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Aerial roots of tropical rain forest trees: the consequence of seedling establishment on fallen logs

Pierre Binggeli

Summary

It has been widely considered that aerial roots of tropical forest trees arise from adventitious roots and provide mechanical support and/or a "breathing apparatus". Observations in a submontane rain forest in Tanzania have demonstrated that they are most frequently a consequence of seedling establishment on fallen logs in tree fall gaps. The rotting logs of fallen trees provided a substrate for the regeneration of 3.3% of the trees recorded in a forest plot.

Introduction

Aerial roots are a common in tropical forests, stilt roots being one of the most noticeable types. Stilt roots arise adventitiously on the lower parts of stems, pass through the air and root usually in the ground (Usher, 1966; Jeník, 1978). Their morphology differs greatly among species, their characteristics being affected by the heights of their emergence on the trunk, by anatomical characters of their primary body, and by the rate of secondary thickening (Jeník, 1978). A similar form may be achieved by quite different developmental pathways in different species (Tomlinson, 1983).

Stilt roots occur in a wide range of taxonomically unrelated species, including gymnosperms and angiosperms. They are well represented in mangroves (*Rhizophora*), swamp forest trees (*Uapaca paludosa*, *Xylopia staudtii*, *Pandanus*), and trees of inundated river banks (*Cecropia*, *Uapaca heudelotii*), but they are also present on trees growing on well-drained soils (e.g. *Santiria*, *Musanga*, *Cecropia*, *Xylopia*, *Pandanus*) (Schnell, 1970). Because stilt roots are often recorded in fresh-water swamps and mangrove forests, it has frequently been suggested that they provide mechanical support to trees on soft marshy soils and/or that they are a mechanism for developing an above-ground aerating system in anaerobic substrates (Tomlinson, 1983). Their occurrence on well-drained soils has been explained as giving a more stable base to shallow rooting of trees on such surfaces (Schnell, 1970).

Stilt roots are found in several species of palms and may be produced at the seedling stage and throughout the life of the plant or only after the seedling stage. Their significance is not clear, and Dransfield (1978) found no relationship between their occurrence and habitat, except perhaps for *Verschaffeltia splendida*, in which they are regarded as an adaptation for self-support on steep, unstable hillslopes in the Seychelles, or in *Socratea exorrhiza*, where stilt roots allow seedlings and juveniles flattened by falling trees to move out from underneath (Bodley & Benson, 1980).

In well-drained primary forests stilt-rooted trees are uncommon, but they occur quite regularly in secondary forest in Western Africa in which all the species with stilt roots have been classified as light-demanders. It has also been noted that stilt-rooted individuals of particular species in the same or different habitats display such roots to different degrees (Richards, 1957). To explain the occurrence of stilt roots on secondary forest species, Kunkel (1965) suggested that stilt roots lift the tree upward and prevent suppression by surrounding trees. While Kaufman (1988) supported the view that stilt roots as well as buttresses in small-gap species may provide the trees with a 'head start' in growth and may provide support in swampy situations, Jeník (1973), in his review of stilt roots, claimed that they are usually genotypic adaptations, but sometimes arise through injury or tidal erosion; Jeník's opinions have gained support (Kahn, 1977). Jordan (1985) suggested that some stilt-rooted individuals of secondary successional species may have originated through the germination of seeds on fallen tree logs. He proposed that these seedlings initially derive their nutrients from the decomposing trunks and, as the trunks disappear, the roots penetrate downwards into the soil. The aim of the present paper is to demonstrate that the majority of stilt-rooted trees in an African submontane rain forest have indeed arisen through germination on fallen logs and discuss the role of fallen logs in forest regeneration.

Study site and methods

The observations were carried out in March 1987 and April 1989 in the evergreen submontane forest of the East Usambaras in Tanzania. The East Usambaras are part of the East African Montain Arc and are situated 60 km from the Indian Ocean. The climate is seasonal with a long rainy season from March to June and a shorter and usually less regular rainy season from October to December. The climate, the soils (deep ferralsols) and various aspects of forest ecology are described in Hamilton & Bensted-Smith (1989). The sampling sites were situated in Amani-Sigi, Amani West, Kwamkoro and Kwamsambia Forests Reserves at altitudes between 950 to 1050 m and were the same as those used for studies of forest dynamics and invasion of an aggressive introduced tree species, *Maesopsis eminii* Engl. (Binggeli, 1989). Observations to determine how stilt roots develop were made using three strategies. First, 98 treefall gaps of various ages and containing logs at different stages of decomposition were surveyed. In each gap the presence of seedlings, saplings and mature trees on fallen logs, stumps and soil mounds (raised during treefalls) was noted and the occurrence of stilt roots recorded. Second, the presence of stilt roots was recorded in relation to the same features on trees with a GBH>15cm in an area of more or less undisturbed forest measuring 63 x 80 m in Kwamkoro Forest Reserve. Finally, the logs of several trees logged, but not removed, by pitsawyers in early 1987 were revisited in March 1989 and evidence of tree establishment on these logs was gathered.

Results

In submontane forest on the East Usambaras stilt roots were observed on *Ficus* spp. and four other species: *Anthocleista grandifolia* Gilg, *Myrianthus holstii* Engl., *Polyscias fulva* (Hiern) Harms and *Syzygium guineense* (Willd.) DC. C.K. Ruffo (Personal communication) has also observed stilt roots on *Macaranga capensis* (Baill.) Sims. Fig. 1 shows an alignement of stilt rooted trees and the remains of a decomposed log (estimated diameter 80cm) which was a result of a tree fall on a ridge of Kwamsambia Forest Reserve. The first tree (*Anthocleista*) has small aerial roots and is growing on the partially decomposed section of the fallen log. The position and morphology of the aerial roots of the next two trees (a *Polyscias* and an *Anthocleista*) show clearly that the seedlings became established on the undecayed log and that the roots grew around the log to eventually reach the ground. After decomposition and partial disappearance of the stem the trees kept growing but, the position of the *Polyscias* is precarious and the tree is leaning sideways. Beyond those three trees there are another two individuals (one *Polyscias* and one *Anthocleista*) with very similar growth forms. Other fallen logs with varying degrees of wood decomposition, were observed and the above pattern was confirmed. For example in Kwamkoro Forest Reserve a *Myrianthus* 1.7 m high was found growing on a decaying log of a Newtonia cut 9 years previously. The sapling became established on the side of the log, 30 cm above the ground and had sent one root down around the log into the soil. These observations support the view that stilt-rooted trees in the montane forest may result from a capacity to regenerate on logs of fallen trees.

Figure 1. to be added

All the species in the above examples are short-lived and light-demanding and grow only in forest gaps. Nevertheless, they are not the only species capable of establishment on logs. Two common primary forest trees, *Newtonia buchananii* Gilb. & Bout., a long-lived light-demanding species, and *Allanblackia stuhlmanii* Engl., tolerant of more shaded conditions, were also found growing on the remains of decayed logs. Only the latter sometimes exhibits stilt roots. At the time of establishment of these two species the log would probably have been soft and would have already partially collapsed and neither species would need to produce stilt roots to reach the ground surface. Two young *Newtonia* saplings were observed on the rotting log among the trees shown in Fig. 1. Seedlings of *Maesopsis* have been observed in great numbers on well decayed logs but never seem to survive more than a few months. In contrast successful establishment has been recorded on soil root mounds.
In the plot surveyed in the Kwamkoro Forest Reserve only four species representing 3.3% of the 362 trees had stilt roots (Table 1). By far the commonest stilt rooted species was *Myrianthus holstii*.

Table 1. Occurrence of trees with stilt roots, and of trees without stilt roots growing on logs, stumps, and soil root mounds over an area of 63 x 80 m in Kwamkoro Forest Reserve.

Species	with aerial roots	with aerial roots, position of establishment, on			
		log	stump	mound	ground
Myrianthus holstii	8	-	-	1	17
Anthocleista grandiflora	2	-	-	-	1
Polyscias fulva	1	-	-	-	8
Syzygium guineense	1	-	-	-	1
Alsodeiopsis stuhlmanii	-	1	-	-	1
Xymalos monosporo	-	-	1	-	9
other tree spp.	-	-	-	-	347
total	12	1	1	1	362

Discussion

The ability of seeds to germinate, and of tree seedlings to grow on fallen logs, leading to the production of stilt roots has not previously been described for tropical forests, although Jordan (1985) has suggested that it is likely to occur. This process of stilt-root production has, however, long been known to occur in temperate forests (e.g. Willkomm, 1887; Hackiewics-Dubowska 1936; Falínski 1986). In the Boubiner Urwald (Bohemia) known for its stilt-rooted trees, Prusa (1985) found that 4.5% of the living *Picea abies* displayed stilt roots, or 2.4% of all trees, a figure similar to the one found in the East Usambaras.

In the East Usambaras tip-up root mounds are uncommon because trees usually snap, rather than become uprooted (Binggeli, 1989) and root mounds are therefore unimportant microsites for tree regeneration. A few *Anthocleista* were observed on tip-up root mounds, and it was often the case for the introduced *Maesopsis*.

Several authors (Richards, 1957; Schnell, 1970; Jeník, 1973) have argued that stilt roots would increase the stability of trees growing on hard soils where rooting depth is assumed to be limited. The leaning *Polyscias* in Fig. 1 illustrates that stilt roots are actually detrimental to the stability of the tree, and Taylor (1989) has shown that trees in the East Usambaras do not have such shallow roots as is often claimed for tropical forests, giving them enough stability without the need of special morphological adaptations in sub-canopy short-lived species. As shown earlier, the claim that all stilt roots arise adventitiously from the tree trunk (Richards, 1957; Jeník, 1973; Kahn, 1977) is spurious.

It can be suggested that most or even all tree species displaying stilt roots in well drained African tropical forests, and particularly species listed, for instance, by White (1983) for young secondary forests of the Guineo-Congolian region and Kunkel (1965) for the high and secondary forests of Liberia, are in fact a result of their regeneration on fallen logs. Also some of the trees with stilt roots in tropical swampy forests may have originated in a similar fashion. Harmon *et al.* (1986) have stressed the importance of coarse woody debris in terms of tree recruitment in temperate forests, which in the tropical zone seem to have so far been ignored. They suggest that (a) decayed logs increase water holding capacity, (b) seedling burial by litter accumulation is less on logs than on forest floor, because of a decreased herb and bryophyte cover, (c) establishment on fallen logs may reduce herbivory, and (d) concentration of fallen logs may form natural exclosures. In some temperate forest, fallen logs are essential for tree regeneration, for instance in old-growth Pseudotsuga-Tsuga forest of the Pacific Northwest 98% of *Tsuga heterophylla* seedlings were rooted on rotten wood that covered 6% of the forest floor (Christy & Mack, 1984). Because of frequent water-logging, tip-up root-mounds may in fact be with the fallen log the only safe microsites for seedling establishment of some tropical tree species, and in case the mound becomes eroded the tree may display stilt roots. Clearly in such areas detailed investigations should be undertaken to ascertain whether this is the case.

The logs of fallen trees are only one of four habitats which have been identified as available for tree seedling establishment in treefall gaps in the East Usambaras (Binggeli, 1989); the others are the mineral soil of the uprooted tree base, the humus soil along the fallen log and the crown zone of the fallen tree. It was observed that in large treefall gaps most tree seedlings become established in the humus zone, but that, in general, all species were observed to favour more than one type of substrate. This explains why the production of stilt roots in some species is facultative. In fact, in the East Usambaras few tree species regenerate on fallen logs. It appears that only in case of regeneration failure and rapid spread of ground vegetation, will the fallen log become the only safe micro-site for further seedling establishment.

In tropical forests with well drained soils stilt-rooted trees

(Fig. 2) may be used as one of the clues for the existence of past treefalls, a technique which has been used in North American forests (Lorimer, 1985), and recently in the East Usambaras (Binggeli, 1989).

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Article's history
This article was submitted for publication and rejected. Then Table 1 was added and before further improvements could be made, life moved on.