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TREE PROSTHESIS FOR CROWN ACCESS.

We studied the reproduction biology and population genetics of six co-occurring species in *Shorea* (section Mutica, Dipterocarpaceae). In equatorial Asia, the emergent dipterocarp trees and several in other families flower gregariously, supra-annually. We needed to manipulate flowers, including cross-pollination, of at least three trees more or less simultaneously and in complete security, with both hands and arms free. An engineering company designed for us an artificial tree limb, strong enough to bear the weight of a botanist hoisted on its extremity. The limbs, or booms, consisted of five standard commercial aluminum alloy tubes, that could be combined to extend up to 22 m. We discuss the advantages and disadvantages of canopy sampling with the boom.

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WATER AND NUTRIENT RELATIONS OF THE UPPER CANOPY IN DIPTEROCARP AND HEATH FORESTS OF BRUNEL

Tropical rain forest in Brunei (NW Borneo) includes two types, dipterocarp and heath forest. Although these forest types occur in close proximity, their structure and vegetation types are distinct. The ecological mechanisms responsible for these differences remain elusive; we are investigating the relative importance of differences in water and nutrient uptake as a possible basis for this phenomenon.

During a wet season, we measured sap flow (heat pulse technique) in ten conspecific canopy and subcanopy trees at a dipterocarp and a heath forest site. Simultaneously, on a single day for each tree, diurnal collections were made of sap in crowns of five conspecific trees at each site. Sap was analyzed for TKN, TKP, Ca and K. A second experiment was conducted at the dipterocarp site, using canopy dominant *Dryobalanops aromatica* Gaertn. F., to investigate the effects of tree size on flow and composition of sap and to establish the optimum sap flow sampling period.

Distinct diurnal patterns of sap flow and nutrient content were apparent in most trees. For *D. aromatica*, mean daily sap flow ranged from 5 to 300 kg tree⁻¹ d⁻¹. Dividing sap flow by stem area best eliminated tree size effects. Nocturnal sap flow in *D. aromatica* ranged from 5 to 46% of daily totals. Sap nutrient concentrations tended to track sap flow rates. Results for sap flow and nutrient content are discussed in terms of nutrient delivery to tree crowns, and comparisons are made between forest types.

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MODELING AND SIMULATION OF CANOPY ARCHITECTURE.

The CIRAD Plant Modelling Laboratory, is composed of a team of 20 researchers specializing in four different fields (botany, agronomy, mathematics, computer graphics). Our belief is that a well-balanced interaction of these disciplines is necessary to establish the fundamental principles of growth simulation of plant architecture. In practice, several successive stages are necessary for the correct simulation of a given plant :

- (1) Botanical field observations provide precise qualitative data concerning the architecture of a plant and its growth pattern.
- (2) The plant is then numerically measured.

(3) The third phase is the creation of a reference axis which takes into account the different laws obtained from the plants, as well as their architectural evolution.

(4) The last phase is plant simulation on a graphic station.

The present state of our investigations, as well as their applications in the understanding of canopy architecture, diffusion of assimilates, inter- and intra- crown interactions, light penetration, secondary growth of the axes, ... will be presented.

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CONTESTED RESOURCE: MANAGING RATTAN HARVESTING FOR FOREST CONSERVATION IN KERINCI-SEBLAT NATIONAL PARK, SUMATRA.

Tropical forests are rapidly vanishing throughout Southeast Asia due to conversion to agriculture and commercial timber harvesting. In Kerinci-Seblat National Park (KSNP) in Sumatra, Indonesia, a lack of access to irrigated ricefields, insufficient yields from degraded hillside farms and limited wage labor opportunities leave many households with few livelihood sources other than to collect rattan or to convert forests to farms within the park. In this paper, we focus on the management potential of one species of rattan, *Calamus exilis*, a small-diameter, coppicing cane used in local handicrafts and basketry, and collected illegally in KSNP. Our studies suggest that *C. exilis* may be suited to sustained-yield harvesting at four-year intervals, and to co-management of rattan harvesting in designated extractive zones by local rattan collectors and artisans along with park officials. Managed harvesting of rattan represents a potential means of relieving pressure to convert forest lands, while simultaneously providing some poor households with a sustainable livelihood.

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ETHNOBOTANY AND ECONOMIC BOTANY OF EPIPHYTES, LIANAS AND OTHER HOST-DEPENDENT PLANTS: AN OVERVIEW.

Epiphytes, lianas, and parasitic plants provide foods, fibers, medicines, and other materials for both traditional and modern societies. In a review of the ethnobotanical literature (particularly from the Neotropics), I found 776 useful species of these host-dependent vascular plants representing 363 genera and 70 families. These include widely employed taxa, such as vanilla (*Vanilla planifolia*) and passion fruit (*Passiflora edulis*), and others with significant regional importance, such as yoco (*Paullinia yoco*) and ayahuasca (*Banisteriopsis caapi*). Three of the most significant plants in northwestern Amazonia are lianas. Among the more important families containing host-dependent species are Araceae, Cucurbitaceae, Fabaceae, Orchidaceae, and Vitaceae.

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PLANT RESPONSES TO RESOURCE GRADIENTS AND MICROCLIMATE IN FOREST CANOPIES.

Trees typically maintain heliophilic, relatively expensive, desiccation-resistant foliage above and cheaper, less H₂O-retentive leaves capable of higher quantum yields lower in crowns in response to vertically graded supplies of photons and moisture. Often extensive, canopy-dependent flora, (the epiphytes), substantially increase this complexity with major, system-wide consequences in many frost-free, humid forests. Lacking access to soil, these plants face much more exaggerated environmental gradients

including some involving mineral nutrients. Accumulating data to be discussed indicates that this flora possesses a correspondingly greater range of resource-capturing and stress-avoiding mechanisms than the supporting trees, i.e., exhibit greater ecophysiological differentiation. These plants in turn provide diverse and abundant resources for much additional biota; by their ecophysiological variety and utilization of sometimes unusual resource bases, substantially augment important whole-system processes like productivity and nutrient stocking. Forest biodiversity is certainly increased by the overlay of epiphytic vegetation, but even more by the considerable fauna supported. Fuller appreciation of forest structure and function therefore mandates more information about the epiphytes, particularly their capacity to partition ecospace and support other biota in the humid tropical forest.

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CANOPY WALKWAYS IN TEMPERATE AND TROPICAL FORESTS: TECHNIQUES FOR THEIR DESIGN AND CONSTRUCTION

Walkways offer a permanent and relatively inexpensive method of access to forest canopies for long term and collaborative biological studies. A new concept in walkway construction was developed utilizing two modules (a bridge and a platform) that can be reiterated in different patterns to suit different sites and budgets. This modular construction has been successfully employed in several forest sites: temperate deciduous forests at Williams College (MA), Hampshire College (MA), Coweeta Hydrological Station (NC); and tropical evergreen rainforest in Blue Creek, Belize for the Jason Project.

We describe the relative costs, design features, and potential scientific opportunities of our modular walkway construction, and some of the canopy research currently underway utilizing these structures.

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THE FUNGAL COMMUNITY ASSOCIATED WITH NEOTROPICAL EPIPHYTE ROOTS.

During a survey of the fungi associated with epiphytic plants (Araceae, Bromeliaceae, Orchidaceae, Piperaceae and Polypodiaceae) native to La Selva Biological Station, Costa Rica, we made numerous isolations from surface sterilized roots. The Basidiomycotina was represented in the Orchidaceae by species of *Ceratrhiza*, *Geotrichopsis*, *Melanotus* and unidentified clamped hyphae. The Ascomycotina was represented by a large number of Fungi Imperfecti, including the Ingoldian aquatic *Tetracladium*, and a new species of *Acrogenospora*, in the Hyphomycetes. Numerous isolates of *Pestalotiopsis* and *Colletotrichum* species comprised the majority of the Coelomycetes recovered. The Xylariaceae and Nectriaceae were the major groups of Ascomycetes isolated. Recent work by Hedger, Lodge, Petrini and others has started to reveal the ecological importance of fungi in the canopies of tropical rainforests. Enumerating and analysing the components of the mycobiota in this habitat presents a major challenge as the taxa are mostly microscopic and require painstaking isolation procedures that introduce serious sampling bias to results. Our isolates represent a small part of the spectrum of the mycorrhizal, saprophytic and parasitic fungi that play important roles in sequestering, transforming and translocating nutrients among the primary producers in the epiphytic habitat.

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EFFECTS OF FOREST DEGRADATION ON FRUIT-FEEDING NYMPHALID BUTTERFLIES IN AN ECUADORIAN RAINFOREST.

In most lowland tropical-forest butterfly communities 25 to 30% of the species richness is accounted for by the taxonomically well known fruit-feeding nymphalids. A 12 month trapping study was undertaken to document the effects of habitat degradation on vertical distribution, species richness and abundance within and among habitats, seasonality, and habitat preference for fruit-feeding nymphalids. The study site comprised a 200 hectare section of forest in Amazonian Ecuador that ranged from old second growth to primary forest that was connected to larger tracts of intact forest. Preliminary analyses suggest that: a) species richness was non-asymptotic after 12 months of trapping in all habitat types; b) in contrast to Central America, species richness and abundance at the Ecuador site was highest in the understory; and c) species richness was lower within intact forest, and there were fewer species restricted to it. Finally, mark-release-recapture techniques suggested that many of the species considered live over six months; some species appear to move considerable distances during their life; others appear to reside in a small fraction of the forest without showing significant movements.

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CONSEQUENCES OF CANOPY ARCHITECTURE FOR ANIMAL COMMUNITIES AT TWO SPATIAL SCALES.

Canopy architecture has the potential to affect animal communities and interactions at several spatial scales. Data collected during a nine-month study of insectivorous *Anolis* lizards, their prey, and three habitats (foliage, crown airspace, gap airspace) in Puerto Rican rainforest canopy suggests two spatially complementary hypotheses: (1) At small scales, the distribution of hiding places as determined by arthropod habitat structure may determine the size distribution of arthropods and hence which size arthropods are preyed upon most by anoles. (2) At larger scales, the position of canopy relative to gaps may determine the dynamics of two-species communities of anoles. Steeper slopes in log-log regressions of arthropod abundance vs. body size for more open habitats combined with strongest responses to lizard removal shown by arthropods with the greatest total biomass support the small scale hypothesis. The spatial distribution of anole abundances relative to wind direction and gap location combined with the temporal dynamics of two-species anole communities support the second, larger scale hypothesis.

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A SAFE, FLEXIBLE AND NON-INVASIVE TECHNIQUE FOR CLIMBING TROPICAL TREES.

This technique, adapted from the aid-climbing methods practiced by rock climbers, provides an alternative to climbing with spikes or having to shoot a line from the ground over a limb high above. The technique is simple and easy to learn and, once practiced, can serve as an efficient and safe method to access the canopy of a large tree. Wearing a rock-climbing sit-harness, the climber ascends the trunk using an etrier in combination with a selection of nylon webbing slings and carabiners, pulling a climbing rope up at the same time. The technique is applicable to trunks up to about one and a half meters in diameter, or to heavy lianas growing on even larger trunks. These methods can be used not only to gain access to nearly any large tropical tree but also provide one with the ability to move about in that tree with relative safety and ease. The climber is always attached to the trunk or major limb of the tree by at least one nylon

webbing sling, so makes the climb in safety. With practice, a climber using this method can ascend from ground level to thirty or forty meters up in the forest canopy in an hour or less.

This technique has advantages over climbing with spikes in that trunks of larger diameter can be climbed and the trunk of the tree is left undamaged. It has the advantage over firing a line into the canopy in that time is not wasted untangling the fishing line of missed shots from frequently dense vegetation. More importantly, it avoids the possibility of the climbing rope being secured over an unsafe, rotting limb.

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USE OF LIGHTER-THAN-AIR VEHICLES FOR ACCESS TO THE UPPER CANOPY OF TROPICAL FORESTS.

In view of the importance of tropical forest canopies, strenuous technical efforts should be made to improve the methods of access available to scientists. One method is the use of lighter-than-air vehicles, i.e. airships, or powered balloons. If helium is used as the lifting gas, a small airship (of about 200-600 cu. metres in volume), can be powered by electric motors, to provide a quiet, mobile, platform for one/two scientists to explore the upper canopy. This aerial taxi system would be cheaper and quieter than the previous use of larger thermal (hot air) airships, ultralights and helicopters. A project is currently being initiated in Sabah, Malaysia, to fly a 400 cubic metre, electric powered airship to evaluate its usefulness for tropical forest studies. The limitations of the system, concerned with wind effects and maneuverability close to the canopy, will be carefully assessed.

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ARTHROPODS OF THE SUBCANOPY IN THE NEOTROPICAL FOREST.

Observations of tropical forest insect canopy collections indicate that discrete faunules of beetles are arrayed among microhabitats. Biodiversity is a function of the number of microhabitats in which evolution of small life forms might express itself. The number of microhabitats is a function of the number of habitats. The number of habitats is a function of latitude, altitude, soil types, and drainage patterns. Biodiversity should be greatest in equatorial lowlands with a complex and dynamic hydrological history. By surveying the quality and quantity of microhabitats within a forest type, the number of species occurring in a particular habitat could be estimated.

The insecticidal fogging technique was used to collect the beetles from the different microhabitats at Pakitza, Peru from 1988-1992. By constructing species accumulation curves for each family-level and trophic group in a microhabitat, the number of species can be estimated when an asymptote is reached on the curve. This type of collection and data analysis can be compared across microhabitats. By comparing microhabitats across several sites, estimating biodiversity can be made manageable.

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PHYSICAL MECHANISMS OF CANOPY-ATMOSPHERE EXCHANGE.

Micrometeorologists track the course of turbulent gusts that ventilate the canopy to estimate canopy-atmosphere exchanges of water vapor, heat, and CO₂. Meteorological techniques, inherently nonintrusive and amenable to automatic measurement, are useful to determine such important quantities as

whole-canopy water use efficiency, net carbon fixation, and pollutant deposition. Canopy researchers may be interested in the gusts themselves. It has long been recognized that turbulence is organized, with relatively large amounts of transport occurring in short periods of intense activity. For example, infrequent strong gusts may be essential for seed and pollen dispersal. We present observations of air motions and associated changes in microclimate to illustrate what these intermittent motions look like, how they are measured, and how they interact with the canopy physical structure. Examples drawn from observations of tropical, midlatitude and boreal forests illustrate the degree to which the canopy can isolate its interior from the ambient air above and how this isolation changes throughout the day and throughout the year. The types of air motions that occur in the canopy are shown to be related to the canopy air density profile, itself a reflection of the canopy biomass structure.

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CROWN STATUS OF TROPICAL TREES.

Trees that make up the canopy of tropical forests are assumed to be adult, i.e. capable of sexual reproduction, usually on an annual basis. There is an implicit assumption that each is contributing to the next generation roughly in proportion to its size, and size is usually measured as trunk or crown diameter. In a quick survey of trees with trunk diameter >30 cm in a mapped 50 ha plot on Barro Colorado Island in Panama, we found that only about 15% of these trees had completely intact crowns with no liana cover while at least 43% are either more than half smothered with lianas or have less than half of a full crown (regardless of crown diameter). Because unhealthy trees usually have little or no regular reproductive output, we suggest that (in static view) nearly half the trees in the forest may be non-contributors to the next generation and non-contributors to flower/fruit-feeding animals, even while they occupy considerable biomass in the forest ecosystem. From a forest-dynamics viewpoint this may be a temporary -- but long-term -- condition of an aging forest stand.

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THE EFFECTS OF PATHOGENS ON JUVENILE MORTALITY IN TROPICAL TREES.

Tree disease may be an important factor affecting the structure of tropical forests. When understory juveniles are susceptible to the same diseases that affect adult, canopy-sized trees, disease-related mortality of juveniles may affect the spatial pattern of recruitment of juveniles into larger size classes. In lowland tropical forests in Panama, some plant diseases are more severe in the understory than in the canopy, while others are not. In one example, a fungal canker disease of trees in the family Lauraceae on Barro Colorado Island is more severe on juveniles than on canopy-sized adults. Juvenile mortality is nearly always greater in cankered than healthy trees, and disease-related mortality is important in regulating the population dynamics and spatial distribution of susceptible species in this family.

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THE DISTRIBUTION OF PLANT FUNCTIONAL TYPES WITHIN AND BELOW A RAIN FOREST CANOPY.

An understanding of the comparative ecology of the rain forest canopy is limited by existing descriptive classification methods based on floristics and broad vegetation structure. A case study is presented that illustrates how a formalized set of plant functional attributes (PFA's) can be used to compare the functional (and hence dynamic) characteristics of canopy plants between geographically remote areas where the taxa may differ. It is argued that PFA's can be used to describe the rain forest canopy-to-ground profile as a compressed-environmental gradient that may be compared with more extensive eco-regional gradients from mesic to arid extremes.

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ECOLOGY OF FRAGMENTED CANOPY REMNANTS OF TROPICAL RAIN FOREST.

Soil exposed by deforestation prevents the establishment of rain forest plants, leaving these species restricted to remnant fragments of variable size. Rain forest trees isolated in pastures and crop-fields are a common landscape feature in Los Tuxtlas, Mexico, where pastures used for more than 20 years are still dotted with remnant trees. In 33 active pastures totalling 190 hectares, we found 74 rain forest species present as isolated trees. Average density was 3.3 isolated trees per pasture hectare (± 2.3 s.d.), with a great variability among pastures (range: 0.4 to 12.9 trees/ha).

Each isolated tree generates a "dark spot" in the pasture, which represents a "safe site" for the establishment of rain forest plants. Under the canopy of 50 isolated trees we found 105 rain forest species, which do not grow in open pasture sites. In addition, 59 species of epiphytes and hemiepiphytes were registered on 38 isolated trees. Although the canopy cover of these trees only accounts for 1.6% of pasture area, the effect on pasture heterogeneity is substantial. We assert that isolated trees are key elements for the management and conservation of rain forest biodiversity in highly fragmented landscapes such as those dedicated to cattle ranching.

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REPRODUCTIVE BIOLOGY OF SRI LANKAN DIPTEROCARPS.

Floral biology, pollination ecology and breeding systems of five, ecologically partially sympatric, endemic *Shorea* (section *Doona*) species were examined from canopy platforms in Sinharaja rain forest in Sri Lanka.

The canopy dominant species belonging to the local group *Thiniya* flowered annually while those of the *Beraliya* group were supra-annual. Flowering episodes among species were partially overlapping but sequential; however, within a given population of a species they were always synchronous. *Apis dorsata* and *A. cerana* were the principal pollinators of these fragrant, white-flowered species that open diurnally displaying bright yellow cylindrical anthers. Near synchrony in ripe fruitfall of the sequentially flowering edible beraliyas imply reduction in seed predation through predator saturation. Breeding

experiments reveal that all five species favor outcrossing to selfing. Floral biology and pollination ecology of the more speciose Sri Lankan *Shorea* (section *Doona*) are shown to be different from those of the corresponding congeners (section *Mutica*) of the aseasonal Malaysian rain forests.

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IMPACT OF BROWSING BY OKAPI, A LARGE MAMMALIAN FOLIVORE, ON CANOPY SEEDLINGS IN ITURI FOREST, ZAIRE.

Herbivory by large mammals has been ascribed a dominant role in vegetation dynamics in temperate and savanna ecosystems. The okapi, a forest giraffe, is a prominent large herbivore in the closed, moist semi-evergreen forests of eastern Zaire. Treefall gaps are preferred foraging habitats for okapi. Gaps are also a scarce regeneration site for some canopy species. Exclosure experiments and plantings in recent blowdowns were used to determine whether large mammal browsing limits establishment of seedlings (< 1.5 m height) of four uncommon heliophilic successional species and one shade-tolerant canopy dominant. All species were browsed by okapi, but three of the four heliophiles were preferred. Seedlings on plots protected from okapi were browsed by insects and small mammals. As a result there was no difference in browsing pressure in and out of exclosures. Rapidly growing heliophile seedlings were more likely to be browsed by any herbivore than were shaded individuals. Successful establishment of heliophile seedlings is likely due to the interaction of shade and browsing pressure.

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LATERAL SHADING AND THE DIFFERENTIAL INTERCEPTION OF ANGULAR DIRECT-BEAM RADIATION AMONG NEIGHBORING TROPICAL RAINFOREST CANOPY TREES.

Non-diffuse direct-beam solar radiation is a critically important resource in closed-canopy tropical rainforests. The competitive advantage of shading is most commonly considered in the form of subcanopy light attenuation. The objective of this study was to quantify lateral shading of angular direct-beam radiation among neighboring canopy trees as a function of changing sun position, and then consider its effects on long-term patterns of canopy tree growth and turnover. The study involved (1) three-dimensional modeling of a tropical rainforest canopy in northeast Queensland, Australia using photogrammetric data derived from aerial stereopairs taken from a low-flying aircraft in 1976; (2) applying a ray-tracing program to the 3-D model to simulate lateral shading for the seasonal daily courses of solar zenith angle and solar azimuth at the site; (3) computing the direct-beam radiation totals intercepted by >500 neighboring canopy trees on the basis of a modified parameterization model and field-based measurements of radiation inputs to a tower positioned above the canopy; (4) using the intercepted direct-beam totals to define each tree's survivorship probability and growth potential; and (5) analyzing the predicted changes in relation to the changes observed in stereopairs taken of the same canopy in an overflight sequence 18 years later in 1994. The finding of significant differences in direct-beam radiation intercepted by neighboring trees was considered in relation to the hypothesis that canopy trees subject to lateral shading may be the most susceptible to windthrow and toppling because of their tendency to develop asymmetric crowns characterized by uneven weight distributions.

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CANOPY BIOLOGY PROGRAM IN SARAWAK.

Mixed dipterocarp forests in Sarawak are the richest tropical rainforests with quite high species diversity of trees, although environmental conditions there change greatly in an unpredictable manner. In March 1993 we constructed the canopy observation system that is comprised of two tree towers of heights > 50 m and walkways of a total length of 300 m in Lambir Hills National Park. Using this system, we started the long-term monitoring of plant phenology and insect population dynamics and the study of interaction between plants and animals in plant reproduction. We clarify pollination syndromes at a community level and find importance of bees and beetles in this region and study effects of pollinators' foraging behavior on genetic structures of plants by microsatellite DNA. We also find clear distribution patterns of insects in the canopy vertical structure and their seasonal patterns. We will show that simultaneous studies of both plants and animals greatly increase information to understand each side and that mutualistic interactions that are allocated at different canopy layers and in different seasons are the important mechanisms to maintain high biodiversity of both sides.

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WHY DO TROPICAL AMERICAN RAIN FORESTS HAVE MORE LARGE FLOWERS THAN TROPICAL AUSTRALIAN RAIN FORESTS? - A VISUAL TOUR OF AUSTRALIAN FLORA.

Comparisons of canopy-flower size, major canopy-pollinators and major canopy-tree species in tropical American and tropical Australian rain forests, reveal striking differences.

In French Guyana, 16.9% of canopy-tree flowers (n = 236) were rated as large as against 7.8% in north Queensland (n = 544). Medium- to large-size bees are major pollinators in tropical America whereas flies and beetles are prominent in tropical Australia. Differences in pollinating guilds are associated with differences in canopy-tree families. In much of tropical America, the three legume families tend to dominate the canopy spectrum in terms of species whereas in Australia, Myrtaceae and Lauraceae dominate.

Evolutionary trends suggest a tendency for a greater presence of larger and more visually conspicuous flowers, together with shorter flower-life in tropical American forests as against the Australian tropical forests where the conspicuous, individual-flower display seems less important to attract the major suite of pollinators.

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PHYSIOLOGICAL DIVERSITY AMONG SHADE-TOLERANT SPECIES.

From a physiological perspective, rainforest trees are distinguished as either gap-requiring or shade-tolerant. Most of the species and most of the individuals are shade-tolerant, but physiological differences among shade-tolerant species have received little attention. We have analyzed a variety of physiological responses among shade-tolerant trees with short-lived and long-lived leaves. In many species, chloroplast development is delayed until the end of leaf expansion, a pattern that we term delayed greening, whereas other species have normal greening. In mature leaves, induction of photosynthesis is significantly more rapid in species with short-lived leaves. In a comparison of acclimation to light-gap conditions of two species, we found no substantial differences in physiology, although the species with short-lived leaves had

much faster leaf production rates than the species with long-lived leaves. Minor differences were found for light-saturated photosynthetic rates. During an unusually stressful dry season, the species with long-lived leaves experienced little stress whereas the species with short-lived leaves experience severe water stress. Differences in osmotic potential, susceptibility to cavitation and root pressure also were observed. In summary, we have found substantial physiological differentiation among shade-tolerant plants suggesting that physiological differences may explain, in part, the high diversity of woody, rainforest plants. Furthermore, some characteristics, such as delayed greening, may be adaptive for shaded saplings but not for canopy adults.

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STRANGLER FIG SEEDLING ESTABLISHMENT IN THE RAIN FOREST CANOPY OF BORNEO - IMPLICATIONS FOR THE MAINTENANCE OF *FICUS* SPECIES DIVERSITY.

Factors affecting the establishment of strangler figs (*Ficus* spp. in subgenus *Urostigma*) on host trees were studied in lowland mixed dipterocarp forest in Gunung Palung National Park, West Kalimantan, Indonesian Borneo. A survey of figs with roots to the ground revealed highly significant differences between some sympatric fig species in establishment site height, canopy level occupied, and host taxa, suggesting that fig species are specialized for specific canopy microenvironments. Forty-five dipterocarps climbed with single rope technique were used as experimental sites to study *Ficus stipenda* germination and establishment in natural sites and artificial planters in the canopy. The presence of substrate with good moisture retention (soil, rotting wood, moss) was the most important factor for germination. Successful establishment was extremely rare, with only 0.04% of 6720 seeds planted in natural sites showing steady growth after 12 months. Knot holes were the best establishment sites, but occurred at a frequency of less than one per tree. Water stress was the most critical factor for seedling growth in the canopy. Additional mortality factors included herbivory and seed harvesting by a newly discovered species of arboreal *Pheidole* ant present in 24% of trees surveyed. Based on seed rain measurements around fruiting fig trees, the probability of seeds hitting safe sites in the canopy was calculated to be very low. Several factors were thus identified that help explain the rarity of strangler figs in contrast to the number of potential host trees in the rain forest. Numerous fig species appear to coexist with little interaction, each limited in abundance by the various constraints on successful seedling establishment. This could help to explain the maintenance of species diversity in the genus *Ficus*.

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RAIN FOREST CANOPY LARGE SCALE MAPPING: TECHNIQUES, APPLICATIONS AND PROSPECTS.

The markedly high variability and complexity of the rain forest canopy hamper our understanding of how to interpret patterns on broad scales (e.g., remote sensing) in terms of processes operating on finer scales (e.g. forest patches, tree crowns, branching patterns). Either floristically, structurally, or in term of dynamics, research work dealing with such spatial heterogeneity emphasizes the need for a refined cartographical representation of the canopy ecosystems and the development of monitoring procedures.

Large scale ground-based and aerial mapping techniques are presented and applications are discussed on the strength of results obtained so far in SE Asia and Africa. They emphasize the importance of detailed base maps of the canopy that could be useful tools in studies undertaken by other canopy researchers. Relief maps ease establishment of sampling design for biological or physical measurements that themselves lead to the production of ecological maps. Drawn up in parallel with biodiversity inventory

and distribution maps, these data are easily integrated within a geographic information system, allowing further modeling.

The complexity of interactions between the forest and its physical environment make tentative correlations with spectral reflectance variation still not fully understood at such large scale. The high spatio-temporal variability of structural and functional parameters observed in the fine-scale forest patterns make extrapolation to larger areas or smaller scales difficult. Much more research on how patterns and processes at one spatial scale affect those at other scales is highly desirable for models involving tropical rain forest functioning and remote sensing techniques. Specific mapping methods adapted to the dynamic nature of the canopy have still to be developed and applied.

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THE POPULATION BIOLOGY OF HEMIEPIPHYTES.

Hemiepiphytes are epiphytic plants with connections to the ground, and shrubby or tree-like crowns anchored to particular spots on their hosts. Hemiepiphytes vary in growth forms (pendent, scandent, shelf-like, erect forms), impact upon their hosts (from lethal to relatively benign), and degree of dependence upon hosts (obligately, facultative, and accidental). In this presentation we focus on issues such as: the uneven distribution of hemiepiphytes within a region and microenvironmental conditions; the abundance of accidental and facultative epiphytes in tropical montane and lower montane forests and the evolution of epiphytism; the importance of metamorphic transitions in the root system; host specificity; and the hemiepiphytic role in canopy structure, and disturbance in the canopy. We also discuss the very little knowledge about population biology (life cycles, seed dispersal and establishment sites, safe sites, vegetative propagation and fusion), and the lack of information on hemiepiphyte population structure and demography, growth rates or at least the rates of transition among life history stages, and patterns of spatial distribution.

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SPECIES RICHNESS OF ANTS (FORMICIDAE) IN A TROPICAL FOREST CANOPY, USING INSECTICIDAL FOGGING AND RICHNESS ESTIMATION PROCEDURES.

Ants are the dominant arthropods in tropical forest canopies, but patterns of diversity are poorly known. The diversity of the canopy ant community was examined in Costa Rican lowland rainforest, using insecticidal fogging. eighteen trees were fogged: six *Pentaclethra macroloba*, six *Virola koschnyi*, and six trees each from a different family. The third treatment was to test host specificity, with the expectation that the community sampled from diverse trees would be richer than that sampled from a single species of tree. The species accumulation curve for the combined sample of 18 trees was a convex curve approaching an asymptote. A total of 137 species were observed, 12 of which were known to be "accidentals," species common in adjacent microhabitats (e.g., forest floor). A variety of species-richness estimators were examined. Chao2 estimates of species richness were 160 and 137 species for samples with and without accidentals, respectively, revealing the sensitivity of richness estimates to accidentals. Separate richness estimates for the six samples from *Pentaclethra* and the six samples from diverse trees were similar: 84 and 92 species, respectively. In contrast, the richness estimate for the six *Virola* samples was 134 species, approaching the community total. Possible explanations for this pattern and the implications for sampling canopy ant communities are discussed.

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ATMOSPHERIC DEPOSITION AND FOREST CANOPY STRUCTURE.

Wet, dry and cloud water deposition all contribute to the total atmospheric deposition to a forest. While the canopy has little influence on the amount of wet deposition it receives (at least on a local scale), the structure and physiology of the canopy can strongly influence the rate of dry and cloud water deposition. Atmospheric deposition is related to total canopy surface area in a nonlinear fashion, and the spatial arrangement of canopy structural elements influences both the amount and distribution of deposition. Efficiently depositing species like cloud droplets and nitric acid vapor show very strong vertical profiles in a forest, while fine particulate material shows almost no vertical variation. Models and measurements have provided a reasonable understanding of the vertical distribution of deposition within a forest, but the lateral variation remains poorly understood and beyond the capabilities of current models. Recent studies suggest that lateral variation is very significant at the tree, stand, and landscape scales, such that neighboring trees and adjacent stands may experience very different rates of deposition. Gaps and edges are extremely important features governing the lateral variation in deposition rates.

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TEMPORAL AND SPATIAL VARIABILITY IN HERBIVORY BETWEEN NEOTROPICAL AND PALEOTROPICAL RAIN FOREST CANOPIES.

Long-term measurements of herbivory in the canopies of rain forest trees were compared between two continents. A construction crane was used to monitor defoliation of seven tree species at one site near Panama City, Panama; and single rope techniques in conjunction with a canopy walkway system were used to measure foliage removal on five species in three sites at New South Wales and Queensland, Australia. In total, over 3000 leaves were monitored within the canopy community on each continent. Spatial variability in herbivory was examined both vertically within a crown and horizontally throughout a forest stand. Temporal analyses were completed for one-, four-, and nine-month cumulative periods (and up to 12 yrs for Australian leaves). Although data collection is still underway, we define the sampling protocols used in our comparative studies after one year. Leaf consumption was highest on young leaves, shade leaves, and soft-leaved species. Herbivory in rain forest canopies ranged from 3% to as high as 42% annual foliage removal for different species. We report elements of variability in sampling that may affect comparative studies and suggest ways to minimize these possible artifacts. The spatial and temporal variation of herbivory may have profound effects on the maintenance of tree-species diversity in rain forest canopies.

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DIVERSITY AND DISTRIBUTION OF *GUZMANIA* (BROMELIACEAE) IN ANDEAN SOUTH AMERICA.

Guzmania sensu lato is a genus of more than 170 species with a center of diversity in NW South America. Most species are found as epiphytes in wet forests, at elevations of 700 to 2000 meters. Observations of pollination are uncommon but the genus appears primarily ornithophilous ("hot" colors, tubular corollas). However, numerous night-flowering, presumably chiropterophilous, taxa are known. Many species of *Guzmania* may be sympatric at very favorable sites. Natural hybrids are known but are not common. The genus contains many narrow endemics as well as widespread taxa.

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THE THREE-DIMENSIONAL STRUCTURE OF AMAZON AND CONGO BASIN SMALL MAMMAL COMMUNITIES.

Virtually no data exist on the vertical distribution of small mammals in tropical rainforests. We used indigenous climbing methods and a simple pulley system to intensively census the canopy fauna at several primary forest sites. These included an upland forest site in the central Amazon, several upland and floodplain forest sites in the western Amazon, and a site in the northern Congo basin. At each site, canopy-based trapping revealed one or more strictly arboreal taxa. The overall degree of arboreality of component small mammal species was quantified by calculating for each taxon the proportion of the total captures that occurred in the canopy vs. on the ground. All forests showed a markedly bimodal pattern of arboreality; most species were trapped in the canopy or on the ground, but not at both heights. Approximately 95% of the taxa captured had greater than 75% of their captures recorded at one height or the other. Canopy-dwelling species were most prevalent in the central Amazon (approximately one-half of the species pool) and were least prevalent in the Congo forest (approximately 20% of the species pool). In each forest, one or two species were numerically dominant, i.e. they were considerably more common than any other species. A numerically dominant taxon was present both in the canopy and on the ground at the Congo site, but occurred only on the ground in the western Amazon and only in the canopy in the central Amazon. Ecological factors contributing to the vertical distribution of small mammal diversity and abundance are discussed.

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IMPORTANCE OF TISSUE CULTURE TECHNIQUE FOR CONSERVATION OF ENDANGERED BRAZILIAN BROMELIADS FROM ATLANTIC FOREST CANOPY

The epiphyte tank bromeliads *Vriesea fosteriana* and *V. hieroglyphica*, native from S.E. Brazil, are endangered by deforestation and harvesting as an ornamental. Tissue culture technique substantially increases the multiplication rate of these plants essential to any replacement program and to conserve some bromeliad populations from Atlantic Forest (Espírito Santo and São Paulo States). In vitro seed germination of *V. hieroglyphica* can be used as a tool in obtaining a large quantity of seedlings from embryos that would normally have produced only one plant.

Particularly for *V. fosteriana* the in vitro culture of young leaves resulted in a large number of new leafy shoots which can be easily separated and rooted. Mutants were not observed. The best levels of growth regulators were analyzed for each species. Efforts to conserve endangered bromeliads require knowledge of efficient methods for propagation as described in this work.

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EXPLORING FOR PLANT DIVERSITY IN THE CANOPY OF A FRENCH GUIANAN FOREST.

Although many methods are now employed for inventorying the diversity and studying the ecology of the rain forest canopy, climbing with the aid of French tree spikes has been highly effective for documenting the vascular plant diversity of a forest in central French Guiana. Botanical exploration of this forest would have been incomplete without exploring the canopy because 64% of the vascular plant species are efficiently collected only

from above the ground. More complicated climbing methods (e.g., ropes, balloons, cranes, walkways, miniature helicopters, etc.) are too expensive and not mobile enough to allow for complete botanical inventory within the budgets and time available for most floristic studies. Although the use of spikes for the collection of botanical specimens does some damage to trees, tree mortality is probably low. The slightly increased mortality adds little to the already high turnover time of lowland tropical forests and consequently is expected to have no negative impact on plant and animal diversity.

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PLANT PHENOLOGY AND ALLOCATION IN RESPONSE TO SEASONAL AND VERTICAL LIGHT GRADIENTS IN THE UPPER CANOPY OF A TROPICAL DRY FOREST.

Spatial and seasonal variation in light and functional leaf characters were studied in the canopies of seven species of trees over two years in a dry tropical forest near Panama City, Panama. Access to the upper canopy was with a 42 m tall construction crane with a boom with 50 m radius. Light gradients in the canopies of the tallest trees were very steep, with up to two orders of magnitude decrease in irradiance from the outside to 1 m inside the canopy. Generally, irradiance decreased with decreasing height above the ground. Diffuse light was higher than in the canopy and subcanopy immediately beneath the canopies of emergent trees. Irradiance was lowest beneath vines occupying gap openings. Across all species, leaf nitrogen concentration, construction cost, mass per area, and assimilation capacity scaled linearly with leaf longevity. When early successional species were excluded, the relationship among functional characters was more closely related to season of leaf production and light availability than to leaf longevity. Variation in functional characters across seasons and light environments was more continuous than discrete for each species.

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MATING PATTERNS AND GENETIC STRUCTURE IN TROPICAL TREES.

A growing body of evidence suggests that although outcrossing predominates in many canopy tree species, inbreeding can be extensive, especially in populations that are low in density or that have been thinned (e.g. selectively logged). Comparisons of age/size classes reveal that inbreeding, depression and heterotic selection are important in maintaining genetic diversity within populations of most of the species examined. The implications of these results will be discussed in relation to conservation management.

NADKARNI*, N., The Evergreen State College, Olympia, WA; COXSON, D., University of Northern British Columbia, Prince George, BC, CANADA; CLARK, K., University of Florida, Gainesville, FL; SCHAEFER, D., University of Puerto Rico, San Juan, PR.

NUTRIENT CYCLING IN MONTANE CLOUD FOREST CANOPIES: WHAT WE KNOW AND WHAT WE NEED TO INVESTIGATE.

Studies on the role of forest canopy components in nutrient cycling have documented that epiphyte biomass is often small relative to total ecosystem pools, but can exceed host-tree foliage. Because of their physiology and their location at the atmosphere-vegetation interface, epiphytes can enhance the interception

and retention of wet and dry deposition (especially cloud water), transform gaseous sources to available forms of nutrients (via fixation) and reduce mobile nutrient loss by the suppression of certain microbial processes (e.g., nitrification). We propose research directions of the highest priority: 1) learn how to scale up from within-tree to ecosystem- and landscape-level spatial scales by developing sound statistical techniques; 2) establish long-term studies of forest canopy dynamics using experimental approaches; and 3) initiate simultaneous studies in a wide range of forest types with harmonized techniques to generate a comparable pool of data.

NADKARNI*, N., The Evergreen State College, Olympia, WA; PARKER, G. G., Smithsonian Environmental Research Center, Edgewater, MD; CLEMENT, J., The Canopy Institute, Olympia, WA; McCONNELL, M., Museum of Science, Boston, MA.

INITIATION OF AN INTERNATIONAL CANOPY NETWORK: DISCUSSION ON INTERDISCIPLINARY AND INTERCONTINENTAL LINKS TO ENHANCE FOREST CANOPY RESEARCH, EDUCATION, AND CONSERVATION.

The burgeoning scientific interest in forest canopies is evidenced by increasing numbers of scientific publications, the growing array of canopy access techniques (e.g., tower cranes), and creation of pathways to enhance communication among subgroups of canopy scientists (e.g., Canopy Research Network electronic mail bulletin board). Recent educational activities have also been created to inform the general public of the importance of canopy organisms and interactions (e.g., JASON canopy project in Belize). These research and educational efforts could be combined to provide a powerful tool for conservation of forests ecosystems and to push forward our understanding of forest canopies. However, no central center or organization now exists to store and process canopy information, serve an advocacy role, or facilitate communication among the many fields canopy science encompasses. This discussion will open a dialogue to initiate a formal canopy organization.

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CLIMBING TO THE CANOPY, A MIXTURE OF ARBORIST, CLIMBER AND CAVER METHODS.

This session will be targeted at the beginner research/climber. Demonstrations will include the following:

- I. INSTALLING YOUR ROPE IN A TREE.
 - (A) Wrist Rocket (B) Throwing Ball (C) Pole (D) Ape Climbing
- II. CLIMBING TECHNIQUES
 - (A) Taut Line Hitch (B) Rope Walking (C) Butt Strap Harness (D) Jumars and Atriers.
- III. DESCENDING TECHNIQUES
 - (A) Figure 8 Rappel (B) Taut Line Hitch Rappel (C) Down Climbing with Ascenders.

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CONSERVATION OF EPIPHYTES ON THE YUCATAN PENINSULA.

About 100 epiphytes of the Orchidaceae, Bromeliaceae, Cactaceae, Araceae, Piperaceae and several ferns occupy the canopy and tree trunks of the various tropical forests of the Yucatan Peninsula. We have established the geographic distributions of these epiphytes, and at the same time we classified them by habitat type: tall rainforest, semi-evergreen, subdeciduous, deciduous, and inundated forests, as well as mangroves. The number of epiphyte species varies among forests. The low-statured inundated forests, unique to the peninsula and the least disturbed, are home to about 45% of the epiphyte species. The destruction of the epiphyte habitats through deforestation and various developments as well as overcollection of some species have made conservation ever more necessary.

The many types of perturbations of the tropical forests occur at different rates. With more than 50% of the original forest gone, the Peninsula's natural areas, which number an impressive eight, will give some protection to the epiphytes. We will discuss the population status of about 50% of the species studied, the conservation of the different forests and their canopies and their importance to the survival of the epiphytic species, the recolonization aspects of the disturbed forests, and some conservation measures involving the government agencies, research institutions, the populace at large and campesinos.

PARKER, G. G., Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037.

CANOPY ACCESS WITH CONSTRUCTION CRANES.

Construction cranes can be effective tools for forest canopy research, particularly for reaching the formerly inaccessible outer canopy. They are most appropriate for prolonged, intensive study of areas on the scale of hectares. Cranes can provide truly three-dimensional mobility throughout large volumes of canopy space, restricted only by the presence of large limbs and branches. Heavy loads of people, equipment, and instruments can be hoisted and kept securely on station for taking samples, making measurements, and servicing experiments. Many kinds of cranes with various configurations and coverage geometries are suitable for a variety of access needs. For example, tower cranes, with jibs completely above the forest, provide low-impact access from above and are useful for studies in wide areas of the outer canopy. Truck-mounted hydraulic cranes, with jibs angling through the crowns, are suitable for access from roads or forest edges.

PARKER, G. G., Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037.

STRUCTURE AND MICROCLIMATE OF FOREST CANOPIES.

Canopy structure influences atmospheric exchanges of material and energy, the environment within forests, and the habitats of canopy organisms. I review general structural features and microclimates of closed forests and examine how structure influences forest environment. Some trends in studies of canopy climate are considered. First, canopy structure is not uniformly measured: structural comparisons between forests are difficult to make. Next, observations of forest microclimate often focus on mean values (usually at few locations and slow time scales); thus, ecologically meaningful variation is difficult to assess. More studies are needed on transitional environments (e.g., edges), transient regions (light gaps), and zones with wide environmental fluctuations (the outer canopy). Finally, studies in stands of simple structure have produced useful models of canopy interactions (e.g., for the interception of radiation, momentum, and

precipitation). Now, more attention is needed to non-ideal situations: mixed-species forests, multiple-cohort stands, forests in fragmented landscapes, and those with deciduous seasons.

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INTEGRATIVE CANOPY METHODS - THE FUTURE OF THE RAFT/DIRIGIBLE.

Appropriate techniques are required for a pluridisciplinary and a multi-scale approach of the canopy so that several levels of organization of the system can be handled simultaneously. A brief history of the development of our method is followed by a presentation of the future of the Raft/dirigible. Canopy access techniques available today do not duplicate each other; they are all reliable and have different advantages and disadvantages. In one such technique, the 'Treetop Raft' uses a combination of three components: a hot air dirigible, a stationary platform (Raft) and a suspended platform (Skimmer or Sled). Each device has its own functions, but can serve different purposes when combined with another. As equipment in its own right or as tools for the development of other methods of ecological analysis, the 'Treetop Raft' is an adaptive system whose many functions can evolve according to scientific requirements, thus making use of the system's extreme versatility.

The originality of the Treetop Raft technique lies in its mobility. It is also the only apparatus designed to be moved not only from one site to another in the same area of forest but also from one country to another. It could thus be used in combination with other types of access to canopy (fixed, or difficult to move), or reserved for long-term research programs on a specific site.

Combined with the advantages of other permanent methods of access (crane, walkway, tower), integrative and comparative methods could be developed enabling comparison between canopy research sites, research on large areas of forest, and then intercontinental comparison.

PERRY, DONALD R., Rainforest Aerial Tram, COSTA RICA.

ECOTOURISM AND ITS POTENTIAL IMPACT ON THE COSTA RICAN RAINFOREST CANOPY.

The Rainforest Aerial Tram is a synergistic relationship between Research, Education and Tourism. The centerpiece of this facility is a 1.3 kilometer-long lift system. Twenty cars carrying up to six people each will ride the 2.6 kilometer cable loop traveling low through the forest on the outbound leg and through the canopy on the return. The project owns 420 hectares of private nature preserve that shares a 3.5 kilometer border with Braulio Carrillo National Park. The site is fifty minutes by car from San Jose, the capital of Costa Rica. The transect begins in secondary forest that quickly turns into rich mid-elevation rainforest (400-500 meters elevation). Subjective estimates suggest the site possesses one of the richest canopy communities in Costa Rica. We are establishing a research center that will focus on canopy biology with an emphasis on nocturnal and diurnal studies, designed to include visitor participation. Our objective is to promote both local and international appreciation for the beauty and complexity of the tropical forest ecosystem. Since the canopy needs large trees for its full expression, education will be aimed at forest preservation. It will stress the growing danger that many projects promote logging under the guise of "sustained development": a practice that threatens to destroy the most complex communities of life on our planet.

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TREE FATES IN VINE TANGLES

Vine tangles in forests may persist for decades but are eventually overtopped by trees. Among trees that are not protected by ants, the likelihood of surmounting crown-covering vines seems to depend to a great degree on chance but a variety of architectural and physiological characteristics influence tree fates. Many vine-surmounting trees display rapid extension growth of orthotropic shoots bearing large leaves and a pronounced capacity to form carpets over tree crowns; differences in vine climbing habits and leaf display patterns influence the characteristics of trees capable of growing up through vine tangles.

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REMOTE SENSING OF FOREST CANOPIES.

Remote sensing provides information about forest canopies through a sensor signal resulting from the interactions of electromagnetic energy with canopy components. There are currently many different types of remote sensing devices that utilize various regions of the electromagnetic spectrum over a range of spatial scales. These devices range from field instruments that measure scattered or emitted radiation from a single leaf to Earth orbiting sensors that record images of entire continents.

The canopy structure information provided by remote sensing devices is dependent on the frequency, as well as the spatial resolution used. For example, visible light is readily absorbed by leaves and so gives information about the upper portion of the canopy which is useful for forest type identification. Near-infrared light, on the other hand, is scattered down into and back out of the canopy and is more sensitive to leaf area. Active microwave sensors have the ability to penetrate deeper into forest canopies and have been shown to be sensitive to above ground biomass.

The objective of this presentation is to provide an overview of how remote sensing can be used to assess forest structure at the canopy, stand and landscape levels. Remote sensing images from passive (e.g., optical multispectral imagers) and active (e.g., synthetic aperture radar) sensors will be presented and discussed. Understanding of the structural information present in a remote sensing image can be gained using models of the energy interactions within, and external to, the vegetation canopy. Models that simulate the scattering of optical and microwave energy will also be briefly discussed with regard to the abstraction of canopy structure.

REAGAN, DOUG, Woodward-Clyde Consultants, 4582 S. Ulster St, Denver, CO 80237, and the Terrestrial Ecology Division, University of Puerto Rico, Rio Piedras, PR.

THE EFFECT OF HURRICANE SEVERITY ON CANOPY LIZARD POPULATIONS IN A PUERTO RICAN RAIN FOREST.

The anoline lizard, *Anolis stratulus*, inhabits the canopy of mature tabonuco forest in Puerto Rico at population densities of 21,000-25,000 individuals/ha. These high densities are due, in part, to the fact that individuals occupy small, ellipsoidal home ranges 6-7 m in diameter layered within the 10-14 m thick canopy. When the eye of Hurricane Hugo passed near the Luquillo Mountains of eastern Puerto Rico on 18 September 1989, forests on northern slopes received the full force of the winds, but eastern and southern slopes were partially protected. I conducted surveys to estimate relative abundance and minimum density of lizards and to estimate anole densities at severely affected (Bisley) and less affected (El Verde) sites in tabonuco forest. Surveys were conducted one month following Hurricane Hugo and annually thereafter for

five years. Initial effects were similar at both sites; vertical habitat structure was compressed from 24+ m to 3± m, and *A. stratulus* densities increased at ground level at both sites. Within the first year, *A. stratulus* had re-invaded the closed canopy at El Verde and the regenerating canopy at Bisley. Five years following Hurricane Hugo, the canopy at Bisley was still not closed, and the population density of *A. stratulus* remained below pre-hurricane levels.

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TEMPERATE RAINFOREST CANOPY ACCESS SYSTEMS IN BRITISH COLUMBIA.

Although we now know that forests are among the most important global ecosystems, we do not yet fully understand their complexity. This is particularly true of the coastal, temperate, old-growth rainforests of the Pacific Northwest.

Ecological processes within the canopy and forest floor of old-growth forests in British Columbia are virtually unknown. In B.C. we have, at present, three old-growth forest research sites, each complete with a canopy access system; another is in the planning stages. The first site is in an old-growth Sitka spruce/western hemlock forest in the Upper Carmanah Valley and has already yielded fascinating results over the last three years. The second was recently established in old-growth Douglas fir on southern Vancouver Island on land adjacent to Pearson College of the Pacific, generously donated by the Department of National Defence. Less than 0.5% of this unique dry coastal Douglas fir habitat remains on the southern tip of Vancouver Island. The third was built (April, 1994) on the property of Bamfield Marine Station in an old-growth western red cedar forest community. The fourth is planned for the wet, coastal Douglas fir of the Megin River Watershed. This area is part of the Long Beach Model Forest in Clayoquot Sound, B.C.

This network of canopy access systems is aimed at assisting Canada in reaching one of its national goals, the conservation of biological diversity -- a national commitment since 28 December 1993, when the Rio Convention on Biodiversity came into effect. The possibilities for future, collaborative projects on temperate rainforest canopy research will be discussed.

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THE RAINFOREST CANOPY: A FRONTIER OF EXPLORATION FOR HIGH SCHOOL STUDENTS.

Until recently, the tropical rainforest canopy has been inaccessible to all but the most courageous biologists. Now there are methods for entering the treetops that make such studies easier not only for scientists but also for educators and students who recognize the need for experience in this species-rich ecosystem. There is a growing need for a canopy curriculum for young people, especially for secondary-school students who have both the pluck and the ingenuous enthusiasm for this type of work. Rainforested regions harbor the majority of the planet's biodiversity and much of its productive tissue and, consequently, warrant coverage in science curricula. A detailed curriculum is underway that emphasizes the rainforest canopy as a frontier of exploration for high-school students, and important parts of the project will be presented in this paper for audience review and discussion. Direct and indirect access techniques, examples of research projects, and relevant texts and periodicals will be included.

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SOLUTION CHEMISTRY IN FOREST CANOPIES.

Forest canopies receive water and chemicals from the atmosphere through gas-, liquid-, and solid-phase deposition processes. Uptake, release, and transformations occur within the canopy before transfer to the forest floor. Deposition of water and nutrients can have positive effects on canopy biota by increasing humidity and fertility. Conversely, strong acids, oxidants, and other toxins can have negative effects by stripping cations, altering plant carbon allocation patterns, and damaging living tissues. But forest canopies are not passive receptors of atmospheric inputs. Canopy fertilization increases growth and thus deposition. This leads to positive and negative feedbacks, depending on the nature of the deposited materials. Because of surface area and growth rates, canopy biota respond to peaks in atmospheric inputs. Water is stored, and nutrient pulses are converted to slowly-decomposing organic matter. Similarly, harmful inputs often affect the canopy first. Nitrogen fixation by canopy epiphytes is a unique example of fertilization, as it is directly available only with specialized microbial associations. Nitrogen fixers also require other nutrients not abundant in atmospheric deposition. Those nutrients are derived from the decomposition of terrestrially-rooted plant material in the canopy, leading to nutritional interdependencies. Interactions between forest canopies and their chemical environments will be illustrated with tropical and temperate examples.

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CANOPY INVERTEBRATE COMMUNITIES AND HERBIVORY IN TEMPERATE AND TROPICAL FORESTS.

Arboreal invertebrates contribute to forest canopy structure and function by affecting foliage surface area and nutrient turnover. Many invertebrates respond rapidly and dramatically to environmental changes, making these organisms useful indicators of forest conditions and moderators of ecosystem processes, such as primary productivity and nutrient cycling. I sampled canopy communities in disturbed and undisturbed plots at the H.J. Andrews Experimental Forest in western Oregon (temperate wet forest), Coweeta Hydrologic Lab in North Carolina (temperate wet forest) and the Luquillo Experimental Forest in Puerto Rico (tropical wet forest) to assess responses to disturbance. Canopy communities in regenerating forests at all three sites showed significantly elevated abundances of sap-sucking arthropods, whereas communities in undisturbed forests showed greater abundances of foliage-chewing arthropods, predators and detritivores. Foliage losses to chewing herbivores was low (<10%) at all three sites and appeared to be related to tree species abundance, perhaps interacting with unmeasured chemical characteristics. Ancillary studies indicated significant effects of herbivory on canopy hydrology and nutrient cycling processes.

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INSECTS IN TEMPERATE FOREST CANOPIES: WHAT'S UP?

Studies of temperate forest canopy insects have tended to focus on population dynamics of a few economically important species, with less work on community-level phenomena. Seasonality influences pattern and process in temperate forests very strongly, and has been a major research focus. Temperate canopy insect communities (especially among Lepidoptera) often comprise suites of species having discrete life histories and other traits providing alternative means of dealing with a rapidly changing environment. Herbivorous insect species influence each other in both negative and positive fashion, and natural enemies are implicated as important numerical and selective influences on canopy herbivores. Recent work

indicates that the influence of these factors cannot be identified in isolation: plant quality, seasonality, and natural enemies all interact to determine insect densities and community structure.

The number of forests in which insect communities are characterized is so small as to make generalization difficult. No study has been replicated at the forest or ecosystem level, and many studies are totally unreplicated and of dubious statistical value. This situation is marginally better than that for tropical forests, in which singular observations and natural history anecdotes dominate. Canopy biology will not become a "mature" discipline until it progresses beyond observation and biotic survey to the use of replicated sampling and experimental designs and a greater focus on experimental studies of processes. Improved canopy access is needed for this to happen.

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STUDIES OF TROPICAL AND TEMPERATE CANOPY ARTHROPODS: PAST, PRESENT AND FUTURE.

The arthropod fauna associated with tropical forests, and in particular, those associated with the canopy of trees have been the subject of intensive study by entomologists at the Natural History Museum in London. This paper will discuss the most important results from several key studies: i) the arthropod community associated with oaks in Richmond Park, England; ii) community structure of Bornean and Sulawesi arthropods. It will also examine the role that canopy arthropod studies can play in understanding the processes that lead to loss of biodiversity through forest fragmentation and loss with preliminary results of a project focusing on changing biodiversity with forest use and management in Cameroon.

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BENEATH BIODIVERSITY: FACTORS INFLUENCING THE DIVERSITY AND ABUNDANCE OF CANOPY MITES.

Mites (Acari), the smallest of the arthropods, are the most abundant, and perhaps the most diverse, of the arthropods that inhabit the leaves and the small stems that compose the outermost canopy of Australian rainforests. Most of this acarofauna graze on microflora or prey on mites and small insects; herbivores are sometimes abundant, but relatively low in diversity. Foliar mite species diversity and abundance was highest on structurally complex leaves, especially those with leaf domatia or erect tomenta. Experimental blocking of access to leaf domatia on 12 species of plants reduced both the abundance and diversity of foliar mites. At four tropical rainforest sites in north Queensland, hairy leaves averaged nearly three times as many species as smooth leaves. Smooth leaves with little surface structure were inhabited by relatively few mites, especially during periods of heavy rains. However, small stems become an aquatic habitat during the rainy season and many of the mite species appear to be adapted to a seasonally aquatic existence.

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CENTINELAN EXTINCTIONS: EXTIRPATION OF NORTHERN TEMPERATE OLD-GROWTH RAINFOREST ARTHROPOD COMMUNITIES.

Arthropod biodiversity is being investigated in the Carmanah Valley on Vancouver Island, British Columbia. Examination of several species, many of which are not yet described from this intact old-growth forest indicate that this structurally complex habitat acts as a reservoir for biological diversity. Nowhere is this more apparent than in the canopy, where the fauna has finely partitioned the tree, both with regard to habitat type and phenology. Microhabitats exploited by this arboreal arthropod fauna are not replicated in any of the other forest sites that we examined. That these species form a taxonomically discrete community clearly demonstrates that removal of this habitat will forever change the structural and functional aspects of these ecosystems and initiate species extinctions.

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RICH EDGES IN FOREST CANOPIES AND ACACIA SHRUBLANDS.

The effects of canopy gaps on forest understory communities are well documented. However, there has been almost no documentation of the effects of gaps on the canopies themselves. Recent research has shown that portions of crowns adjacent to gaps undergo rapid growth, implying an increase in available carbohydrate (due to increased sunlight). It is reasonable to hypothesize that this would also lead to increases in flowering, fruiting, and epiphytic growth in these same crown portions. Limited data from a temperate forest indicate that this is true. If so, gap-edge tree crowns could be hot spots of resource availability for folivores, floral visitors, frugivores, epiphytes, and associates of these species. As yet we have no documentation of these hot spots or how deeply their effects penetrate into the adjacent parts of the canopy. Using examples from 'gaps' (glades) in an acacia shrubland in East Africa, I show how similar hot spots have highly variable effects on the community, depending on the traits considered. I then consider parallels with forest canopy gaps, and possibilities for future research.

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PLANT PHENOLOGY AND PLANT-ANIMAL INTERACTIONS OBSERVED IN A TROPICAL LOWLAND FOREST IN SARAWAK, MALAYSIA.

Two tree towers (45 m and 55 m in height) and nine spans of walkway (300 m in total length) were constructed in Lambir Hills National Park in Sarawak, Malaysia, to observe plant phenology and plant-animal interactions. Reproductive phenology of 190 individuals was observed during August 1992-December 1993, and reproductive and flushing phenology of 498 individuals during May 1993-May 1994. This observation continues. In August 1992, general fruiting was observed and 40.5% of sample individuals set fruit. Most of the trees that set general fruiting did not produce in 1993, but some trees set fruit in continuous two years (*Sindra beccariana*, *Scaphium longipetiolatum*). The cycle of fruiting was shorter than one year in some trees (*Coelostegia griffithii*, *Mezzettia* sp.), but long-term observation is necessary to detect the periodicity on fruiting of those species. The rate of the individuals which showed flushing was high in May-June (50-60%) and low in June-December (40-50%). Fruiting in a non-general flowering year was fairly high in May-August (around 10%) and low in August-December (5-8%). Flowering individuals

in a non-general flowering period were low in rate (less than 5%) all year around. The rate of flowering individuals of species pollinated mainly by medium sized stingless bees and of species pollinated by small diverse insects fluctuated at low level all year around. The rate of flowering individuals of beetle-pollinated species was high in May and decreased toward December. Those species pollinated by leaf cutting bees bloomed only in May-August, and this period matched the flushing season of canopy trees.

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ECOLOGY AND DEMOGRAPHY OF VASCULAR EPIPHYTES.

Epiphytes comprise about 10% of all vascular plants. While little studied in the past, epiphyte ecology has received much attention in recent years. Generalizations concerning the ecology of such a large group of plants are difficult, and I do not intend to outline the entire knowledge of the field in my talk.

Instead, I want to focus on some selected topics of epiphyte ecology and ecophysiology, present unpublished data of my own research, and highlight promising lines of study. I will emphasize topics such as long-term carbon gain, responses of gas exchange to drought-stress, demography (growth, survival, recruitment patterns) of epiphytes as well as aspects of community ecology such as succession, competition and host specificity.