parker and T. B. Smith, Seed dispersal by *Ceratoxymna* hornbills in the Dja Reserve, Cameroon, *J. Trop. Ecol.* **14**, 351–371 (1998).