The Ecology of Tropical Rain Forest Canopies

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With the advent of increasingly sophisticated techniques for access, tropical forest canopy research has burgeoned in the last few years. Although an enormous amount of basic descriptive work remains to be done, canopy research is now entering a more advanced and ecological phase.

Until recently, most of our knowledge about forest ecosystems has been based on observations from ground level. These ground-based perceptions are summarized in a comment by Alfred R. Wallace[1]

> Overhead, at a height, perhaps, of a hundred feet, is an almost unbroken canopy of foliage formed by the meeting together of these great trees and their interlacing branches; and this canopy is usually so dense that but an indistinct glimmer of the sky is to be seen, and even the intense tropical sunlight only penetrates to the ground subdued and broken up into scattered fragments . . . it is a world in which man seems an intruder, and where he feels overwhelmed . . .

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Biological information about canopies changed very little from Wallace's day until – exactly one hundred years later in 1978 – Don Perry published a method of climbing into tropical tree canopies using ropes and technical climbing apparatus[2]. Although Perry was by no means the first researcher to climb into canopies, the use of single-rope technologies heralded a rapid expansion of canopy research involving a range of apparatus including towers, walkways, platforms, cranes and dirigibles[3–5]. Having overcome many of the logistic limitations of access into tall trees, we can now do field work and formulate hypotheses in an above-ground heterogeneous three-dimensional system.

Historically, most ideas about forest ecology were developed in temperate regions. By contrast, most work on forest canopies has been pioneered in the tropics. The reasons for such sudden interest in tropical canopy research are two-fold. First, tropical tree canopies are the most complex of any forest type. Second, the threatened extinction of tropical organisms (many of which live in the canopy) has provided incentive to study them before they disappear[6] (but see Ref. 7).

Having solved many of the problems of access, canopy biologists are now designing new sampling techniques and formulating hypotheses. They face the difficulty of working in a large three-dimensional space. How are organisms detected and sampled in such a heterogeneous environment, where humans are rendered less agile? In a scenario similar to the expansion of coral reef fish ecology in the 1970s with the advent of SCUBA, canopy biologists are developing sampling protocols to account for the spatial, temporal and substrate heterogeneity of their environment[3,8].

The development of canopy research has been affected by several spatial and temporal constraints of this habitat, including: (1) differential use of this geometric space by canopy organisms; (2) heterogeneity of substrate; (3) variability in ages within the canopy (e.g. soil/plant communities accruing in uneven layers on branches, leaf cohorts between sun and shade regions), (4) variability in microclimate of the atmosphere–canopy interface; (5) the high diversity of organisms (many unnamed); (6) development of protocols to quantify processes in the canopy environment. Many aspects of canopy research are so new that results are not yet published.

In this review, we highlight several areas of research that have been enhanced by canopy access. We define three major types of canopy research, each of which requires different logistics and experimental design: studies of plants, studies of animals and studies of canopy processes (e.g. photosynthesis, herbivory and nutrient cycling).

Sessile organisms: trees, vines, epiphytes and epiphylls

Studies of sessile organisms in forest canopies pose fewer logistic difficulties than other aspects of canopy biology. The biggest obstacle is access to growing shoots and reproductive parts, many of which occur in the uppermost canopy. Some methods (e.g. raft[5] and crane[8]) facilitate access to these upper regions. Shade-tolerant plants such as bromeliads and other epiphytes are often accessible in the mid-canopy region. Epiphytes and epiphylls colonize branches and leaves, respectively, in moist canopy regions. Nevertheless, their diversity, distribution and abundance is not well documented[9], and data on growth, recruitment and survival are few (but see Refs 10, 11).

Trees are the major substrate of the canopy ecosystem, and tree species – their architecture, limb strength, surface chemistry and texture – play fundamental roles in shaping the canopy community. Tree architecture is far more varied in the tropics than in the temperate zones, and the patterns of reiteration of canopy branches and their implications for canopy processes are not well understood in either region[12,13]. Over time, as canopy branches grow, the communities within them increase in complexity. For example, patches of leaves, heterogeneous in their age structure, foliage quality and distribution[14], attract different populations of insects both within and between tree crowns: herbivores prefer shade leaves over sun leaves[14,15]; and patches of canopy vegetation (e.g. palms versus vines) may host entirely different populations of insects[16]. Similarly, branching patterns affect the communities that form around them. Branches that are steeply inclined have less accumulation of canopy plants (and consequently canopy soils and insects) than branches that grow horizontally (S.W. Ingram, MA Thesis, University of California at Santa Barbara, 1989).

Branching patterns, in turn, are indirectly affected by the location of a tree. Berner, who is studying the interactions between branch growth patterns, disturbance and plant community dynamics[17], found that trees on slopes produce more asymmetrical branch growth patterns as compared to trees on level ground, due to increased light influx into tree crowns on hillsides. But the steep slopes also result in more disturbance and higher mortality for trees growing there. Similar differential tree growth and mortality occur around the margin of a tree gap, apparently prolonging the successional process[18].

The first comparisons between ground-level observations and direct measurements of canopy architecture are under way in Panama[8]. The 'surface' of tropical forests appears much more irregular and dynamic than most measurements from the ground would indicate, and is more heterogeneous than in temperate forests, partly because of the larger number of tree species. This has implications for canopy–atmosphere interactions, and for population dynamics of organisms in the upper canopy. For instance, precipitation reaching the understory layers can vary severalfold depending on the angle of incidence of rainfall[19]. Canopy topography affected the flux of wind-blown insects in Puerto Rican rain forest canopies, contributing to the regulation of *Anolis* lizard populations (R. Dial, PhD Thesis, Stanford University, 1992). Other environmental (e.g. light, sunflecks, wind-below-crown level) and biological factors (e.g. density of vines, distribution of flowers, populations of canopy leaves and subsequent organisms that inhabit them) are affected by tree growth and canopy architecture.

Crown shyness gaps between trees arise from dieback of the outermost branches due to wind-shearing[20] or shading of adjacent crowns[21]. The amount of spacing between tree crowns may have profound effects on the dispersal of canopy organisms, providing pathways for flying organisms both between tree crowns and between canopy layers, but inhibiting the horizontal passage of climbing animals and plants. The unusual diversity of gliding animals in Asia has been attributed to the relative scarcity of lianas in this region, which many animals use as 'highways' to cross from one crown to the next[22]. As crowns become more widely dispersed (particularly in windy regions), lianas themselves have more difficulty extending laterally from tree to tree[20]. Vines may comprise one quarter of all leaves in the forest of Barro Colorado Island, and one individual of *Entada monostachya* has been recorded to connect the crowns of 64 canopy trees[23]. Indeed, to describe vines as sessile is sometimes inappropriate, because of their fast growth, mobility and foraging behavior as they search for light[24]. Techniques other than climbing have been employed to study vines, such as the use of winches in Australia to haul *Calamus* down from the canopy and measure its growth[25]. We are only beginning to understand the complex dynamics of tree and vine growth in relation to canopy processes.

Mobile organisms in canopies

Most studies of vertebrates have been made from ground level – an adequate vantage point for diurnal mammals and some birds. But access into the canopy has led to the discovery of unexpectedly arboreal proclivities in some rodents, whose behavior was not obvious from the ground. Malcolm used the peconha Indian method (strap between the feet) to look at edge effects on small mammals in the canopy of lowland forest near Manaus, Brazil[26]. He found that species exhibit distinct height preferences, and more mammals were arboreal than terrestrial. In a Costa Rican cloud forest, Langtimm also found stratified height preferences for different species of small mammals[27].

Ornithologists face the challenge of trying to capture (as well as to observe) birds in tree crowns. In New Guinea, Bechler hoisted nets up and down tall poles to quantify birds of paradise in the canopy (B. McP. Bechler, PhD thesis, Princeton University, 1983). More recently in Peru, Munn used a large slingshot to position aerial mist nets in emergent trees as high as 40–60 m[28]. Bierregaard and Lovejoy found that birds will increase the size of their territories vertically to compensate for forest fragmentation[29]. Using single-rope techniques, Nadkarni and Matelson documented 193 species of birds using epiphytes in tree crowns[30].

Reptiles and amphibians in tree canopies have been studied in Puerto Rico. Reagan[31] developed sampling techniques to monitor *Anolis* lizard populations in tree canopies. Dial (PhD Thesis, Stanford University, 1992) performed some of the first experimental studies on populations of lizards in tree canopies; he excluded lizards from tree crowns and found a marked increase in abundance of insects, their food source.

Studies of invertebrates in tropical forest canopies have perhaps created more controversy than any other aspect of canopy research. Early studies by Erwin[32] in tropical forest canopies raised the estimates of the total number of species on Earth from one million to 30 million within a decade; however, this high figure has recently been questioned[33]. Fogging experiments by Erwin in Brazil produced 1080 beetle species in four lowland rainforest canopies, and 83% of the species were restricted to only one forest type[34]. Sampling small flying organisms with statistical reproducibility is difficult, and Erwin's methods have taken many years to develop[35].

Since the first canopy fogging in Brazil, forests in several other regions have been similarly assessed for insect diversity, including Borneo[36], Venezuela[37] and Australia[38]. The enormous spatial and temporal variability, as well as artefacts of sampling, make studies of canopy arthropods difficult, and the volume of data collected requires many years to analyse.

Fig. 1. Malaysian scientist S. Appanah in a canopy boom at Pasoh Forest, Malaysia. The boom can be moved readily and here is used to reach fruits of a dipterocarp tree. This method has wonderful potential but is seldom mentioned in the literature. *Photo supplied by Mark Moffett.*

Processes in forest canopies

In forest trees, reproductive biology is predominantly a canopy phenomenon. The surprising importance of thrips in the pollination of dipterocarps was discovered using a boom for canopy access[39] (Fig. 1). The staggered pattern of dipterocarp flowering and fruiting requires insect pollinators that can rapidly increase in numbers to accommodate the intermittent flowering periods[40]. Comparisons of levels of allozyme diversity between high- and low density populations of tree species show that low-density populations have less allozyme genetic diversity, yet maintain higher levels than would be found in most temperate plants[41]. Perhaps this can be attributed to long-distance pollinators for many tropical canopy trees, and further canopy investigations are required. Fruit-dispersal syndromes involving vertebrates have been studied in forest canopy in Borneo[42], although most work was conducted with binoculars[43], and – like pollination studies – require many hours of observation.

Measurements of herbivory and the heterogeneity of both foliage quality and herbivore distribution have been enhanced by canopy access. In earlier studies, where defoliation was sampled only by harvesting lower-canopy leaves, both the extent and the patchiness of herbivory was underestimated[44]. Herbivores consume significantly less foliage in the upper crowns (sun leaves) as compared to the lower crowns (shade leaves), but young leaves (especially in the shade) are often completely consumed[45]. Differences in recorded herbivory levels can arise from artefacts of sampling[46], although canopy access has increased the accuracy of results[44].

Access to tree crowns has stimulated interest in canopy nutrient cycling, particularly with reference to epiphytes[9]. Nadkarni and Matelson have documented the importance of wind-blown fine litter in providing nutrients for epiphytes[47], and consider epiphytes a vital component of canopy communities. Many epiphytes are rare or endangered, and with the destruction of their tropical forest environment, research on them (as well as other canopy organisms) is urgently needed. Epiphytes were recently the subject of an international symposium[48], but their population biology and life histories are still poorly known.

Other processes, such as photosynthesis, have been reviewed for vines[20] but less extensively for other canopy foliage (but see Ref. 8) The interaction of most canopy processes – in particular, large-scale canopy dynamics – is not yet understood. Much of the groundwork, however, has been completed to facilitate the extrapolation of small-scale studies to larger-scale community population dynamics (e.g. from leaf to canopy, from organisms to populations, from flower to entire crown), and from short-term observations to long-term phenomena (e.g. from seedling mortality to recruitment patterns in tree crowns, from measurements of light levels to gap dynamics and photosynthesis, from litterfall patterns to nutrient cycling processes).

Prospects

Canopy research has emerged as a new dimension to our study of ecosystems. In the tropical rain forests, where canopies are more complex than any other forest type, modern techniques of access have made it possible to address hypotheses concerning biodiversity and community ecology in the canopy.

The next decade will be critical, as attempts to document the biodiversity and ecology of rain forest canopies accelerate before habitat fragmentation and deforestation take their toll. We advocate parallel studies of temperate versus tropical canopies, and aquatic (e.g. coral reefs) versus terrestrial ecosystems, all of which will illuminate the mechanisms for differences in species diversity and community structure.

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