Aeolanthus biformifolius De Wild.: A Hyperaccumulator of Copper from Zaïre
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Source: *Science*, Feb. 24, 1978, New Series, Vol. 199, No. 4331 (Feb. 24, 1978), pp. 887-888
Published by: American Association for the Advancement of Science
Stable URL: https://www.jstor.org/stable/1745275

possible that the planktonics were outcompeted by the nonplanktonics.

Evidence presented here supports the hypothesis that larval ecology has an effect on evolutionary rates. Along continental shelves, nonplanktonic, low dispersal species are easily isolated by local barriers during periods of regression. The subsequent increase in rates of extinction and speciation decreases average species longevity. Planktonic, high-dispersal species are less frequently isolated and tend towards long species duration. In any group of organisms, however, evolutionary rates will be influenced by a number of factors. Within the ecologically and morphologically uniform group of Lower Tertiary volutids, species longevities are primarily controlled by a combination of two factors, dispersal and environmental tolerance. Whether these factors control mollusks in general or even other families of gastropods is yet unknown, because many other ecologic controls must be taken into account.

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10. Jackson (*4*) and Scheltema (*7*) presented a model for the effect of larval dispersal on biogeography and evolutionary rates of transoceanic species. Species with long-lived planktonic larvae easily maintain gene flow between populations, which suppresses geographic isolation. Moreover, local environmental disturbances have little effect on the entire species population because of its wide distribution, hence extinction rates are lower. The result is that long-lived planktonic species have high longevity but low speciation rates. On the other hand, species with short-lived planktonic larvae may occasionally traverse a barrier such as an ocean basin, but are generally unable to maintain genetic communication. Thus, populations diverge and geographic speciation may result. Local environmental disturbances are likely to affect the entire species, giving rise to high extinction rates. In this case, short-lived planktonic species have high extinction rates and high speciation rates (low longevity).
11. Shuto's (*9*) criteria are size of embryonic whorl and shape and ornamentation of protoconch whorls. Primarily, a small and pointed apex indicates a planktonic larval stage while a large and blunt apex is characteristic of nonplanktonic forms.
12. The volutid nomenclature of Palmer and Brann (*14*) was adopted. Only species that passed the following criteria were used: (i) a part of their range must include Alabama, Mississippi, Louisiana, or Texas, (ii) only fully named species were used (for example, not *Athleta* sp.), (iii) species based on a single unique specimen or species poorly described and in which the sole type has been lost were disqualified, and (iv) all subspecies were included under the specific name.
13. Published reports on nannofossils and planktonic foraminifera allow correlation of Gulf Coast Paleocene-Eocene stratigraphy with the new Paleocene time scale of J. Hardenbol and W. A. Berggren (*Bull. Am. Assoc. Pet. Geol.*, in press). For a similar scale, see W. A. Berggren, *Lethaia* **5**, 195 (1972).
14. Species occurrences were taken from K. V. W. Palmer and D. C. Brann [*Bull. Am. Paleontol.* **48** (1965–66)] and L. Toulmin (*Ala. Geol. Surv. Monogr. 13*, in press).
15. Maps were drawn from W. L. Fisher [*Trans. Gulf Coast Assoc. Geol. Soc.* **19**, 239 (1969)], C. J. Mann and W. A. Thomas [*ibid.* **18**, 187 (1968)], and data compiled by the author from county geological reports.
16. The single long-lived nonplanktonic-eurytopic species is a problematical form present in one formation in the Upper Paleocene and one formation in the Upper Middle Eocene. Whether it is truly a single species is questionable, but it passed all the criteria of (*12*) and so is included.
17. I thank R. Dodge, E. Kauffman, D. Rhoads, N. Sohl, V. Tunnicliffe, and K. Waage for comments and criticism. Thanks go to J. B. C. Jackson and R. Scheltema for discussion.

20 October 1977

Aeolanthus biformifolius De Wild.: A Hyperaccumulator of Copper from Zaïre

Abstract. Aeolanthus biformifolius *(Labiatae) from Shaba Province, Zaïre, has been shown to be a hyperaccumulator of copper. The copper content of the total plant during the rest period after the rainy season was 1.3 percent (dry weight basis) and is easily the highest copper concentration ever found in living material. This species should be classified as a "copper flower" because of its exclusive occurrence over mineralized ground.*

Numerous studies have been concerned with the vegetation associated with copper mineralization in south-central Africa, namely, Shaba Province, Zaïre (*1, 2*), and the "Copper Belt" in Zambia (*3, 4*) and Rhodesia (*5–7*). Several plants have been described as "copper flowers" and are of considerable interest for mineral exploration. Typical copper flowers include *Becium homblei* (De Wild.) Duvign. et Plancke in Zambia and Rhodesia (*3, 6, 7*), *Haumaniastrum katangense* in the vicinity of Lubumbashi, and *H. robertii* around Kolwezi in Shaba Province, Zaïre (*2*). More recently, the copper and cobalt contents of African

Table 1. Copper concentrations (in micrograms per gram, dry weight) in *Aeolanthus biformifolius* compared with values for other accumulator species in south-central Africa.

Species	Location	Organ	Mean copper concentration	Reference
Aeolanthus biformifolius	Shaba (Étoile)	Basal leaves (1/7/77)	2,600	*
A. biformifolius	Shaba (Étoile)	Basal leaves (2/2/77)	2,150	*
A. biformifolius	Shaba (Étoile)	Flower stems (1/7/77)	3,500	*
A. biformifolius	Shaba (Étoile)	Flower stems (2/2/77)	2,150	*
A. biformifolius	Shaba (Étoile)	Corms (1/7/77)	2,600	*
A. biformifolius	Shaba (Étoile)	Corms (2/2/77)	11,800	*
A. biformifolius	Shaba (Étoile)	Corms (3/24/77)	13,700	*
A. biformifolius	Shaba (Étoile)	Whole plant (2/2/77)	10,000	*
A. biformifolius	Shaba (Étoile)	Whole plant (3/24/77)	13,700	*
Ascolepis metallorum	Shaba (Dikuluwe)	Leaves	1,200	(*2*)
Becium aureoviride	Shaba (Niamumenda)	Leaves	210	(*2*)
B. homblei	Zambia	Leaves	324	(*3*)
Crotalaria cornetii	Shaba	Leaves	12	(*9*)
C. peschiana	Shaba	Leaves	268	(*9*)
C. prolongata	Zambia	Leaves	15	(*9*)
Eragrostis boehmii	Shaba (Tilwizembe)	Leaves	78	(*2*)
Fimbristylis exilis	Rhodesia (Copper King)	Leaves	420	(*7*)
Haumaniastrum homblei	Shaba	Leaves	74	(*8*)
H. katangense	Shaba	Leaves	75	(*8*)
H. robertii	Shaba	Leaves	662	(*8*)
H. robertii	Shaba (Mupine)	Leaves	1,960	(*2*)
Indigofera dyeri	Rhodesia (Copper King)	Leaves	890	(*8*)
Pandiaka metallorum	Shaba (Dikuluwe)	Leaves	740	(*2*)
Triumfetta dikuluwensis	Shaba (Dikuluwe)	Leaves	123	(*2*)

*This study.

species of the genera *Haumaniastrum* (*8*) and *Crotalaria* (*9*) have been reviewed. Hyperaccumulators have been recently defined as plant species with a specified elemental content, which in the case of nickel is >1000 μg/g on a dry weight basis (*10*). Until now, the highest recorded copper concentration has been that of *H. robertii* (*2*), although further research (*8*) has shown that it contains considerably more cobalt than copper.

A survey of the copper content of various plants collected from Shaba Province, Zaïre (Table 1), carried out by atomic absorption spectrophotometry, has revealed the existence of a new hyperaccumulator (using the same 1000 μg/g criterion as for nickel): *Aeolanthus biformifolius* De Wild. (Labiatae). This species, which was previously only known from the vicinity to the Luiswishi Mine, has a very marked ability to accumulate copper. We have, however, recently discovered this dwarf perennial growing at the old "Mine de l'Étoile" and at the Ruashi Mine, both in the vicinity of Lubumbashi. From its present known distribution, it must be considered as endemic to the southern part of the Shaban Copper Belt.

There is a seasonal variation in the copper content of individual plant organs of *A. biformifolius*. Concentrations are lowest at the beginning of the rainy season and then increase rapidly with the development of the new corm, which is fully mature by the end of the rainy season some 3 months later. *A. biformifolius* should be considered as a copper flower for the southern part of the Shaban Copper Belt, since it appears to be confined to substrates rich in copper.

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21 September 1977

Tree Branch Angle: Maximizing Effective Leaf Area

Abstract. *In a computer simulation of branching pattern and leaf cluster in* Terminalia catappa, *right and left branch angles were varied, and the effective leaf surface areas were calculated. Theoretical branch angles that result in maximum effective leaf area are close to the values observed in nature.*

The shape or geometry of a living tree has been related to its adaptive strategy for light interception (*1, 2*). The woody framework of branches presents the photosynthetic surface, the leaves, to sunlight in a manner that is primarily, but not totally, related to the photosynthetic efficiency of the leaf and the distribution of light in the environment of the tree. Horn (*1*), on theoretical grounds, has established two basic types of leaf distribution: the monolayer with leaves densely packed in a single layer, and the multilayer with leaves loosely scattered among many layers. Understory trees and forest floor species tend to be monolayered; canopy tree and pioneer species tend to be multilayered. Among crop plants, the shape of the leaf canopy (as determined by branch and leaf arrangement) directly affects light interception and, hence, productivity (*3*). In the simpler system of an individual leaf, the biophysical and adaptive significance of shape and orientation have been studied (*4*). Although the bifurcation ratio (a measure of the degree of branching) was shown to be greater in evergreen broad-leaved trees than in deciduous ones (*5*), there are no published studies that quantitatively relate the parameters of tree branching to the interception of light by the leaf surface. The greatest obstacle to investigations of the adaptive function of branching pattern has been the three-dimensional complexity of tree branches and the varying orientation of the leaves borne by them. We present the finding that, in at least one tree species, the natural limits placed on branching and the asymmetry of branch angles observed in nature are, in fact, very close to theoretical values which maximize the effective leaf surface area (the horizontal projection of the leaf area), a feature with obvious adaptive value.

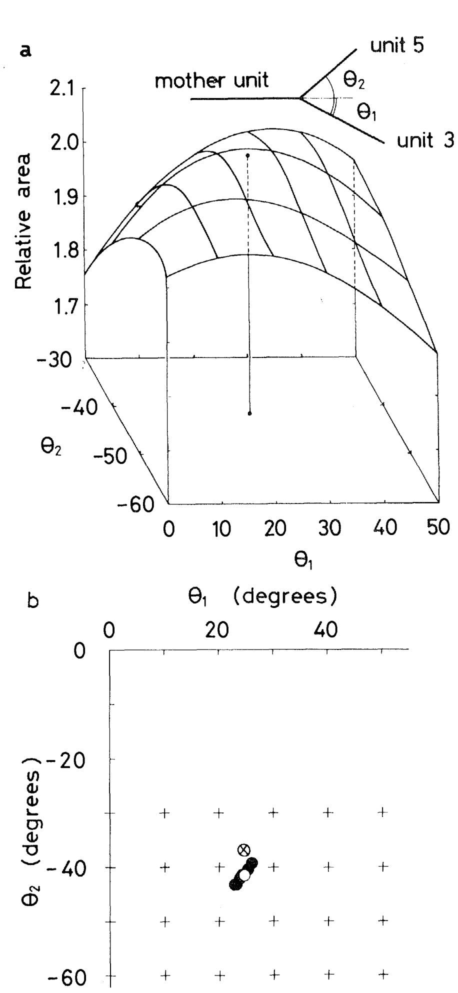

Fig. 1. (a) The effective leaf area versus θ_1 and θ_2. Conditions of the simulations are the same as Fig. 2. The maximum effective leaf area is shown by a vertical line indicating the optimal θ_1 and θ_2. Inset: explanation of branch angles θ_1 and θ_2. (b) Comparison of the actual θ_1 and θ_2 (⊗) with the optimal values derived from simulation in Fig. 2c. The conditions of the simulation are the same as Fig. 2. Results obtained with the six different values for the leaf disk radius between 0.7 and 0.9 (●), instead of 0.8 (○), are shown.

The tropical tree *Terminalia catappa* L. (Combretaceae) has certain architectural features that make it ideal for quantitative studies of branch pattern and leaf surface area. Its distinctive pattern of growth and development, *Terminalia*-branching, is widespread among tropical dicotyledonous trees (*6*). The tree, basically, consists of an erect leader axis with tiers of three to five lateral branches that result from periodic outgrowth of axillary buds and form a characteristic pagoda shape to the crown. The older lateral branches are horizontal and dorsoventrally flattened. Each lateral branch complex is composed of a repeating series of branch units, and each of these bears a cluster of horizontal leaves at its distal end (*7*). Therefore, most of the leaf surface of the tree is presented as a series of flattened layers, each one equivalent to a monolayer; these are well spaced along the trunk. Branching in *Terminalia* has already been studied quantitatively, and average values of different morphological parameters have been calculated (*8*). These ac-

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