

Reports

Canopy Roots: Convergent Evolution in Rainforest Nutrient Cycles

Abstract. *Accumulations of living and dead epiphytes in the canopy of rainforest trees provide an aboveground nutrient resource. A wide range of host tree species in both temperate and tropical rainforests gain access to these nutrients by putting forth extensive networks of adventitious roots beneath the epiphyte mats they support.*

Rainforest vegetation that grows on heavily leached soils of low nutrient content requires efficient mechanisms of nutrient transfer and retention (1). Nutrient transfer from vegetation to the forest floor occurs by decomposition and subsequent uptake of timberfall and litterfall and via canopy leaching by precipitation (2). I have discovered an additional transfer pathway in the tree canopies of both temperate and tropical rainforests. Host trees put forth adventitious roots that run beneath thick mats of accumulated organic material and the epiphyte community they support. These roots give host trees access to canopy nutrient resources which are normally unavailable to the host tree and surrounding vegetation until they enter the soil-litter component.

Mild temperatures and high precipitation on the Olympic Peninsula (Washington State) support an ecosystem known as the "Olympic rainforest," which is similar in some respects to tropical rainforests. Young soils of the river valley terraces are poorly developed and have low nutrient content (3). The abundant rainfall (3600 mm/year) promotes profuse growth of epiphytes—that is, plants deriving support but not nutrition directly from other plants. Epiphyte mats up to 30 cm thick are formed on host tree boles and branches, high above the forest floor. These mats, composed of live and dead epiphytes (bryophytes, lichens, club mosses, and ferns), intercepted host tree foliage, and decomposing bark, generate a canopy litter and humus nutrient resource.

Recent field observations, made with the use of modified mountain-climbing techniques (4) in the canopy of mature

big-leaf maples (*Acer macrophyllum* Pursh) in the Hoh River Valley of the Olympic Peninsula revealed that some trees put forth an extensive network of adventitious roots which penetrate these canopy detrital mats (Fig. 1). Such morphological features as abundant root hairs, unsubsized and rapidly regenerat-

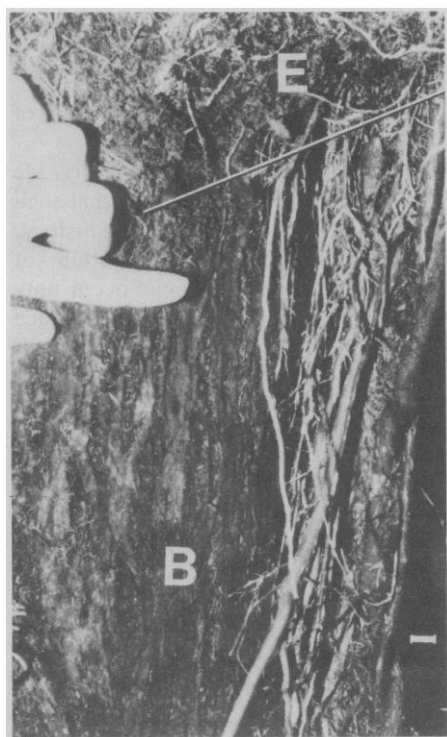


Fig. 1. Canopy roots exposed after stripping epiphytes from vertical surface of a big-leaf maple bole (65 cm in diameter at breast height). The finger points toward mass of roots clinging to bark (B) 18 m above forest floor. Roots are normally enmeshed in thick accumulation of epiphyte and detrital mats (E) (above line at top of photograph). Scale bar, 1 cm.

ing root tips, and the presence of endomycorrhizal hyphae and vesicles inside the roots, are evidence of their role in nutrient transfer. They differ from the "aerial roots" described for some tropical trees (5) in that they develop only beneath a layer of moist organic matter and their gross morphology does not differ from their subterranean counterparts. Thus, they contrast with the aboveground roots of such trees as mangroves, which function in gas-exchange and anchorage, clasping roots of tropical lianas, "column roots" of strangling figs, and "stilt roots" of tropical palms.

Canopy roots occur on three of the seven major tree species present in the Hoh Valley. I have found canopy roots on 92 individuals (of 170 sampled) of big-leaf maple and 23 (of 44 sampled) of vine maple (*Acer circinatum* Pursh). These two species carry the heaviest epiphyte loads in the Olympic rainforest. Mature individuals of red alder (*Alnus rubra* Bong.) also exhibit this habit. Well-developed nitrogen-fixing nodules have been found on alder canopy roots 20 m above the forest floor. Young or exposed trees of these species that do not carry well-developed or contiguous epiphyte mats have no such canopy root systems. Canopy roots have not yet been found on black cottonwood (*Populus trichocarpa* Torr. & Gray), nor on any of the conifer species [*Tsuga heterophylla* (Raf.) Sarg., *Picea sitchensis* (Bong.) Carr., and *Pseudotsuga menziesii* (Mirb.) Franco].

A typical mature and heavily covered big-leaf maple (100 cm in diameter at breast height) had canopy roots originating at 18 points along the bole, from 2 to 20 m above the forest floor. Some of them extended up to 10 m out along branch systems before epiphyte mats and roots terminated. Five canopy root systems branched off in both upward and downward directions; two of the latter had grown completely down the trunk and penetrated the forest floor soil, joining the belowground root system with no alteration in appearance. They ranged in size from root tips with root hairs (2 to 5 mm in diameter) to large, heavily subsized woody roots (8 cm in diameter).

Canopy roots originate from junctions of a branch system (live or dead) with the host tree trunk. Often a lump or callus surrounds the point of origin. Thin sections confirmed continuity of the root with the host tree vascular system; roots originate well inside the xylem.

The same adaptation would be expected on host trees in other ecosystems where nutrients are similarly limited and epiphyte loads heavy. Fieldwork in the

montane cloud forest (1850 m) of the Monte Verde Reserve in Costa Rica has revealed at least 22 species of trees with canopy roots. As in the temperate site, they sprout adventitiously from the boles and branches of host trees and run beneath the constantly moist bryoflora and accumulated organic matter. Canopy roots have recently been reported on two tree species in a Hawaiian cloud forest (6) (*Metrosideros collina* and *Cheirodendron trigynum*). Canopy-rooting species in the tropical environment are taxonomically diverse: for example, Lauraceae (*Ocotea* spp.), Flacourtiaceae (*Xylosma* sp.), Araliaceae (*Didymopanax pittieri*), and Cunoniaceae (*Weinmannia pinnata*). Thus, convergent evolution occurs (i) among geographically distant ecosystems and (ii) between some of the component woody taxa.

Discovery of this phenomenon forces a reconsideration of the nature of the relation between epiphyte and host tree, a subject of debate for many years. Although by definition epiphytes do not take nutrients directly from host trees (as parasites do), they have been implicated in host tree decline (7). Epiphytes have been termed "nutritional pirates," as they can intercept and tie up in their own biomass those nutrients borne in dust, precipitation, and canopy leachates, which would otherwise be available to host trees. However, in rainforest ecosystems where nutrients are readily leached from soil and canopy (and lost to all ecosystem members), tying up nutrients in epiphyte biomass does not "rob" or deny host trees of atmospheric nutrients. Rather, it immobilizes them within the system, and at worst delays their availability to host trees. Those trees with extensive networks of canopy roots gain access to the arboreal nutrient source generated and retained by epiphytes. In fact, epiphytes may substantially contribute to host tree nutrient status by trapping and retaining atmospheric nutrients.

The implications of canopy roots extend beyond the relations between epiphyte and host tree to the more general questions of ecosystem nutrient dynamics and their interrelations. Root distribution and morphology indicate that more direct nutrient transfer between canopy and forest floor vegetation is taking place than previously considered. Canopy roots provide an efficient mechanism for nutrient recycling with smaller amounts of nutrients lost to other ecosystem components or leached from the entire ecosystem. For vegetation growing on heavily leached soils, such a

mechanism would contribute to the nutrient conservation and retention capacity upon which rainforests depend.

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8. I thank C. Grier for support, D. Paulson for photography, W. Haber for tropical plant identification, D. Benzing for comments, A. M. Glyph, and the Monte Verde community. J. Agee and the National Park Service provided technical and financial assistance in the Olympics, and the Organization for Tropical Studies and the Tropical Science Center helped greatly in Costa Rica. This research was supported by a University of Washington graduate research fellowship, a U.S. Forest Service cooperative aid agreement, a Sigma Xi grant-in-aid, and a research grant from the U.S. Man and the Biosphere Secretariat.

20 February 1981; revised 18 April 1981

Predation Through Geological Time: Evidence from Gastropod Shell Repair

Abstract. *Warm-water marine gastropods from soft-bottom habitats show an increase in the incidence of breakage-resistant shell characteristics over geological time. The hypothesis that breakage became a more important component of selection in the middle of the Mesozoic Era is supported by the finding that frequencies of breakage-induced shell repair increased from the Pennsylvanian and Triassic periods to the Cretaceous, Miocene, and Recent.*

Shell breakage by predators may be a more important agent of selection today than it may have been in the Paleozoic and early Mesozoic eras. This idea was presented as a hypothesis (1) to explain the Middle Mesozoic rise in the incidence of breakage-resistant shell characteristics and the concomitant decline of structurally weak features (2).

In order to test this hypothesis, we assessed the incidence of sublethal shell damage at various times in Earth history. Selection favoring the evolution of breakage-resistant shells can occur only if individuals in a population reproduce after they have suffered nonlethal shell-breaking attacks (3). If all breakage were lethal, there would be no selection between weak and strong shell variants, and no shells would show the scars that record nonlethal injury. High frequencies of sublethal damage imply that the shell, together with other defenses, is effective in protecting the gastropod against locally prevailing shell-breaking agents. The higher the frequency of sublethal shell damage, the greater is the likelihood that selection will maintain or enhance shell armor (3). Although it is impossible to measure the intensity of this selection, the hypothesis that shell breakage became a more important component of selection after the Triassic Period in the Mesozoic would be supported if the frequency of breakage-induced shell repair began to rise at that time (3, 4).

The exceptional preservation required to detect shell repair is rare, especially in Paleozoic and Mesozoic gastropods. Nevertheless, we obtained bulk samples of gastropods from two pre-Jurassic and three post-Jurassic time units (5). All species lived in sands and muds in warm shallow marine waters. A scar on the shell's exterior is the jagged trace of the outer lip where the latter was damaged and subsequently repaired by the mantle edge. For each species at each locality, the frequency of repair (defined as the number of scars per shell) was calculated for predetermined size classes as well as for the complete sample, which included all shells with one dimension greater than 5 mm. If a species was represented in a time unit by more than one sample, each sample was treated equally, and a mean frequency of repair was calculated. A single frequency of repair was used for each species in comparisons of repair between time units. Geographical and habitat variation of repair within and between species was evaluated in gastropods from the Pennsylvanian and Recent (3, 4). Although this variation is great (Table 1), it is less than the variation between time units.

Analysis of complete samples revealed an increase in the incidence of repair among gastropod species from the Pennsylvanian (late Paleozoic) and Triassic (early Mesozoic) to the Cretaceous (late Mesozoic), Miocene (late Cenozoic), and Recent (Table 1). This trend is statis-