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SHORT COMMUNICATION

Mangroves: where's the understory?

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With one exception, every pristine tropical forest more than a few metres in height has understory vegetation that contains numerous vascular plant species that grow and reproduce there, but never become canopy members. Likewise with one exception, all pristine lowland tropical forests have numerous species of vines (lianas) (e.g. Gentry 1983, Peñalosa 1984, Putz 1983, 1984a, b). The exception in both cases is the mangrove swamp forest (Figure 1). Mangrove forest the world around is conspicuous for the absence of reproducing understory herbs and shrubs, and for the absence of the vine life form. If you grow rooted to the soil in a mangrove swamp, you are a tree and the reproductive members of your population have their crowns in the canopy of the forest. Equally conspicuous is the total absence of any reference to either this phenomenon or its possible causes in the voluminous mangrove forest literature (e.g. Chapman 1976, 1977, van Tine & Snedaker 1974, Watson, 1928). It is almost as though ecologists are so pleased with not having to deal with an understory that its remarkable absence is passed over with relief.

The evolutionary move into the intertidal mud-flat successional habitat has occurred numerous times in numerous plant families. What has kept herbs and understory shrubs from likewise evolutionarily moving into the mangrove forest understory? What has kept vines out of the canopy? Why is the understory occupied at best by a few stunted juveniles of the habitat overhead, such that the view through a mangrove forest understory (Figure 1) is largely of sun-dappled and shaded trunks, stilt roots, pneumatophores and little foliage? Even the succession in a mangrove tree fall is carried out entirely by canopy-member species. The mangrove fern, *Acrostichum* spp. (Gomez 1983), is the closest thing to a mangrove understory herb, but even this halophile seems to be dependent on direct sunlight to be fully reproductive on salty substrates and usually grows in full sunlight.

Hypothesis 1. Plants with low light resources cannot accumulate enough fast enough to meet the metabolic demands of the drain of the machinery and morphology for salt tolerance.

This hypothesis is based on energy budget considerations and on the Vietnam defoliation 'experiments'. It was a common outcome in Vietnam that various species of adult mangroves were killed by a single chemical defoliation while many species of terrestrial forest trees required several chemical defoliations to be killed. Consistent with this hypothesis is the observation that no species of mangrove is intra-crown synchronously deciduous, even in coastal areas so dry that nearly all the terrestrial forest trees are deciduous. For example, in Santa Rosa National Park, in the dry Pacific coastal lowlands of northwestern Costa Rica, there are four species of mangrove trees (Janzen & Liesner 1980); all four stand evergreen against a deciduous adjacent forest during the dry season. However, mangroves do have their roots continually in water or wet soil; continuously available water also favours evergreen behaviour. If this hypothesis is an accurate statement of what matters to a plant growing in strongly saline soil, it suggests why mangrove trees generally do not extend into northern latitudes. Since long-lived canopy-level vines very commonly start vegetative life in shaded forest understory, their absence from mangrove forests may be partly explained by this hypothesis, but certainly their absence from the early stages of mangrove succession is not explained. Likewise, such a hypothesis does not explain the general absence of herbs from insolated early successional mangrove vegetation.

Hypothesis 2. The herb, shrub and vine life forms are intrinsically incapable of growing in saline soils.

I find this hypothesis particularly unconvincing because young mangroves are in fact shrubs and there is at least one species of neotropical mangrove vine (liana), *Phryganocydia phellosperma* in the Bignoniaceae (Gentry 1982).

Hypothesis 3. The characteristically small seeds of herbs, shrubs and vines do not generate a sufficiently robust seedling to withstand the abiotic conditions and/or grazing conditions of a mangrove swamp.

I find this hypothesis unconvincing because (1) the potential mangrove understory plants could evolve large seeds or be selected from among large-seeded species (mangrove trees regularly have very large seeds), and (2) there are many heavily disturbed and grazed terrestrial and freshwater habitats that are rich in understory herbs and shrubs. However, just as I have hypothesized that a shortage of the resources associated with sunlight restricts the ability to avoid or tolerate salt, a similar shortage of these resources may severely restrict the reserves available for defensive chemistry and large crops of large seeds.

I have neither the facilities nor background to explore this question further. However, it is a glaring trait of mangrove swamps and its exploration might well lead to new insights about the limits to the biological abilities of organisms.

Figure 1. (A) Mangrove forest understory at low tide: Bako National Park, Sarawak, Malaysia. (B) Black mangrove (*Avicennia germinans*) forest: Santa Rosa National Park, Guanacaste Province, Costa Rica. All foliage in the photograph is *A. germinans*. The ground is covered with a dense stand of living pneumatophores growing upwards from the roots of the mature trees overhead.

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