Inside CTFS

Center for Tropical Forest Science
Smithsonian Tropical Research Institute

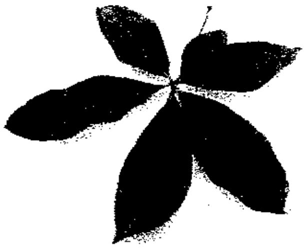
LETTER FROM THE DIRECTOR

# Setting Standards

*Elizabeth C. Losos*
*Director, Center for Tropical Forest Science*

Standardized data at a global scale have long been a key attribute of the Center for Tropical Forest Science. Only recently, though, through the analytical workshop series hosted by CTFS, has the true value of data standardization been realized. Each year, a working group of 30 - 35 scientists from 13 CTFS sites spend the better part of a month carrying out identical statistical analyses on each of their Forest Dynamics Plot databases and directly comparing their data.

Our special feature on 'Habitat Association' in this issue of *Inside CTFS* illustrates findings emerging from the CTFS working group. Workshop participants have applied the Torus Translation Test, a new statistical technique developed by Kyle Harms, to evaluate the degree to which relatively common species are associated with particular habitats in a Forest Dynamics Plot. Harms previously showed that about one-third of the species in a seasonally moist forest plot in Panama had significant associations with topographic features. In this issue, scientists reveal that, in a dry forest in India, nearly two thirds of the species appear to be significantly associated with topographically-defined habitats. In a seasonally wet forest in Cameroon, the proportion of species rises to over two-thirds, and in an everwet forest in Sri Lanka, it jumps further to four-fifths. Similar analyses by the CTFS working group are currently being carried out on plot data from Thailand, Ecuador, Puerto Rico, Colombia, Philippines, Sarawak, and peninsular Malaysia.



The working group as a whole has also begun working on cross-site analyses of habitat association across multiple Forest Dynamics Plots. Of course such global comparisons are tricky – how can one define meaningful habitat categories for such a diverse group of plots? Broad comparisons necessarily ignore the rich detail possible in single-plot analyses. Yet such multiple-site comparisons, in conjunction with single-site studies, will allow us to develop an understanding of which edaphic, climatic, and biogeographic factors lead toward increased or decreased habitat specialization at a global scale.

Standardized data collection, which was previously confined to tree measurements within CTFS, has now been extended to seeds, seedlings, soils, and hydrology. In 1987, Joe Wright and colleagues in Panama started a seed trap and seedling plot census within the 50-ha BCI Forest Dynamics Plot. Trap contents were collected on a weekly and bi-weekly basis for more than 15 years, and have been used with the tree data from the plot to vastly increase our understanding of dispersal and recruitment. More recently, three additional sites have added comparable seed trap and seedling censuses to their sites – Puerto Rico in 1992, Ecuador in 2000, and peninsular Malaysia in 2001. In this issue of *Inside CTFS*, scientists report on the progress of the two most recently established programs.

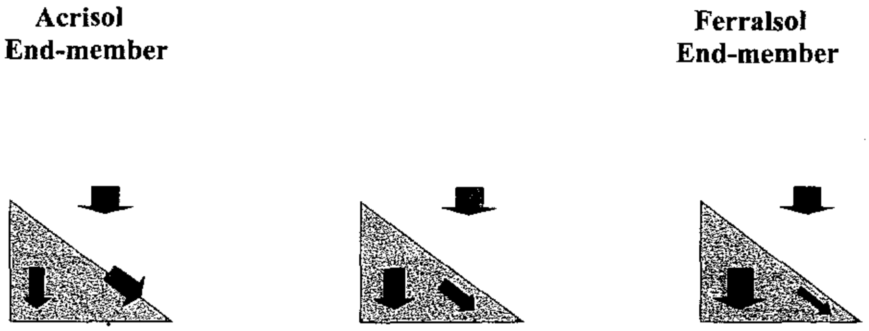
Within the abiotic world, Jim Dalling, Kyle Harms, Bob Stallard, and Joe Yavitz, along with colleagues at many of the CTFS sites, have initiated a study of the influence of the physical environment on tropical forest structure and dynamics within nine of the large plots. Standardized edaphic and hydrological measurements will enable scientists to study the effects of soil-borne resources on the variation in forest structure and turnover rates observed among plots. In this issue, Stallard reports on the hydrology component of this project. With each new standardized protocol, the CTFS network comes closer to deciphering which factors drive forest diversity at a truly global scale. ❧

INSIDE THIS ISSUE... HABITAT ASSOCIATIONS FEATURE

# HOW DOES WATER MOVE IN THE VARIOUS FOREST DYNAMICS PLOTS?

*Robert Stallard - University of Colorado, US Geological Survey,*
*and Terrestrial Environmental Studies Program of the*
*Smithsonian Tropical Research Institute*

Almost every characteristic of a humid tropical landscape is affected, shaped, and often controlled by the movement of water through, and sometimes over, soils on its way to streams. The distribution of vegetation, soil, and many organisms evolve, in turn, through complicated interactions and feedbacks, often involving the movement and distribution of water. Soils, because of their integrative nature, may be the best recorder of this interaction over longer time scales. Topography (hillslope form) and geology are central to this interaction. The styles of hydrologic, erosional, and biogeochemical processes are fundamentally different in flat versus steep terrains. Physical erosion on steep terrain is supply- or weathering-limited, for which physical transport processes - mostly surficial erosion by water - remove much of the loose material created by the breakdown of bedrock (weathering), and thus soils tend to be thin on the steep slopes leaving bedrock-derived nutrients easily accessible by plant roots. Under especially wet conditions, soils on steep slopes can erode catastrophically causing soil avalanches. On gentle slopes, by comparison, physical erosion is transport-limited, for which downslope transport processes cannot move all the loose material created by weathering, causing thick soils to develop and evolve, sometimes for millions of years. On these gentle slopes, bedrock-derived nutrients are not so easily accessed by roots.



Despite the important role of topography (hillslope form) and geology on water and nutrient movement, current ecosystem models of carbon and nutrient cycles lack a physically realistic topographic component. The prevailing perception for nutrients cycling in tropical-forest ecosystems is one for which nutrients are retained through intense and efficient recycling involving: leaching from leaves, branches, and decaying biomass; subsequent interception by soil organic matter, microorganisms, mycorrhizea, and roots; and then reincorporation into vegetation, with minimal leakage into groundwater and rivers. This view is fundamentally columnar in design, with mass nutrient exchanges being moved from the top of the canopy straight down to the bottom of the soil profile; whereas, in natural settings, on all but in thick permeable soils, much of the mass of nutrients and bedrock weathered products moves laterally downslope.

Recent research indicates that a vertical flowpath model is not consistent with field observations of storm-water flow in tropical forests. Instead, during major storm events in typical tropical sites, overland and near-surface waters flow moves much of the storm water directly to streams, bypassing plant roots. This water can transport elevated concentrations of potassium and nitrogen.

The figure below shows Elsenbeer's (2001) functional classification of tropical forest soilscapes using hydrologic flowpaths. Arrows indicate water movement overland and through soils. Arrow thickness indicates relative proportions. Surface lateral flow is found in hilly catchments with shallow bedrock where the saturated hydraulic conductivity (the ability of water to move through soil - $K_S$) decreases rapidly in the soil profile. Two end members are define: One is an Acrisol, which is an acidic, well-leached soil with a clay-enriched lower horizon, and the second is a Ferralsol, which is also acidic and is even more thoroughly leached, composed largely of quartz, the clay kaolinite, and the oxides and hydroxides of iron and aluminum. The "Acrisol" end-member pattern would be expected in Lambir, Sarawak, Malaysia and Sinharaja, Sri Lanka where two CTFS Forest Dynamics Plots occur. Deep lateral flow (as indicated in the "Ferralsol" end-member) should be found where Ks remains high through the soil profile. This pattern has been seen at the Ducke Reserve, near Manaus, Brazil, and is expected in Yasuni, Ecuador, two other CTFS sites. The intermediate condition of near-surface lateral flow is seen at Barro Colorado Island in Panama.

Although the movement of water through humid tropical forest catchments affects the soils, vegetation, nutrient movement, and runoff chemistry, only few small-scale catchment studies (10-1000 ha) exist that allow broad comparisons in tropical ecosystems, due to inconsistencies in sampling and analytical approaches. CTFS' global network of Forest Dynamics Plots are ideal for such studies due to their large size and standardized nature, but up until now few catchment studies have been carried out within them. As part of a recently funded, three-year research project entitled "Collaborative Research: Effects of Soil-borne Resources on the Structure and Dynamics of Lowland Tropical Forests" [Principal Investigators: Jim Dalling (University of Illinois, Urbana-Champaign), Kyle Harms (University of Louisiana), Robert Stallard (University of Colorado), and Joseph Yavitz (Cornell University)], we hope to address some of the

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# SPECIES-HABITAT ASSOCIATION AND DIVSERSITY AT KORUP, CAMEROON

*George B. Chuyong - University of Buea*
*David Kenfack - University of Missouri at St. Louis*
*Duncan Thomas - University of Oregon*

Considerable attention is being paid to how tropical forests maintain high tree diversity. Variation in habitat specialization in these tropical species has been proposed as one of the principal mechanisms that facilitate the maintenance of diversity. The focus of the last two CTFS analytical workshops was on habitat associations. Participants drawn from within the CTFS network of Forest Dynamic Plots (FDPs) had the opportunity to explore vast FDP datasets to determine whether local habitat specialization allows for species coexistence among tropical trees.

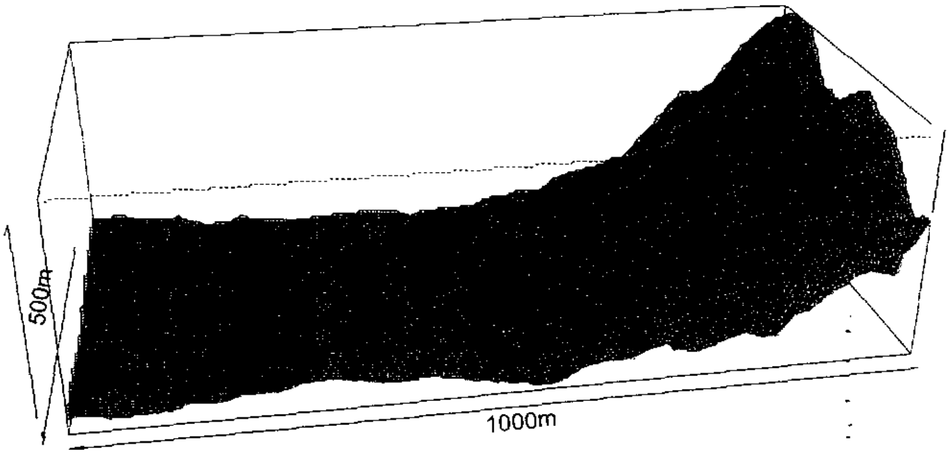

**Figure 1.** Three-dimensional map of the Korup Forest Dynamics Plot, Cameroon

The 50-ha Forest Dynamics Plot located within Korup National Park, Cameroon, is representative of the pristine Atlantic coastal forest of Western and Central Africa. This plot is unique among the CTFS network of plots in that it receives one of the highest annual rainfalls (over 5000 mm) but has a severe dry season spanning 2-3 mos. (monthly rainfall averages <100 mm), topographic features that greatly influence local conditions such as moisture availability, and soil type and properties that determine site quality and productivity.

We used the 50-ha Korup Forest Dynamics Plot (KFDP) to examine the following: (1) major habitat types as defined by topographic variables, (2) stem density and species diversity within the different habitat types and (3) the strength of species-habitat associations.

Seven habitat types were delineated based on the combination of mean elevation, slope and convexity of individual 20m x 20m quadrats: riverside, low depressions, low flat, high gully, bench, steep slopes, and ridge top. Mean Fisher's Alpha index (FAI) was computed for each habitat category to determine the level of species diversity and the Torus Translation Test was used to evaluate the significance of species-habitat associations.

Of the 310 species

*Continued on page 10*

## Torus Translation Tests: Trees on a Donut

*Kyle E. Harms - Louisiana State University*

The torus-translation method is a flexible procedure for judging the statistical significance of spatial associations within a mapped study plot. We developed the method to examine species-specific patterns of association with discrete habitats, while avoiding one of the common pitfalls of habitat-association analyses, that is, failure to account for the autocorrelation that characterizes most spatial patterns in the natural world.[1] Positive spatial auto-correlation is present at a chosen scale of observation when pairs of sites a given distance apart are more similar than randomly selected pairs of sites from any distance apart; this is usually manifest in nature as neighboring sites being more similar than sites distant from one another. A double-dose of autocorrelation confronts analyses of habitat association, since habitat variables, as well as the locations of conspecific trees, are spatially autocorrelated within large plots. Torus Translation Tests of habitat association incorporate observed spatial structure of both habitats and trees to avoid the spatial-autocorrelation pitfall.

The objective is to assess the probability that the observed levels of association among habitats for an individual species could have occurred by chance, and this is done by creating a null distribution of expected values of association for the focal species and each habitat.

For a given species of tree, a Torus Translation Test of association with discrete habitats requires: (1) a measure of habitat association (for example, species density or basal area in each habitat); (2) a map of the plot fully gridded into equal-sized squares, each assigned to one of a set of pre-determined habitats; and (3) the coordinates of the individuals of the focal species within the plot. For example, one might choose to use the density of stems as a measure or indicator of association of the focal species with a given habitat. In this case, the observed density of the focal species in a given habitat would be compared to the null distribution of expected densities of the

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# SPECIES-HABITAT ASSOCIATIONS IN THE FOREST DYNAMICS PLOT AT SINHARAJA, SRI LANKA

*C.V.S. Gunatilleke, Shameema Esufali, and*
*I.A.U.N. Gunatilleke - University of Peradeniya*
*Kyle E. Harms - Louisiana State University*
*David Burslem - University of Aberdeen*

Species distribution in relation to habitats is central to understanding the maintenance of species diversity in tropical rain forests. To understand how species are distributed among different habitats in the 25-ha Sinharaja Forest Dynamics Plot we first differentiated habitats based on similar topographic features of elevation, slope, and convexity of each of the 625 20 m x 20 m quadrats. Slope within the plot ranged from 0 to 40.9° and convexity ranged from -9.3 to 7.9. To group quadrats into habitats, two levels were considered for each topographic feature. These features included: **low** and **high** elevation quadrats based on the median, **steep** and **less-steep** slopes also based on the median, and **spurs** and **gullies** based on greater or less than zero convexity. On this basis, eight habitats (Fig. 1) were identified and named as i) high steep spurs, ii) high less-steep spurs, iii) high steep gullies, iv) high less-steep gullies, v) low steep spurs, vi) low less-steep spurs, vii) low steep gullies, and viii) low less-steep gullies. The extents of these habitats varied as shown in Table 1.

We then compared the differences in (i) vegetation structure as given by density and basal area, (ii) floristics as given by species richness and Fisher's alpha diversity index, and (iii) the dispersal patterns of abundant and less abundant species, > 1 cm dbh. Of the 205 free-standing species identified in the 25-ha Sinharaja Forest Dynamics Plot, only 125, with more than 100 individuals, were selected for analyses.

The differences in density, basal area, species richness, and Fisher's alpha among habitats are given in Table 1. The high elevation spurs had a greater density and basal area than other habitats. Species richness and Fisher's alpha were lower in the high-elevation habitats. These structural and floristic differences appear to be related to the overwhelmingly high abundances (17,000 – 22,000 individuals) of the leading dominant species (*Humboldtia laurifolia* [Leguminosae], *Agrostistachys intramarginalis* [Euphorbiaceae], and *Mesua nagassarium* [Guttiferae]) in the high elevation spurs, and a paucity in the abundance of the leading dominants (*Garcinia hermoni* [Guttiferae], *Agrostistachys hookeri* [Euphorbiaceae], *Psycotria nigra* [Rubiaceae]) in the low elevation habitats (6000-8000 individuals).

### *Specialist and Generalist/Neutral Species*

Of the 125 species that were subjected to the Torus Translation Test (see Harms, this issue), 99 (79%) were positively and/or negatively associated with the different habitats. Sixteen were positively associated with one or more of the high elevation habitats; 12 of these were also negatively associated with either one or both low elevation gullies. Sixty-five species were positively associated with the low elevation habitats; 28 of which were negatively associated with one or two of the high elevation habitats. The species positively associated with habitats may be considered specialists. Among them, those that also showed negative associations with any other habitats may be considered highly specialized, as exemplified by the high steep spur specialists *Mesua nagassarium* [Guttiferae], *Shorea worthingtonii* [Dipterocarpaceae], *Agrostistachys intramarginalis* [Euphorbiaceae], and the high less-steep spur specialist *Humboldtia laurifolia* [Leguminosae]. Some examples from the low-elevation habitats include *Bhesa ceylanica* [Celastraceae], *Palaquium canaliculatus* [Sapotaceae], and *Urophyllum ellipticum* [Rubiaceae]. Among the 18 species that showed only negative associations, 11 (including *Shorea distica*, *Shorea affinis*, and *Shorea congestiflora*) were under-represented in the low elevation habitats and seven (including *Anisophyllea cinnamomoides*

| Habitat Categories | Habitat Characteristics | | | | |
|---|---|---|---|---|---|
| | Area (ha) | Mean no. of trees per quadrat | Mean basal area ($m^2$ per quadrat) | Mean no. of spp. per quadrat | Mean Fisher's Alpha per quadrat |
| **High Elevation Habitats** | | | | | |
| High steep **spurs** | 4.2 | 409 ± 11* | 2.36 ± 0.08 | 46.7 ± 0.8 | 14.6 ± 0.4* |
| High less-steep **spurs** | 2.7 | 402 ± 13* | 2.26 ± 0.10 | 47.9 ± 1.2 | 15.1 ± 0.6 |
| High steep **gullies** | 4.3 | 322 ± 10 | 1.90 ± 0.07 | 47.0 ± 0.7 | 15.5 ± 0.4 |
| High less-steep **gullies** | 1.3 | 357 ± 18 | 1.81 ± 0.11 | 51.7 ± 1.9 | 17.2 ± 0.8 |
| **Low Elevation Habitats** | | | | | |
| Low steep **spurs** | 2.1 | 368 ±14 | 2.05 ± 0.09 | 56.9 ± 1.7 | 20.4 ± 0.9 |
| Low less-steep **spurs** | 2.4 | 352 ±18 | 1.88 ± 0.09 | 54.0 ± 1.5 | 19.7 ± 0.8 |
| Low steep **gullies** | 1.9 | 322 ±17 | 1.51 ± 0.07 | 53.4 ± 1.3 | 19.4 ± 0.8 |
| Low less-steep **gullies** | 6.2 | 220 ± 6* | 1.22 ± 0.04 | 49.6 ± 0.8 | 21.1 ± 0.4* |

**Table 1.** Comparison of the structural (density and basal area per quadrat) and floristic (species richness and Fisher's alpha diversity per 20 m x 20 m quadrat) characteristics among habitats, in the 25-ha Sinharaja Forest Dynamics Plot. Total number of free-standing species identified in the plot was 205. Significance among the respective values column-wise were tested using a Torus Translation Test. * = Significant at p<0.05.

[Anisophylleaceae], and *Cullenia ceylanica* [Bombacaceae] were underrepresented in the high-elevation habitats. The remaining 26 species that did not show any positive or negative association with any of the eight habitats may be considered as generalists or neutral species, which were distributed in all habitats, showing no preference to any of them. The six most abundant generalists were *Myristica dactyloides* [Myristicaceae], *Diospyros acuminata* [Ebenaceae], *Mangifera zeylanica* [Anacardiaceae], *Shorea stipularis* [Dipterocarpaceae], *Chaetocarpus coreaceus* [Euphorbiaceae] and *Diospyros hispidus* [Ebenaceae].

### *Distribution Patterns of Abundant and Less Abundant Species*

The habitat preferences of the abundant species and the less abundant species (> or < 800 individuals/25-ha, respectively) were also compared. Of the 99 species that showed positive and/or negative associations with one or more of the eight habitats in the plot, 41 were abundant and 58 were less abundant (Tables 2 and 3).

Among the positively associated species, 10 abundant species (e.g. *Mesua nagassarium* [Guttiferae], *Palaquium petiolare* [Sapotaceae], and *Hydnocarpus octandra* [Flacourtiaceae]) and six less abundant species preferred one or two of the high elevation habitats; 23 abundant species including *Palaquium canaliculatus* and *Urophyllum ellipticum* [Rubiaceae] and 42 less-abundant species preferred one or two of the low elevation habitats (Table 3). Some species in these categories were also negatively associated with one of the remaining habitats, indicating that they were underrepresented in them. A total of 18 species, eight abundant and 10 less abundant, showed only negative associations with certain habitats. In this category, seven species in the high-elevation habitats and 11 species in the low-elevation habitats were underrepresented.

| | No. of species (+) associated with each habitat | | No. of species (-) associated with each habitat | |
|---|---|---|---|---|
| **Habitat Category** | Abund. Spp. (41) | Less Abund. Spp. (58) | Abund. Spp. (41) | Less Abund. Spp. (58) |
| **High Elevation Habitats** | | | | |
| High Steep Spurs | 3 | 0 | 6 | 15 |
| High Less-Steep Spurs | 2 | 5 | 6 | 12 |
| High Steep Gullies | 4 | 1 | 0 | 7 |
| High Less-Steep Gullies | 3 | 0 | 0 | 2 |
| **SubTotal** | **10** | **6** | **10** | **25** |
| **Low Elevation Habitats** | | | | |
| Low Steep Spurs | 3 | 2 | 0 | 1 |
| Low Less-Steep Spurs | 4 | 7 | 1 | 1 |
| Low Steep Gullies | 5 | 8 | 5 | 6 |
| Low Less-Steep Gullies | 18 | 29 | 13 | 6 |
| **SubTotal** | **23** | **42** | **13** | **11** |
| Total no. and (%) of **significantly associated species** in each category | **33**<br>(80%) | **48**<br>(83%) | **23**<br>(56%) | **36**<br>(62%) |

**Table 2.** Proportions of species positively- and negatively-associated with eight habitats, both for abundant (> 800 individuals / 25 ha) and less abundant (100-800 individuals / 25-ha) categories. Individual species can be associated with more than one habitat type. Habitat associations are based on the Torus Translation Test using a two-tailed probability test at $p < 0.975$ level.

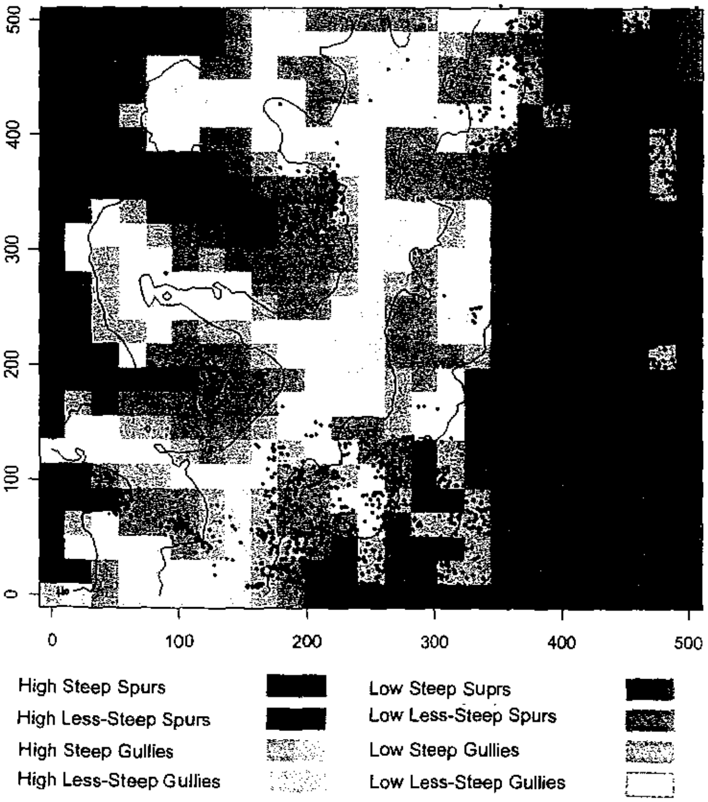

**Figure 1.** Distribution of habitats in the Sinharaja Forest Dynamics Plot and the distribution of individuals > 5 cm dbh of the leading dominant canopy species *Mesua nagassarium* (dark gray dots), representing 7% of all individuals in the plot, abundant in the high steep spurs and high less-steep spurs. *Mesua ferrea* (light gray dots) is more or less restricted to the high steep and less-steep gullies.

From the results of this study we conclude that there is a high degree of specialization of species to the different habitats in the Sinharaja Forest Dynamics Plot. Even within an elevational range of only 125 m, the upper elevation habitats had a higher density and basal area, but were floristically poorer compared to the lower elevation habitats. In the high elevation habitats, the very high densities of the three dominant species suggest their differential success on soils of lower levels of moisture and nutrients. In addition, their seedlings and saplings may tolerate higher levels of understory light in these upper slopes and ridges. On the other hand, in the lower elevation habitats, where soil moisture and nutrient levels may be relatively higher, the greater diversity of species may be due to a larger pool of species capable of successfully establishing on the lower-

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# DISTRIBUTIONS OF TROPICAL DECIDUOUS FOREST TREES IN MUDUMALAI, SOUTHERN INDIA

*Robert John - University of Georgia*
*H.S. Dattaraja - Centre for Ecological Science, Indian Institute of Science*

Niche-assembly theories propose that habitat specialization is the principal mechanism for maintaining tree diversity in tropical forests, but relatively few community-level tests of this hypothesis have been undertaken, and there is no evidence that tropical trees indeed occupy unique niches. Here we report tests of habitat associations from a tropical deciduous forest in Mudumalai Wildlife Sanctuary, southern India. We examine tree distributions in the 50-ha Mudumalai Forest Dynamics Plot plot as well as in 18 1-ha plots from a 321 $km^2$ area in Mudumalai. The study area is remarkably heterogeneous in rainfall, topography, soil types, and disturbance regimes, with corresponding differences in forest types. The length of the dry season is nowhere less than five months, hence trees are essentially deciduous, but evergreen thorny scrub forest occurs in the driest parts.

| Habitat | Area (ha) | No. of Trees/Ha | Basal Area /Ha $(m^2)$ | No. of Species/Ha | Fisher's Alpha | No. of Associations/Species | |
|---|---|---|---|---|---|---|---|
| | | | | | | Positive | Negative |
| *Streamside* | 7 | 558±67 | 21.4±1.9 | 37±3 | 8.91 | 10 | 8 |
| *Low-Elevation* | 21.5 | 465±52 | 25.1±1.8 | 31±4 | 7.48 | 2 | 2 |
| *High-Elevation* | 21.5 | 540±47 | 25±1.6 | 27±3 | 5.98 | 2 | 5 |
| *Plateau* | 21.5 | 457±32 | 25±1.9 | 29±3 | 6.89 | 8 | 6 |
| *Slope* | 21.5 | 540±66 | 24.8±2.1 | 29±3 | 6.56 | 4 | 7 |
| *Negative-Convexity* | 16.8 | 541±82 | 25.9±1.5 | 31±3 | 7.15 | 1 | 2 |
| *Positive-Convexity* | 26.2 | 475±50 | 24.8±2.1 | 29±3 | 6.81 | 8 | 7 |

**Table1.** Associations to habitats defined by slope, elevation, convexity, and proximity to streams. Fisher's alpha was calculated for the mean number of trees and species.

Gradient analyses have shown that rainfall accounts for over 90% of the variance in species composition between these plots. Tree densities vary widely, with only 300-600 trees/ha (trees ≥ 1 cm dbh) in the scrub forest and dry deciduous forest to over 1500 individuals in the moist deciduous forest. The expected number of species per 300 trees ranges from about 15 to 45 (Hurlbert's rarefaction measure). With low tree densities and a higher level of dominance than tropical moist forests, a large proportion of the species in our samples are rare. Of 70 tree species in the 50-ha plot, 47 had <50 individuals and 34 species had <25 individuals (trees ≥ 1 cm dbh).

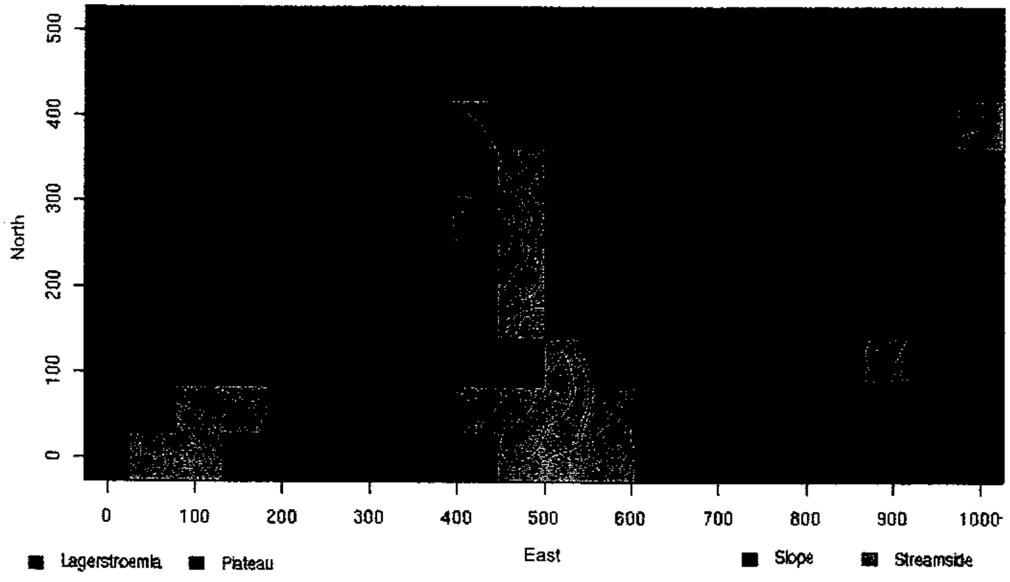

**Figure 1.** Regions defined by species compositional differences using TWINSPAN. Lagerstroemia indicates regions where *L. microcarpa* occurs at high densities.

We tested habitat associations among the 50 most common species in the 50-ha plot using the Torus Translation Test. Habitats were defined based on topography (slope, elevation, convexity) and proximity to seasonal streams. We first segregated the *streamside* quadrats and classified the remaining quadrats as: (1) Slope and Plateau, (2) Low- and High-elevation, and (3) Negative and Positive convexity. The median value was used to differentiate habitats for slope and elevation, and zero was used for convexity. This yielded three separate habitat maps (*streamside* was common to all three maps) against which habitat associations were tested. Since slope, elevation, and convexity were poorly correlated among themselves, we could test these variables individually.

The highest number of significant associations was to the *streamside*

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# Sprouting:
# Research on Sustainable Forest Management in Malaysia

*Matthew D. Potts - Institute on Global Conflict and Cooperation, University of California, San Diego*

A longstanding goal of CTFS is to improve forest management and biodiversity conservation in tropical countries. We are initiating two projects which will help CTFS reach this goal. The first is a three-year project undertaken by myself in collaboration with Jeffrey Vincent (University of California, San Diego), Takashi Kohyama (Hokkaido University), and Dr. Shamsudin Ibrahim (Forest Research Institute Malaysia) to develop species and spatially explicit forest growth models. The second is a five-year multi-disciplinary project developed by Forest Research Institute Malaysia in collaboration with researchers at Harvard University and University of California, San Diego to jointly model the economic and ecological aspects of tropical forest management. An explicit goal of both of these projects is to provide policy makers and economic planners with the necessary tools to make economically efficient and ecologically sound planning decisions.

Both projects will use a 3000 km$^2$ region in the northern peninsular Malaysian state of Perak to develop and parameterize their models. The region forms part of the largest remaining block of unlogged rainforest in peninsular-Malaysia with rich species diversity and high potential timber value. The region also contains the Perak Integrated Timber Complex (PITC) concession that recently became the first timber concession in peninsular Malaysia to be certified as sustainable by the Forest Stewardship Council. PITC has agreed to participate in both projects and will allow for harvesting according to experimental protocols designed to test hypotheses about biodiversity impacts.

The primary focus of the first project is to develop a species- and spatially-explicit forest growth model applicable across a multitude of spatial scales that will jointly provide information on timber yield and biodiversity. The main objective of the second project is the construction and parameterization of a spatially explicit dynamic forest allocation model to investigate the economic and ecological conditions that determine the optimality of segregated versus integrated forest management systems. In segregated management, some areas of the forest estate are managed intensively for timber production while others are set aside for biodiversity conservation. In integrated management, all areas of a forest estate are jointly managed for timber production and biodiversity. The models from both projects will be used to test the hypothesis that rising biodiversity value to humans coupled with inherent nonlinear tradeoffs between biodiversity protection and timber production causes the optimal management approach to change over time.

Extensive ecological and economics research will be undertaken to support both these projects. Field studies of flora and faunal taxa will be combined with existing research and data from the CTFS Forest Dynamics Plots to determine the characteristics of a feasible set of combinations of timber production and biodiversity conservation at different temporal and spatial scales. Hydrological and timber value studies will be used in conjunction with surveys of both revealed and stated preferences of Malaysian households to develop functions that relate timber and non-timber values of Malaysian forests to forest characteristics and socioeconomic factors. Survey results will provide the Malaysian public's willingness to pay for biodiversity conservation as well as the potential tourism value of these forests. These values will help to determine the size, shape, and location of protected and harvested areas.

These projects, while helping to deepen our understanding of fundamental questions in ecology and economics, provide a unique opportunity to better understand the coupled dynamics of human and natural systems while disseminating the resources and research of CTFS to a much broader audience.

*Funding for the first project is being provided by a National Science Foundation Bio-Informatics Post-Doctoral Fellowship. Planning support for the second project was provided by the United Nations Development Programme Global Environment Facility with on-going funding being sought from the United Nations Development Programme Global Environment Facility, National Science Foundation, and International Tropical Timber Organization.*

# Trapping in the Yasuní Forest Dynamics Plot

*Nancy C. Garwood - The Natural History Museum*

Early in 2000 we placed 200 traps in the Forest Dynamics Plot (FDP) of Yasuní National Park, Ecuador. Our prey were not the furry denizens of the forest but plant reproductive parts – flowers, fruits and seeds. We join an expanding network of researchers at other FDP sites using similar methods. Our aim is to understand the environmental and biotic factors that determine the timing and success of plant reproduction in Yasuní and other tropical forests. Here we contrast our early results from the 'aseasonal' forest of Yasuní with long-term work in the highly seasonal forests of Barro Colorado Island (BCI), Panamá.

The relationship between the strongly seasonal climate of BCI and the seasonal patterns of plant and animal reproduction there has long been a focus of study. But, because climatic factors such as rainfall, temperature, humidity, and solar irradiance are often correlated in the seasonal tropics, it is difficult to tease apart the proximate mechanisms that trigger reproductive events and the ultimate evolutionary causes selecting for these patterns. One way to disentangle these factors is to compare sites that have different climates.

We chose Yasuní as a second site because its climate, which lacks a dry season, was considered aseasonal. In the absence of clear climatic cues, we predicted that plant reproduction would also be aseasonal. However, climate data collected since 1995 show considerable variation within and between years and more seasonality than suspected. Mean annual rainfall is about 2800 mm, which is very similar to the 2600 mm that BCI receives each year. In Yasuní, no month receives < 100 mm of rainfall and dry periods are < 3 weeks long, but there is typically more rainfall in May and June and less in August and September. In contrast, BCI has a relatively severe 4-month long dry season. Both sites have strong annual cycles in solar irradiance.

We erected 200 traps, each 0.5 $m^2$, in February 2000 near trails within the Yasuní Forest Dynamics Plot. The sampling method is identical to that used by Joe Wright and colleagues within the FDP on Barro Colorado Island (BCI) since 1987. The only difference is that we counted the contents of the traps every two weeks at Yasuní, not every week as done on BCI. The team spent the 'extra' time building up a voucher collection of reproductive parts and learning to identify the parts to species. This was a formidable task because the flora is hyperdiverse – there are about 3.5 times more tree species in the FDP at Yasuní than at BCI – and there had been little previous work on fertile parts at Yasuní, as most of the plot identifications are done on sterile material. In addition, we established 20 transects, each 100 $m^2$, along trails outside the FDP to determine the timing of seedling emergence, a method I used previously on BCI. Seeds were

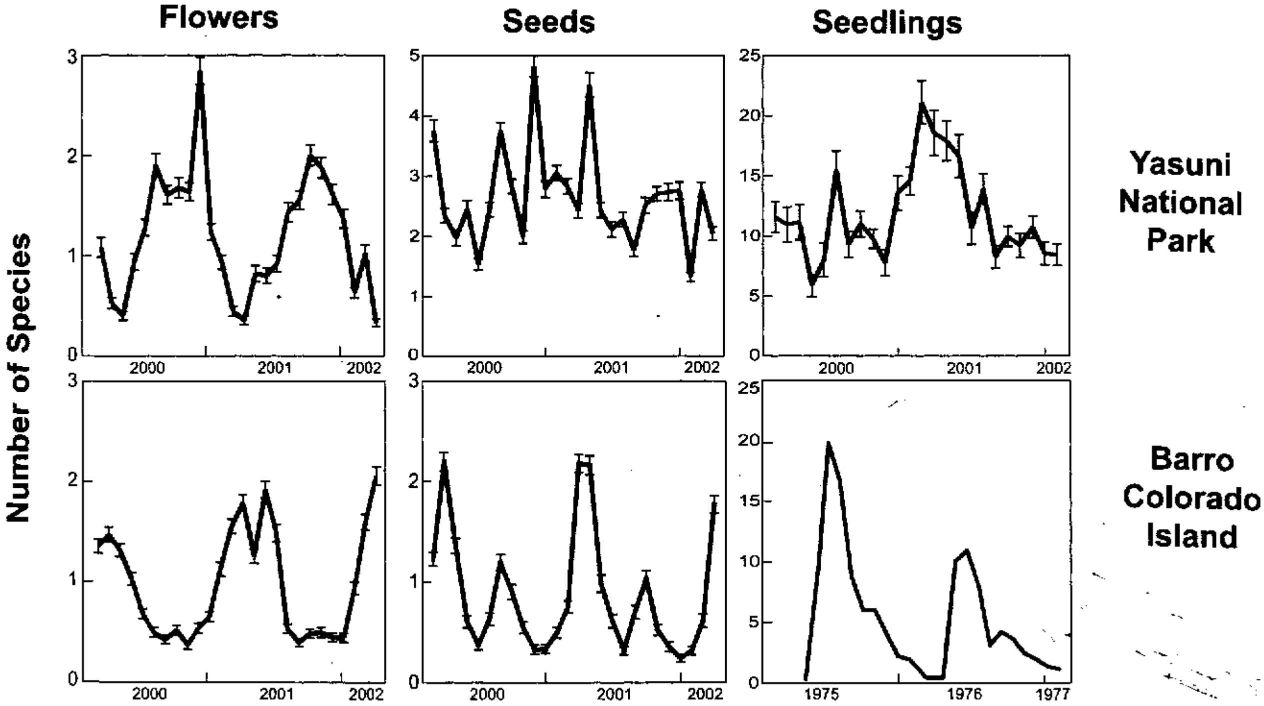

**Figure 1.** Timing of flowering, seed dispersal, and seedling emergence over two years at Yasuní National Park and Barro Colorado Island. Number of species is shown as the mean species per trap (α, SE) or transect for each phenophase (n=200 except n=20 for seedling emergence). All data are from March 2000 to April 2002 except seedling emergence from BCI, which is from April 1975 – March 1977 (the only years for which data are available). Data sources: Yasuní (this study); BCI flowering and seed dispersal (S.J. Wright, unpublished); BCI seedling emergence (N.C. Garwood, unpublished). Reproduced from V. Persson (*in prep.*).

# Phenology During Two General Flowering Events in Pasoh Forest Dynamics Plot, Malaysia

*Yu-Yun Chen - University of Georgia*

Researchers have been fascinated by the magnitude and unpredictability of "general flowering events" in Southeast Asia. In general flowering years, many tree species simultaneously produce a large amount of seeds, while they produce no seed in non-general flowering years. Unlike most tropical forests where flowering and fruiting occur regularly on annual and/or sub-annual bases, general flowering in Southeast Asia occurs at varying supra-annual intervals and is generally thought to be triggered by regional climatic fluctuations. Although general flowering events have been known for a long time, there are few long-term, community-wide, quantitative studies of this phenomenon.

To better understand the role of general flowering in the maintenance of tree diversity, a long-term seed rain study was established in Pasoh Forest Dynamics Plot, Malaysia, in August 2001. The purpose of the study is to investigate patterns of seed production, seedling dynamics, dispersal, and recruitment limitation and to test general flowering-related hypotheses proposed to explain the high diversity of tropical forests.

The methodology for this study is identical to the seed rain and seedling dynamics study on BCI and Yasuní. A total of 247 seed traps were set up along the existing trails in the plot and three 1 x 1 m seedling plots were located on the sides of each trap, except for those in gaps, which had four seedling plots. Seed traps were censused weekly with all reproductive plant parts identified to species (or morpho-species), and sorted into one of six categories: mature fruit, seed, capsule, fragment, young fruit, and flower. The presence of flowers and counts of all other categories were recorded.

Unexpectedly, two sequential general flowering events, one in August 2001 (2001 GF) and another in March 2002 (2002 GF), have occurred since the start of this study with fruit production occurring in March 2002 and October 2002, respectively. We documented which species and individuals reproduced; the temporal synchrony of flowering and fruit fall; and levels of pre-dispersal and post-dispersal seed predation on *Shorea* [Dipterocarpaceae] seeds. The fate of seedlings was also monitored after seed

*Continued on page 12*

| | 2001 GF | 2002 GF |
|---|---|---|
| Total number of species | 308 | 521 |
| Empty traps* | 5265 (68.8%) | 758 (9.89%) |

**Table 1**. Comparison of general flowering in 2001 and 2002.
* *The percentage of empty traps is calculated as: number of empty trap records / total trap records (247 traps x 31 trap censuses).*

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also germinated in the growing house built for the project to identify seedlings collected along transects and to obtain germination data.

Results from the first two years of our study are shown in Figure 1. At Yasuní, flowering showed a strong unimodal annual cycle, contrary to our initial predictions of aseasonality. No seasonal cycles were detected in seed dispersal and seedling emergence, although the means varied considerably throughout the study period. At BCI, as reported in earlier studies, flowering and seedling emergence showed a strong unimodal annual cycle while seed dispersal demonstrated a bimodal cycle. At both Yasuní and BCI, the mean number of species flowering per month is positively correlated with solar irradiance, but only on BCI is flowering also negatively correlated with rainfall. This supports the hypothesis that flowering in tropical forests is timed to maximize capture of solar energy for reproduction. An alternative hypothesis, that timing of flowering minimizes disruption of pollinators by rainfall, is rejected for Yasuní but not BCI.

Seedling emergence is highest in the first half of the rainy season on BCI, but occurs throughout the year in everwet Yasuní (Figure 1). Previously on BCI, I have shown that there is a selective advantage to germinating early in the rainy season. This can be achieved either by dispersing non-dormant seeds, which germinate quickly, at or just before the beginning of rainy season or by dispersing seasonally dormant seeds late in the rainy season, which lose dormancy and germinate by the following rainy season. I would argue that, with seasonal constraints on germination largely removed at Yasuní, seasonal seed dormancy will be absent and hence the timing of seed dispersal will be under stronger biotic than climatic constraints. Further analysis of the trap and germination data will allow us to test these predictions.

*My primary collaborators on the Yasuní project are Renato Valencia of Pontificia Universidad Católica del Ecuador (PUCE) and FUNDACYT, Joe Wright of the Smithsonian Tropical Research Institute, graduate student Viveca Persson from the University of Aberdeen, and technician Milton Zambrano. We are grateful to the Andrew W. Mellon Foundation, Natural Environment Research Council, the Natural History Museum, London, England, and British Airways for funding the Yasuní project, the PIs of the Yasuní FDP for their continuing support, and P. Alvia, M. Priest, G. Villa, and H. Navarrete for much needed assistance. Z. Aquilar and P. Barriga completed their Licenciatura theses at PUCE as part of the project. The results reported here are part of a Ph.D. thesis by V. Persson.* ❧

## Korup, Cameroon...

Continued from page 3

with more than 30 individuals within the plot, 210 (68%) showed significant associations (positive or negative) with one or more habitat types. *Homalium sarcopetalum* [Flacourtiaceae] was the only species that was completely restricted to the riverside. All the other species were significantly associated with two or more habitat types. The low depressions, steep slopes, and riverside had relatively high levels of positive and significant associations with 61, 55, and 48 species respectively. Generalists like *Hymenostigia alfzelii* [Leguminosae] and *Cola attiensis* [Sterculiaceae] occurred at random.

Overall species diversity was not strongly correlated with any particular topographic variable. The riverside, low depression, and low flat habitats showed relatively higher species richness, which may be attributable to lower moisture stress during the tough dry season. This finding however should be confirmed with plant-water relation experiments. The lack of a strong correlation between Fisher's Alpha Index (FAI) and the different topographic variables indicates that other site factors are in play and raises questions that will require more research activities within the plot in the coming years. The recently completed soil survey of the entire plot may help determine if soil heterogeneity is a factor that influences habitat specialization.

Our knowledge of habitat preferences of the plants at Korup - particularly those with great potential for the pharmaceutical industry - will guide species collection, and the management and conservation of habitats that harbor these useful plants. ❧

| Habitat type | Area (ha) | No. of Individuals per Ha | No. of Species | Fisher's Alpha index | Significant Associations |
|---|---|---|---|---|---|
| Riverside | 2.08 | 4,701 | 318 | 62.94 | 48 |
| Low depression | 11.04 | 6030 | 410 | 58.22 | 61 |
| High gully | 3.56 | 5193 | 322 | 55.39 | 35 |
| Low flat | 15.24 | 7741 | 439 | 57.57 | 31 |
| Bench | 6.08 | 7052 | 356 | 53.19 | 3 |
| Ridge top | 3.32 | 6329 | 290 | 47.6 | 21 |
| Steep slopes | 8.48 | 6164 | 362 | 52.42 | 55 |

**Table 1.** Stem density, diversity (FAI), and number of species that show significant associations by habitat type.

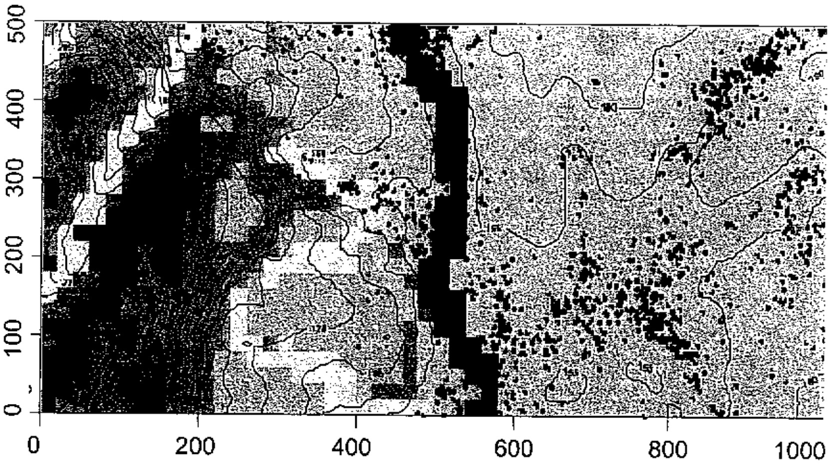

**Figure 2.** Distribution of *Beilschmedia sp.* (small gray clusters) showing significant association with low depressions.

## Torus Translation Tests...

Continued from page 3

focal species in the selected habitat to determine the probability that the observed density could have occurred by chance, given the spatial structure of the focal species' population and the habitats of interest.

To generate the null distributions, the plot map is placed on a torus. A three-dimensional torus approximates the shape of a donut, and placing a two-dimensional map on a torus can be visualized as the two-component process of rolling the map in both east-west and north-south directions so that the entire length of the eastern border of the plot becomes attached to the western border, and the entire southern border adjoins the northern border. Once placed on a torus, the habitat map is then decoupled from the tree map and is shifted (translated) east, west, north, or south across the borders of the plot, while the locations of the trees remain unchanged relative to the plot's borders. After one shift of the habitat map, the number of trees of the focal species is counted in each habitat to give one value for the expected density in each habitat. Each additional shift (translation) of the habitat map provides another estimate of the expected density in each habitat. After many shifts of the habitat map, all the estimates of the expected density in a given habitat together form a frequency distribution that is the null distribution for one species-habitat association. An observed density – from the correct habitat-map orientation – that falls in either of the 2.5% tails of the null distribution would indicate a significant departure from the expected degree of association based on chance.

During the first two CTFS workshops (Bangalore, India 2001; Gamboa, Republic of Panama, 2002) we developed and distributed a Torus Translation Test of habitat association for CTFS plots in the freeware programming language "R." For persons wishing to employ or modify the torus-translation procedure for their own purposes, the R-language code is available through the CTFS office. Three articles in this newsletter make use of Torus Translation Tests, and others have recently appeared in the literature[2]. Modifications of the original method have been developed for continuous environmental variables (A. Itoh, pers. comm.) and extensions are readily apparent for applications beyond habitat-association analyses (for example, to evaluate patterns of interspecific association). ❧

[1] For more information on the original Torus Translation Test, see:Harms et al. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. Journal of Ecology89:947-959.

[2] Recent articles that use Torus Translation Tests include: Bunyavejchewin et al. 2003. Spatial distribution patterns of dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand. Forest Ecology and Management 175:87-101; Debski et al. 2002.Habitat preferences of *Aporosa* in two Malaysian forests: Implications for abundance and coexistence. Ecology 83:2005-2018; Itoh et al. 2003. Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest. Ecological Research 18:311-324.

# CTFS Flourishes in Asia

In January 2003, the Smithsonian Tropical Research Institute and the Arnold Arboretum (AA) of Harvard University signed a memorandum of understanding to strengthen the CTFS Asia Program, known henceforth as the CTFS-AA Asia Program. With newly appointed Scientific Director Dr. Stuart Davies of Harvard, STRI and AA will cooperate in providing expanded core support for the CTFS Asia Program over at least the next five years. For STRI, this partnership was made possible in part through a generous contribution from the Celerity Foundation at Peninsula Community Foundation.

The CTFS-AA Asia program is a regional program of the CTFS global network of long-term Forest Dynamics Plots. The CTFS Asia Program was originally established by STRI in 1992, working in collaboration with Professor Peter Ashton at Harvard. Since that time, the Asia program has been an active research network making significant contributions in areas of tropical forest ecology and botany, local human capacity building, and tropical forest conservation in Asia. The program has now expanded to 11 sites in seven countries. Given the vast expansion of sites and the new opportunities they provide, the program has grown to require additional leadership and supporting resources.

## Sinharaja, Sri Lanka...

*Continued from page 5*

elevation soils. The lower densities of each of the species however, may be due to the inability of their seedlings and saplings to tolerate the shadier understory conditions in these microhabitats, because their juveniles are light-demanders. Long-term studies, combined with experimental manipulations, will help to understand the extent to which each of these factors contributes to the spatial patterns observed in the Sinharaja plot.

*The authors gratefully acknowledge the permission given to work in Sinharaja World Heritage Site and the accommodation facilities provided by the Forest Department of Sri Lanka as well as the generous financial assistance to set up the plot and computerize the database given by The John D. and Catherine T. MacArthur Foundation, the Smithsonian Tropical Research Institute, the Center for International Development of Harvard University, and the National Institute of Environmental Science. The Sri Lankan authors extend a special thank you to Dr. Richard Condit for his invaluable time to teach us how to analyze these large databases rapidly and to Dr. Elizabeth Losos for organizing the workshops held in Bangalore in 2001 and in Panama in 2002 where we learned the methodology and had fruitful exchange of ideas during the preparation of this paper.* ❧

**Habitat Preferences of the More Abundant Species**

| HSS | HFS | HSG | HFG | LSS | LFS | LSG | LFG | No. of Spp | Canopy | Sub Canopy | Understory Tree | Treelet/Shrub |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| + | | | | | | - | - | 1 | | | | *Agrostistachys intramarginalis* |
| + | | | | | | | - | 2 | *Mesua nagassarium,*<br>*Shorea worthingtonii* | | | |
| | + | | | | | - | - | 2 | | | *Humboltia laurifolia* | *Memeculon arnottianum* |
| | + | | | | | | - | 1 | *Shorea congestiflora* | | | |
| | | + | | | | | - | 1 | | *Shorea cordifolia* | | |
| | | + | + | | | | - | 1 | *Palaquium petiolare* | | | |
| | | + | + | | | | | 1 | *Mesua ferrea* | | | |
| | | + | | | | | | 1 | | *Hydnocarpus octandra* | | |
| | | | + | | | | | 1 | | | | *Nargedia macrocarpa* |
| | | | | | | | | 11 | | | | |
| | | | | + | + | - | | 2 | | | *Xylopia championii* | *Memeculon rostratum* |
| | | - | - | | + | | | 1 | *Pseudocarapa championii* | | | |
| - | | | | | | + | + | 1 | | *Semecarpus walkerii* | | |
| - | - | | | | | + | + | 1 | | | | *Syzygium spissum* |
| - | | - | | | | + | + | 1 | | *Palaquium canaliculatus* | | |
| - | | | | | | | + | 4 | *Bhesa ceylanica* | *Semecarpus gardeneri,*<br>*Syzygium wightianum* | | *Psycotria dubia* |
| | - | | | - | | | + | 1 | | | | *Leea indica* |
| | | | - | | | | + | 3 | *Cryptocarya wightiana* | *Chaetocarpus coreaceus,*<br>*Chaetocarpus castanocarpus* | | |
| | | | | | | | + | 9 | *Shorea megistophylla* | *Mastixia tetrandra,*<br>*Syzygium neesianum* | | *Psycotria nigra, Gaertnera vaginans,*<br>*Gaertnera rosea,*<br>*Glochidion acuminata, Litsea longifolia, Allophyllus zeylanicus* |
| | | | | | | | | 23 | | | | |

**Table 3.** Examples of more abundant species showing significant positive (+) and negative (-) associations to different habitats in the 25 ha plot at Sinharaja. (Seven species showing only (-) associations and five species showing only (+) associations are not given in this table).

| | |
|---|---|
| ***HSS*** = *High elevation steep slopes;* | ***LSS*** = *Low elevation steep slopes;* |
| ***HFS*** = *High elevation less-steep slopes;* | ***LFS*** = *Low elevation less-steep slopes;* |
| ***HSG*** = *High elevation steep gullies;* | ***LSG*** = *Low elevation steep gullies;* |
| ***HFG*** = *High elevation flat gullies;* | ***LFG*** = *Low elevation less-steep gullies.* |

# Flowering in Pasoh FDP...

*Continued from page 9*

fall. This article only reports the flowering phenology and fruit-fall patterns of these two general flowering events.

Collections in the seed traps revealed differences in species composition of reproducing species and in the magnitude of general flowering at the community level. In the 2001 GF, 308 species were recorded in the trap census, while 521 species were recorded in 2002 GF. These two general flowering events did not show high consistency in species composition: only 178 species (34%) reproduced in both events (Table 1). Furthermore, the number of empty traps was much higher in the 2001 GF. These facts suggest that the 2002 GF was a stronger event than the 2001 GF.

In addition to the weekly trap censuses, a whole plot survey of all adults in the Dipterocarpaceae familiy showed consistenly higher flowering than in others. Sixteen Dipterocarp species (62%) reproduced in both events, but a much lower percentage of individuals (9%) reproduced in both events; suggesting that there may be resource constraint in reproduction.

We observed temporally staggered flowering for *Shorea* species (Figure 1) in both general flowering events. This is consistent with the flowering sequence described by Chan and Appanah in 1980, Appanah in 1985, and Ashton and colleagues in 1988. However, the flowering period was twice as long in the 2002 GF (23 weeks) as it was in the 2001 GF (11 weeks). Despite this, seed fall during both general flowering events spanned a ten-week period. In the 2001 GF, 45% of the seeds fell within one week, but no such distinct seed-fall peak occurred in the 2002 GF. The highest seed fall week in the 2002 GF received 23% of the seed-fall; only two other weeks each received more than 15% of seed fall.

In summary, although both events showed a staggered sequence of flowering and concentrated seed fall in *Shorea* species, they differed greatly in the magnitude, spatial pattern, and timing. The variations also applied to other species joining the events. In addition, environmental fluctuations added to the complexity of this event. For example, due to a severe drought at the end of the 2001 GF, all but 13 seedlings out of 725 dipterocarp seedlings died. Thus, long-term monitoring on seed production and seedling-establishment pattern in both general flowering and non-general flowering years is necessary for fully understanding the importance of general flowering on forest dynamics and the maintenance of diversity.

*This project was initiated by Drs. I-Fang Sun (CTFS), S. Joseph Wright (STRI), and Stephen P. Hubbell (University of Georgia) with collaboration from Dr. Md. Noor Supardi (Forest Research Institute Malaysia), and is supported by the U.S. National Science Foundation.* ❧

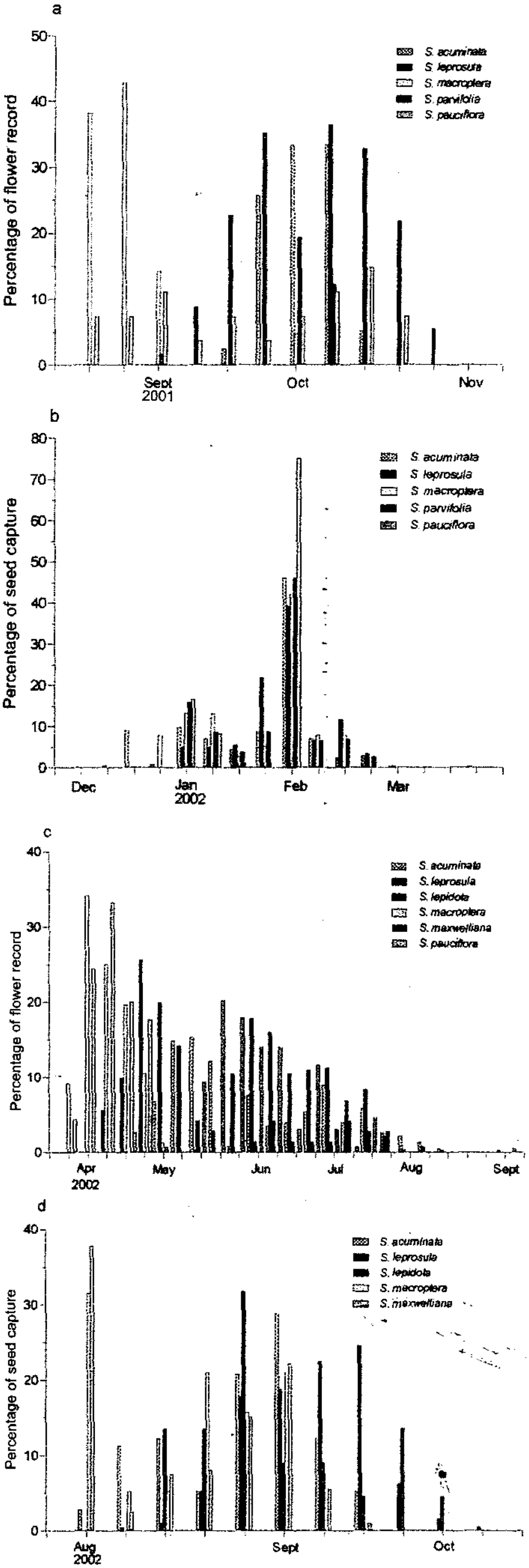

**Figure 1.** Phenological patterns of selected *Shorea* species in two general flowering events: (a) Flowering pattern in 2001 GF, (b) Seed-fall pattern in 2001 GF, (c) Flowering pattern in 2002 GF, (d) Seed fall pattern in 2002 GF.

## Mudumalai, India...

*Continued from page 6*

habitat (18), followed by *positive-convexity* (15), and *plateau* (14). Of the three topographical variables, slope had the strongest effects with 25 associations, followed by convexity (18) and elevation (11). In all, 29 species had at least one significant association to at least one habitat (Table 1). Species positively associated with the *streamside* (e.g., *Dalbergia latifolia* [Leguminosae], *Garuga pinnata* [Burseraceae]) were usually rare, not only in the Forest Dynamics Plot but also in the 1-ha plots, except for one small shrub *Helicteres isora* [Sterculiaceae], which was common in all dry deciduous forest plots. Species that were positively associated with the *streamside* were not positively associated with other habitats.

Three of the four most common canopy trees (*Anogeissus latifolia* [Combretaceae], *Terminalia crenulata* [Combretaceae], and *Tectona grandis* [Verbenaceae]) were positively associated with the *plateau* and the *spurs* (*positive convexity* habitat), and negatively associated with the *streamside*. These species constitute the bulk of the basal area in the dry deciduous forest plots. Several other typical dry forest trees were negatively associated with the *streamside*.

The most common canopy tree *Lagerstroemia microcarpa* [Lythraceae] was not associated with any habitat feature, and occurred only in the moister forest plots at an intermediate abundance. Nowhere was it as abundant as in the region of the Forest Dynamics Plot and its high densities here is intriguing.

We expect the *slope* habitat to be moister than other parts (except the *streamside*), but only three species were positively associated with this habitat. These included an understory tree *Kydia calycina* (Malvaceae), which was extremely abundant in the 50-ha plot and whose distribution and densities in all plots was similar to *Lagerstroemia*.

To test whether these habitat associations resulted in differences in species composition between regions in the plot, we performed a TWINSPAN classification using 0.25-ha quadrats (Figure 1). The four regions defined in Figure 1 display remarkable congruence with habitat associations. Species composition does reflect habitat characteristics, defined as *streamside*, *slope*, and *plateau*. *Lagerstroemia microcarpa* attains very high densities in some regions and although this is reflected in the TWINSPAN classification, the distribution of *Lagerstroemia* was unrelated to topography.

In conclusion, about two-thirds of the species analyzed had significant habitat associations, but many had very similar patterns of associations. These results indicate that the habitat variables examined here do have a significant influence on the abundance and distributions of many species, but they do not support habitat specialization as the primary mechanism that maintains alpha-diversity in this forest. It is, however, possible that our habitat classifications were too simple and coarse-grained to discern differences in habitat preferences, particularly for the less-abundant species included in our analyses. Developing more sensitive methodologies and complementing them with field experimental studies to identify mechanisms constitute an exciting area for future research in Mudumalai. ❧

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## Water flow...

*Continued from page 2*

issues of landscape-scale movement of water though a cross-comparison of a number of Forest Dynamics Plots. The overall project has two primary objectives: (1) characterization of large-scale variation in forest structure and dynamics in relation to soil fertility and water availability, and (2) characterization of local attributes of forests in relation to fine-scale variation in topography, soil fertility, and water availability.

The soil-hydrology component of this project focuses on hydrological processes in the soils, and involves a mix of field-work and modeling. The hydrological fieldwork includes measuring soil permeability and texture, measuring water levels in a stream with gages, and measuring rainfall. This approach has been refined on the Forest Dynamics plot on Barro Colorado Island, where part of the plot is in the catchment of a small stream. The water discharge on this stream is measured and is used to characterize moisture relations for the plot. We plan to use technologies that are relatively inexpensive so that we can replicate the experiment in several locations; hopefully this will eventually include all sites. We are also seeking funds to include stream and rainfall chemistry.

To interpolate our data across each Forest Dynamics Plot, we will also implement simple, physically based hydrological models for each site, using TOPMODEL. With these models we anticipate being able to reconstruct reasonable soil moisture histories, over the duration of the rainfall record, for each 5-meter grid square in each plot. These predictions would describe the moisture conditions that would be experienced by trees within that grid square. Also, we anticipate being able to assess the importance of the overland-flow nutrient-loss pathway at each location.

Stream catchments are the natural units for the study of hydrology in a landscape, and current Forest Dynamics Plots do not conform to stream catchments. In order to correct for this discrepancy, we will have to combine data from our detailed work within the Forest Dynamics Plots with regional data, including vegetation (1-km resolution maps of the world in 1992 derived from the Advanced Very-High Resolution Radiometer [AVHRR] satellite), topography (90-m resolution radar-derived from Space Shuttle), geology (American Geological Institute), and soil (UN Food and Agricultural Organization). For each forest-dynamics plot site, we plan to prepare a map of these data for a 100-km square around the site. These maps will be available to all researchers in CTFS. ❧

# CTFS RESEARCH GRANTS PROGRAM: FUNDING SCIENTISTS THROUGHOUT THE TROPICS

*Marie Massa - Center for Tropical Forest Science*

The CTFS Research Grants Program recently completed its first two rounds of award announcements in November 2003 and April 2003. During these grant cycles, CTFS received 68 grant proposals. In total, $1 million was requested, and out of this pool, 21 proposals were selected for full or partial funding for a total of over $200,000.

The CTFS Research Grants Program is open to all researchers – from graduate students to senior scientists – for projects three months to three years in length. This program, designed to catalyze research linked to the CTFS network of Forest Dynamics Plots, provides opportunities for scientists and students to work in or with data from one or more of the Forest Dynamics Plot. One of the objectives of this program is to attract and support scientists from across the globe, especially countries where the CTFS plots are located.

The next two deadlines for applications are August 29, 2003 and February 27, 2004.
For more information please visit: www.ctfs.si.edu

*The CTFS Research Grants Program is made possible through the generous financial support from the Celerity Foundation at the Peninsula Community Foundation.*

| Summer 2002 Research Proposal Title | Study Site | Principal Investigators |
|---|---|---|
| Growth and survival of trees in relation to canopy closure in a 50-ha neotropical forest plot | BCI | Robert John (India) |
| A Topographic Comparison of Soil Nutrient Status in Relation to Habitat Specialization in the 25-ha Forest Dynamics Plot at Sinharaja | Sinharaja | H.M.S.P. Madawala Weerasinghe (Sri Lanka) |
| Habitat specificity and diversity in the Korup Forest Dynamics Plot, Cameroon | Korup | George Chuyong (Cameroon) |
| Seed Rain in Tropical Forests: Patterns, Causes, and Consequences for Forest Dynamics | Luquillo, Yasuni, BCI, Malaysia | Helene Muller-Landau (USA) |
| Comparing interspecific interactions between tree species in the New- and Old World Tropical Forests | Malaysia & BCI | Christopher Wills (UK) |
| Ecological and evolutionary genetics of two vertebrate-dispersed tropical trees, *Simarouba amara* and *Symphonia globulifera* | Yasuni & BCI | B. Denise Hardesty (USA) |
| Understanding the origin of tropical tree species richness: a phylogenetic analysis of ecological data from Sinharaja's Forest Dynamics Plot | Sinharaja | Elizabeth Stacy (USA) |
| Forest Reserves as Refugia for Human Impacted Biodiversity: A Case Study of the Forest Dynamics Plot in Mudumalai Wildlife Sanctuary, India | Mudumalai | Jayshree Vencatesan (India) |
| Contribution to the taxonomical knowledge of the Myrtaceae, with special reference to the genus *Calyptranthes* Sw., in the Yasuni Forest Dynamics Project | Yasuni | Alejandra Moscoso (Ecuador) |
| Phenologies of Tropical Forests : The Role of Light Limitation | Luquillo | Jess Zimmerman (USA) |

| Fall 2003 Research Proposal Title | Study Site | Principal Investigators |
|---|---|---|
| Reconstructing historical disturbance regimes and forest stand dynamics in the forest mosaic of the Huai Kha Khaeng Wildlife Sanctuary, western Thailand | HKK | Patrick Baker (USA) |
| Comparative Community-wide Studies of Forest Reproduction and Pollinators in Old and New World Tropical Forests | BCI, Yasuni, Khao Chong, Pasoh, Lambir | Rhett Harrison (UK) |
| Seedling Dynamics in Yasuni National Park, Ecuador | Yasuni | Margaret R. Metz (USA) |
| Linking Seedling Drought Resistance with Species Habitat Associations: Dry Season Mortality | BCI | Bettina Engelbrecht & Liza Comita (German) |
| Preliminary Study to Evaluate the Arboreal Species Composition, Abundance and Diversity in the Panamanian Forests | BCI & Panama | Rolando Perez, Salomon Aguilar and Jose Deago (Panama) |
| Pollen dispersal limitation in tropical rainforests: A comparative study in BCI and Yasuni | BCI & Yasuni | Christopher Dick, Frederic Austerlitz & Eldredge Bermingham (USA) |
| Investigation of oomycete fungi believed to be involved in Janzen-Connell effects observed on Barro Colorado Island, Panama | BCI | Jason Watkins (USA) |
| Herbaceous and Epiphytic Flora of the Korup Forest Dynamics Plot in Cameroon | Korup | Louis Zapfack, Gaston Achoundong & Bernard Aloys Nkongmeneck (Cameroon) |
| The *Brownea grandiceps* species complex used to study modes of speciation in understory rain forest trees | Yasuni & Venezuela | Gorky Villa Munoz (Ecuador) |
| A Mechanistic Understanding of the Responses of Soil Carbon Pools in Tropical Forests to Increasing Global Temperatures | BCI, Yasuni, HKK, Khao Chong | Jennifer S. Powers (USA) |
| Comparison of fruit characteristics, dispersal syndromes and seed dispersal in lowland rain forests of the Western Ghats and Sri Lanka | Mudumalai & Sinharaja | Priya Davidar, I.A.U.N. & C.V.S. Gunatilleke (India) |

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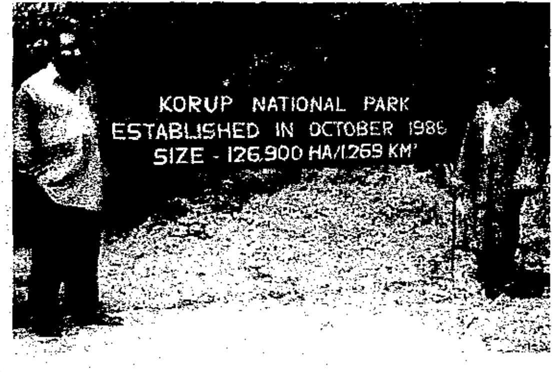
# NEWS SECTION

## KORUP, CAMEROON

Sainge Moses, field director for the Korup Forest Dynamics Plot, received the "CTFS Award for Outstanding Field Service" for his enthusiasm, dedication, and contribution to the Korup program. CTFS would like to recognize the important and essential work of field personnel who make the Forest Dynamics Plot network possible.

The CTFS Stand Table Book Series has also published *Tree Species of Southwestern Cameroon: Tree Distribution Maps, Diameter Tables, and Species Documentation of the 50-Hectare Korup Forest Dynamics Plot* by D.W. Thomas, D. Kenfack, G.B. Chuyong, Sainge N. Moses, E.C. Losos, R. Condit, and N.C. Songwe. For a copy of this publication please contact the CTFS Washington DC office.



The price giving ceremony of Sainge Moses at the entrance of the Korup National Park witnessed by the Assistant State Council for Mundemba

## MUDUMALAI, INDIA

Raman Sukumar, Principal Investigator of the 50-ha Mudumalai Forest Dynamics Plot in India and director of the Asian Elephant Research and Conservation Centre, was recently awarded the Whitley Award for conservation by HRH The Princess Royal - the patron of the Whitley Laing Foundation. Prof. Sukumar was awarded £50,000 at the annual Whitley Awards ceremony at the Royal Geographical Society in London to advance his work with the Asian elephant. His award will help provide support to local farmers to mitigate the impacts of elephants on their lands as well as support the efforts of his field research team, which act to identify threats such as poaching for ivory and monitoring the health of the elephant population. For more information about Prof. Sukumar's research, the Asian elephant or the Whitley Awards please visit: http://www.whitleyaward.org/

## BUKIT TIMAH, SINGAPORE

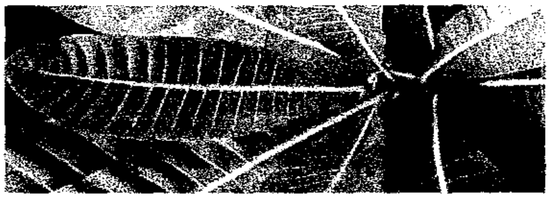
The CTFS Asia Program headquarters at the National Institute of Education – Nanyang Technological University in Singapore celebrates its 10th anniversary. There have been many important milestones for the Bukit Timah research plot in this anniversary year including the successful completion of the recensus of the 2-ha Bukit Timah Forest Dynamics Plot, which was supervised by Khadijah binte Rambe, working closely with Professor Shawn Lum and Dr. James LaFrankie. Data entry for the recensus has also been completed in Singapore. Current plans are underway to begin the addition of 2-ha of secondary forest to the Bukit Timah project.

Luan Keng Wang has also recently joined the CTFS-AA Asia Program team to conduct research on the Bukit Timah plot and to assist with the database management for the plot. Ms. Wang, a native of Singapore, is working on a doctorate at the University of Washington.

## BCI, PANAMA

The Barro Colorado Island field crew is currently carrying out the third annual census of seedlings and small saplings in the BCI 50-ha FDP. In this study, all woody plants greater than 20 cm in height and less than 1 cm dbh are tagged, measured and identified in 20,000 1-m$^2$ quadrats that have been established in the 50-ha BCI FDP. Between the first and second census, 6573 out of 60,292 individuals died (10.9%), and 7170 new individuals were recruited into the census. Mortality rates varied among life forms, with seedlings of shrub and liana species showing the lowest mortality (4.8% and 6.7%, respectively) and canopy tree species exhibiting the highest mortality (19.1%).

Dry and wet season survival of seedlings of 36 species is also being monitored in the seedling census plots as part of a new study to link seedling drought resistance with species' habitat associations in the 50-ha BCI FDP. An initial pre-dry season census was conducted in December 2002 and a post-dry season census was carried out in May 2003. Dry season survival varied greatly among species, ranging from 53 to 100%. Pre- and post-dry season censuses will be conducted over a 3 year period in order to compare seasonal patterns of seedling survival among species with differing degrees of drought tolerance.



## YASUNÍ, ECUADOR

The first recensus of the 25-ha plot started in October 2002 and is expected to be completed in September 2002. Preliminary findings indicate that, on average, there are 1000 new trees per hectare, with some hectares boasting more than 1200 new trees. Based on our experiences from other plots, only about 700 new trees per hectare were expected, thus Yasuní appears to have has a surprisingly high level of recruitment.

New surprises have also been discovered in the taxonomy of species occurring in the plot. Dr. Henk van der Werff of the Missouri Botanical Garden is describing a new genus of Lauraceae based on vouchers specimens collected by Gorky Villa from the plot. Unfortunately the description cannot be completed at this time because more fertile material is necessary but field workers are keeping a close eye on the tree in question.