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142

Above-Ground Branching of the Stilt-Rooted Palm, Eugeissona minor

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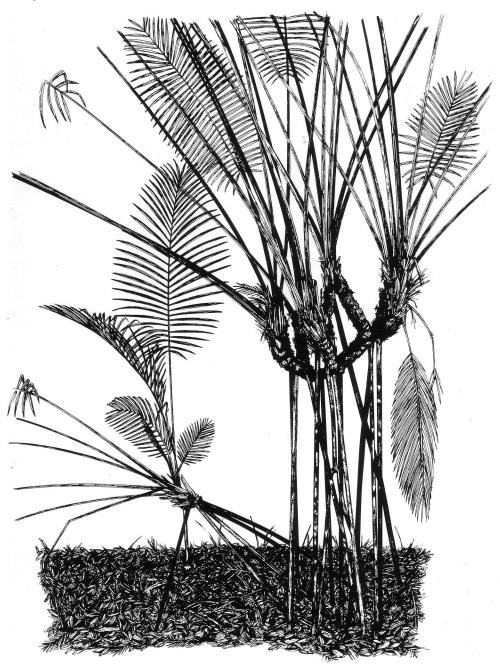
Although branching in palms is not a rare phenomena, it continues to attract much attention (Ridley 1907, Holttum 1955, Dransfield 1978). This sustained interest is perhaps due to the fact that branching in most palms is subterranean and thus not easily observed. In his review of the growth forms of palms, Dransfield (1978) describes one species, Eugeissona minor, which is both branched and stilt rooted, a combination which results in an "elevated yet basically acaulescent branching system." In this paper we offer further observations on the branching pattern of this unusual palm and discuss some of the ecological consequences of this unique growth habit.

Observations were made in Lambir Hills National Park, Sarawak, East Malaysia (4°03'N, 114°03'E). Eugeissona minor is common in mixed dipterocarp forest on gently sloping ridges. A survey of five 0.1 ha plots revealed an average density of 30.2 (sd = 3.3) E. minor plants/ha. Soils in the area are primarily a clay-rich fine sandy loam. The mean rainfall in the nearby town of Miri is approximately 3,200 mm per year (Walter et al. 1975).

The branch system of *E. minor* develops sympodially, with small leaf rosettes (branches) forming adjacent to larger shoots (Fig. 1). Each shoot segment generally initiates one (sometimes two) new rosettes, usually oriented towards the

exterior of the shoot system. Stem segments sometimes achieve 6 cm in diameter and 25 cm in length before branching but interbranch distances are usually less than 15 cm. Mature leaves on large plants are usually 4-5 (6) m long. Unlike palms that branch on or beneath the ground, there are no scale or otherwise modified leaves along the stems of E. minor. Internode lengths average 1.5 cm, except on the terminal flowering axes where interleaf distances up to 16 cm obtain. Although there is no set pattern of branching in E. minor, the stem systems tend to be linearly oriented, often developing a candelabralike appearance (Figs. 1-3). The vertical angle of branching varies between 30° and 80° and does not appear to be related to the height or overall size of the plant. Branching begins at ground level and continues with approximately the same frequency and pattern throughout the life of the plant.

The local Iban name for *E. minor* is "tunjang pipit" meaning the legs of a small bird, which its conspicuous stilt roots certainly resemble (Fig. 3). These roots are 1.5–2.5 cm in diameter and up to 4.5 m long. Locally they are carved into fine walking sticks. Young roots are initiated immediately below each living rosette on all sides of the stem with one root produced every two to three internodes. The roots are oriented within 10–15° of ver-



1. Drawing of a medium size Eugeissona minor plant with one recently detached section.



Close-up of the shoot system after removal of litter showing branch and stilt root initiation.



3. A tall, divided Eugeissona minor.

tical and often become interwoven and closely pressed together. As the roots grow towards the ground the exposed root tip is protected by a thick, shaggy cap. If injured, however, branching proximal to the damaged tip occurs. The mature stilt roots are protected by whorls of 2–4 cm long modified roots which function as spines.

The configuration of the branches and leaves and the cagelike projection of stilt roots trap a substantial amount of leaf litter and other decaying organic matter (Fig. 4) and qualify *E. minor* as a "trash-basket plant" (Granville 1977, Ng 1980, Raich 1983). The extent to which *E. minor* derives nutrients from the entrapped litter, however, is unclear as aerial feeder roots (Nadkarni 1981) growing in the crown litter were not observed. Yet this trapped litter does represent a nutrient source because nearby plants frequently have roots that grow up into *E. minor*

crowns. Termites of several species commonly construct nests within *E. minor* crowns (Fig. 4). Removal of litter and organic debris inevitably turned up carton trails and other evidence of termite activity. In one case a bird's nest was discovered among the branches, stilt roots, and accumulated litter among the branches of a large plant.

A consequence of a growth form which combines branching with stilt roots is the fragmentation of stem sections which occurs as the older portions of the stem decay (Figs. 1, 3). Decomposition of the lower (older) stems often occurs in stilt-rooted palms which then maintain contact with the soil only through their stilt roots (Corner 1966). In *E. minor* this process is accelerated by termites which feed upon the dead roots and stem. Even after the connecting stem section has been severed, interlocking leaves and stilt roots help to keep the plant balanced in its original con-



 An undisturbed Eugeissona minor crown with trapped litter and a termite nest.

figuration. However, stem fragments which are supported by only a few stilt roots eventually become unsteady and fall to one side under their own weight (Fig. 1). The maximum distance traversed is determined by the length of the existing roots which remain anchored in the soil in their original position. The fallen stem sections reorient and produce new, more-or-less vertical stilt roots. Eventually, as the older roots die and rot away, the once intact plant (genetic individual) comes to appear as several independent plants growing 1-3 m or more apart. This process of vegetative reproduction through stem fragmentation is sometimes aided by disturbances such as tree and branch falls which help to unbalance stem sections and push them apart. However, the primary reason for fragmentation lies not with such disturbances but is inherent in the growth habit of the plant.

In order to determine the extent and

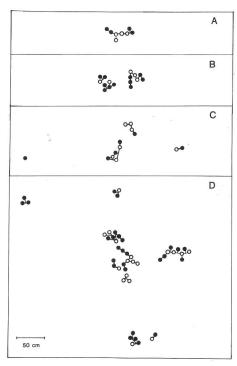


Diagram of four Eugeissona minor plants: A = intact; B = separated; C and D = fragmented. Solid circles represent living apices, open circles represent dead shoots.

frequency of vegetative fragmentation in E. minor, a survey was conducted. The first 50 plants encountered growing within 2 m of a ridge-top trail in an area with abundant E. minor were sampled and the number of living shoot apices, height to the lowest and highest apices, reproductive status, and percent canopy cover overhead were recorded. In addition, each plant was classified as either "intact," "separated" (having at least 2 unconnected stem segments separated by <50 cm), or "fragmented" (having at least one stem segment separated by >50 cm and which initiated new roots in the new location) (Fig. 5). Plants growing within 2 m of each other without showing any clear signs of having once been connected were difficult to classify and were not included

in the survey. Of the 50 plants sampled, 20 (40%) were intact, 13 (26%) were separated and 17 (34%) were fragmented. Six of the fragmented plants had obviously been knocked apart by falling tree branches. The largest horizontal distance observed between two separated sections was 1.9 m.

Fragmentation by decay and natural senescence occurs in many vegetatively regenerating plants (e.g., Leakey 1981). Its significance in the case of E. minor, however, is unclear. Flowering and viable seed production were observed within the study area but seedlings were extremely rare. Furthermore, vegetative expansion in E. minor is somewhat limited in spatial extent and appears effective primarily for exploiting local environmental heterogeneity and surviving disturbances, rather than as a colonizing strategy. On the other hand, fragmentation of E. minor plants does provide some release from withinplant crowding and competition.

Branching in palms, even in the absence of fragmentation, can be considered both as a safety mechanism against terminal bud damage and as a means to offset the disadvantages of apical flowering (Dransfield 1978). Stilt roots have been considered advantageous due to reducing the length of the ground-level establishment phase and thus exposure to terrestrial predators, ability to survive tree-falls (Bodley and Benson 1980), increased stability on steep terrain or in swampy habitats (Corner 1966), and for increasing rooting area (Ashton in Dransfield 1978). The unique co-occurrence of stilt roots and branching in E. minor results in a distinct form of clonal growth and vegetative spread which provides benefits to the plants and confirms the intimate relationship between morphology and demography (e.g., White 1979).

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LITERATURE CITED

- BODLEY, J. H. AND F. C. BENSON. 1980. Stilt-root walking by an iriarteoid palm in the Peruvian Amazon. Biotropica 12: 67-71.
- CORNER, E. J. H. 1966. The Natural History of Palms. Weidenfeld and Nicolson, London.
- DRANSFIELD, J. 1978. Growth forms of rain forest palms. In P. B. Tomlinson and M. H. Zimmermann (eds.). Tropical Trees as Living Systems. Cambridge University Press, Cambridge, Massachusetts.
- GRANVILLE, J. J. DE. 1977. Notes biologiques sur quelques palmiers guyanais. Cah. O.R.S.T.O.M., ser. Biol. 12: 347–353.
- HOLTTUM, R. E. 1955. Growth-habits of monocotyletons—variations on a theme. Phytomorphology 5: 300-413.
- LEAKEY, R. R. B. 1981. Adaptive biology of vegetatively regenerating weeds. *In* T. H. Coaker (ed.). Advances in Applied Biology. Academic Press, N.Y.
- NADKARNI, N. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. Science 214: 1023-1024.
- NG, F. S. P. 1980. Litter trapping plants. Nature Malaysiana 5: 26-32.
- RAICH, J. W. 1983. Understory palms as nutrient traps: a hypothesis. Brenesia 21: 119-129.
- RIDLEY, H. N. 1907. Branching in palms. Ann. Bot. 21: 415-422.
- Walter, H., E. Harnickell, and D. Mueller-Dombois. 1975. Climate-diagram maps of the individual continents and the ecological climatic regions of the earth. Springer-Verlag, N.Y.
- WHITE, J. 1979. The plant as a metapopulation. Ann. Rev. Ecol. Syst. 10: 109-145.