Production of a Second Set of Stilt Roots in Arborescent Palms: A Solution to the Puzzle

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1. Second set of stilt roots emerging from the trunk of an *Iriartea* palm at 1–2 m above the ground at the point of litter accumulation caused by a leaning tree.

Iriartea **and** ***Socratea*****, stilt-rooted palms of the Americas, sometimes develop a second cone of stilt roots. This paper addresses what the significance, if any, of this second cone may be.**

Arborescent palms are abundant canopy components of tropical lowland and montane forests up to 1000–1500 m (Kahn & de Castro, 1985, Peres 1994, Kessler 2000). Their distribution reflects fine environmental gradients that affect the diversity of tropical plants. These gradients are the result of differences in successional status, soil type and nutrient content, and topography (Kahn & de Castro 1985, Chazdon 1995, Clark et al. 1995). As a consequence, palms have developed diverse mechanical features that favor their establishment over a wide range of environmental conditions (Kahn 1986, Rich 1986, Swaine 1983).

Among arborescent palms, Iriarteoid palms are characterized by the production of stilt roots, which form a cone around the stem. In *Iriartea deltoidea* the stilt roots are clustered at the base of the stem, have prominent lenticels, lack thorns, and can grow 1.5–2 m above the ground. Individual palms may reach 35 m in height (Gentry 1993) and are characteristic canopy elements of lowland and mid-elevational tropical forests up to 1000 m. In *Socratea exorrhiza* the stilt roots are well separated, can be very tall (up to 4 m) and are covered by small (0.5 cm) thorns. *Socratea* is more abundant in lowland rainforests; its density decreases with elevation more rapidly than in the case of *Iriartea* (Kessler 2000).

Stilt roots provide support for palms that grow to reach canopy height and are located in very steep topographic conditions. I have found a close relationship between the cone volume of stilt roots and the height of the palm in both species (r^2 = 0.85, P = 0.0001, N = 37 for *Socratea*, and r^2 = 0.82, P = 0.0001, N = 31 for *Iriartea*, pers. obs.) New stilt roots sprout at the top of the cone and are projected down. Old stilt roots die either inside the cone (the first ones that were produced) or in the lower periphery of the cone, and are replaced by new roots emerging from the topmost part of the cone. Stilt roots favor resprouting when the palm has been flattened by falling branches or trees (Bodley & Benson 1980). In addition, the root cone develops early in the life cycle permitting a rapid height increase without loss of stability, which allows an early exploitation of gaps and occupation of canopy space relative to species in which stilt roots are absent (Swaine 1983).

Although most palms produce only one set of stilt roots located at the base of the stem, I have observed several palms developing a second set of stilt roots at significant heights above the ground, sometimes as massive as the root cone produced at the base of the stem (Fig. 1). Why do these palms develop a second set of roots, which obviously do not reach the ground or are useful in providing support or access to nutrients? The solution to this puzzle became evident at Poco Sol Biological Station, Children´s Eternal Rainforest (800 m in elevation), where I observed two individuals 20–25 m in height of *I. deltoidea* each developing a second set of stilt roots 1–2 m above the first root cone. The first individual had a small tree, still alive but leaning on the palm trunk at an approximate angle of 45° touching the point where the new set of stilt roots were produced. The crown of the leaning tree surrounded the palm trunk and favored the accumulation of leaf litter and dirt, and colonization by hemiepiphytes such as *Asplundia* sp. (Fig. 1). The second individual had a well developed second set of still roots 2 m above the first one with none of the roots making contact to the ground. There were evident signs of litter accumulation around the top part of the cone (soil, dead branches, leaf litter and epiphytes established around the top of the cone). It is likely that the accumulation of litter (and eventually soil) induced the production of still roots through their interaction with plant growth regulators such as auxins. In horticulture, it is common practice to induce the production of new stems and roots of ornamental plants by surrounding and tying the stem with an aluminum pocket containing soil mixed with rice husks and other plant material, a technique known as air-layering. This practice is implemented in the propagation of *Dracaena americana* and other monocotyledonous ornamentals exported to international markets. As a result of the exposure to the soil and organic matter mixture, the plant develops new stems and roots at the point in contact with the pocket contents. Similarly, leaning trees or fallen branches that make contact with palm trunks favor litter accumulation, as well as colonization by large epiphytes that also enhance organic matter accumulation, influencing the production of this peculiar second set of stilt roots above the ground at that point in the stem.

Although the development of a second set of stilt roots is not common, I have observed two individuals of *S. exorrhiza* with this second set of aerial stilt roots at considerable height above the ground in Corcovado National Park, Costa Rica, close to San Pedrillo Park Ranger Station (0–15 m in elevation). The individuals were 25–35 m in height and had a well-developed set of stilt roots 10–15 m above the ground similar to the ones forming the cone at the base. In Braulio Carrillo National Park, Costa Rica (Quebrada González, 450 m), I observed one 4 m tall *Cryosophila guaguara* palm developing a second set of stilt roots 50 cm above the first set. In contrast to the *Iriartea* and *Socratea* cases mentioned above, it was likely that being so close to the ground, this second set of stilt roots will replace the first one.

The ability to produce a second set of stilt roots could be of benefit when the palm is overtopped by vegetation around the trunk base, and when plant debris has the potential to interfere with root gas exchange. A second set of stilt roots would favor the palm to grow out of the accumulation of vegetation after a disturbance, even if the palm is knocked down (i.e., Bodley & Benson 1980). This ability may have resulted in the capacity to produce stilt roots above the first set, even when the ground is considerably far below. Although under certain circumstances it bears no advantage, this phenomenon is a reflection of the significant growth plasticity found in tropical palms.

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