A GLOBAL PROGRAMME IN INTERDISCIPLINARY FOREST RESEARCH: THE CTFS PERSPECTIVE

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ASHTON, P. S., BOSCOLO, M., LIU, J. & LAFRANKIE, J. V. 1999. A global programme in interdisciplinary forest research: the CTFS perspective. A research collaboration between forest scientists of tropical Asia and the United States is gathering new statistically comparable data, aimed at furthering an understanding of tropical forests and at translating biological and socio-economic research into results relevant to forest management, economics and policy. The programme is interdisciplinary and long-term in scope. We review its objectives and describe field methods including characteristics of the sites chosen. Achievements to date in both field work and research are summarised. Early research findings point to the human factors that are likely to influence biodiversity, question the view that the quality of logging practices is influenced by the period of the concession, and emphasise the value of managed rain forest as a carbon store. Yet they also reveal great local and regional diversity in the structure and function of the forests, and of the life history characteristics of their tree species.

Keywords: International collaboration - multiple value forests - economic optimisation - sustainable management - interdisciplinary research - statistical comparability - modelling

Introduction

In 1988, the United States Agency for International Development, with advice from the U.S. National Research Council and National Science Foundation sponsored a meeting of forest scientists from Asian nations under the chairmanship of the senior author, to seek consensus on funding priorities for research into the sustainable management of biodiverse resources. Some forty forest scientists, from Sri Lanka and India east to Papua New Guinea, attended.

The concepts of a regional network of research sites adopting standardised protocols, and an interdisciplinary approach, combining social science and silvicultural ecology, were welcomed. Forest ecologists saw the opportunity, for the first time, to make their work policy-relevant. Economists saw an opportunity to mesh their economic analysis with ecological relationships derived empirically. In 1992 the Smithsonian Tropical Research Institute (STRI) created an organ within the Institute, the Center for Tropical Forest Science (CTFS) to coordinate American efforts to advance a global programme following the objectives defined in 1989.

This paper describes how some forest scientists in tropical Asia, in collaboration with a U.S. team, have built a network of sites with the objective of defining generalisable, socio-economic, and silvicultural parameters which might aid rapid diagnosis of forest policy and management prescriptions. It reviews the overall research approach, the findings of some economic, biological and ecological work, and concludes with reflections on future research priorities.

Objectives

Two interdependent objectives of the programme were defined and accepted:

- To estimate the total economic value of examples of the major lowland tropical forest types under the diversity of economic conditions; and to provide evidence to assist policy reform for economically justifiable, sustainable, management of indigenous forests. Continuing economic change, and the likely impact of global climatic change on forest function implies that the programme should be on a continuing basis, analogous to the collection of meteorological data.

- To build and test simulation models of these forests, in order to generate testable predictions of management prescriptions for optimising sustainable yield of their most valued goods and services. These models will eventually incorporate socio-economic as well as forest ecological (including silvicultural, wildlife) data, and will include considerations of biodiversity conservation. It is a truism that, whenever ecological sustainability is of concern, any study addressing forest management and policy issues should be based on a solid understanding of the forces driving forest dynamics and its components. Of course, no better natural laboratory exists to understand species composition, their demographics, growth and dispersal than primary forest.
It is for this reason that the initial focus of the programme has centered on primary tropical rain forests. Models based on such understanding have become valuable tools to generate hypotheses for optimal management. Such hypotheses, however, need to be tested with harvesting experiments.

Data collection

Precise understanding of the relationship between community and species population distribution, structure and function in relation to soil, topography, and intrinsic characteristics such as seed dispersal and density dependence, requires mapping and monitoring large forest samples. These provide the core research facility of the CTFS programme. Extrapolation to landscape or larger scales is an objective for the future. Standardisation of ecological sampling protocols was aided by Hubbell and Foster (1983) at the STRI research forest on Barro Colombo Island (B.C.I.), Panama Canal Zone, and tested at the first Asian site, in Malaysia. Unitary large plots provide the only means for precise mapping of species distributions in relation to soil, for demographic analysis of species' populations, and for analysis of spatial and temporal interaction between populations, including interactions between tree, animal and pathogen populations. Such large plots also provide the opportunity, heretofore unavailable, for rigorous testing of the optimal plot size for working plan, silvicultural, floristic, and other surveys (Condit et al. 1998, Hall et al. 1998). Plot size has been set to capture population samples sufficient for demographic analysis of at least half the tree species contained in it, estimated to be at least one hundred individuals. For practical reasons the largest plots, required in the most species-rich forests where most trees are in low population densities, do not exceed about fifty hectares. In poorer forests, plots of either twenty-five or about sixteen hectares have proven sufficient.

The disadvantage of this approach is in the limited opportunity for replication. In this we follow Richard's (1952) pioneering example, by attempting to find sites on the three continents, which approximately replicate the same combination of environmental conditions. Commonalities of trends along gradients, and among plots whose floras are so independent, we judge to be robust. The data resulting from our programme will provide the quantitative test, and the means to identify commonalities from species-specific and other purely local forest phenomena.

In each plot, all trees > 1 cm dbh are censused; identity, diameter, and spatial position are recorded. Recensuses are carried out every five years. The level survey yields a precise contour map. The methodological protocols, adjusted for forest conditions in Asia, have been described in full by Manokaran et al. (1990).

Periodic workshops have been held to define additional requirements. These include height measurements of a subsample of the stand and key species populations, and measurement of the height of the canopy and principal leaf layers. From these, net production estimates can be calculated by allometry using published data from Pasoh (Kira 1978), correlated with canopy topography and extrapolated photogrammetrically. Seedling and sapling subplots are required for silvicultural
research and demographic analysis. Harvesting experiments are planned in Malaysia, but have not as yet begun.

Standardised protocols for economic analysis are still in process of development. A workshop was held in Chiangmai to this end (Godoy & Bawa 1993), but formulations are not yet agreed upon. On the issue of valuation (attributing a monetary value to goods and services not traded in markets) some progress has nevertheless been made with regards to non-timber forest products (NTFPs). Godoy et al. (1993), after an extensive review of the literature, proposed recommendations on necessary data to carry out complete and comprehensive studies. They noted that existing studies could not really be compared because they accounted for different costs and benefits. Strict protocols for data collection have been developed by Wilkie et al. (1994), piloted by Lubowski in Sri Lanka, and then employed at a bigger scale by Godoy in Honduras. On the issue of the socio-economic determinants of forest use (economic value of NTFP extraction), Godoy and Bawa (1993) summarised assumptions and open questions. For other values (biodiversity, watershed protection, carbon storage, etc.), attempts have been carried out but no standardised protocol to date exists.

Site selection

In each continent, the CTFS network aims to include sites representing the ends and centres of the abiotic gradients which are considered, on the evidence of existing research, to most influence lowland rain forest structure and function. Rainfall seasonality, which is broadly correlated with predictability of killing droughts although El Niño events provide a notable exception in many parts of the tropics, is the principal gradient at regional scale (Ashton 1991). Soil nutrient levels and water economy vary with geology at a more local scale, and along the topographic catena; plots are large enough to include these gradients within them. Frequency and intensity of canopy disturbance may be both regional and local, according to the cause of disturbance which may include typhoons (hurricanes), line squalls, or land slips. In addition, the influence of island biogeographical, historical factors on species richness and diversity is taken into account.

The 1989 meeting in Bangkok, and the long established and distinguished tradition in scientific forestry in Asia, gave early impetus which has resulted in this region having already completed identification of a core network of forests sites, all of which are implemented or in process. Site selection in the Asian tropics has also been aided by its monsoon rainfall climate, with single wet and dry seasons which vary in length in logical progression across the region. The Asian network has therefore come to serve as the global model. Now, additional researchers in the region are volunteering to adopt the CTFS protocols. This is providing the opportunity to expand forest types to include, for example, deciduous and lower montane forests. The U.S. contribution is to assist in regional coordination including training and workshops, data management and analysis, and in funding. At the time of writing, the National Institute of Environmental Sciences (NIES) of Japan and STRI are discussing formation of a joint venture in these respects, and
in funding. A CTFS Director for the region, J.V. LaFrankie, is based at a facility provided by the Nanyang Technological University in Singapore.

A summary of the site network in Asia therefore serves to illustrate the CTFS scheme in practice (Figure 1, Table 1). The relationship between rainfall regime and forest formations in the region is now broadly understood (Champion 1936, Ashton 1991). Such criteria have been combined with socio-economic ones to generate a framework for site selection.

**The socio-economic gradient**

In site selection, an attempt has been made to reflect various socio-economic conditions. The *Pasoh* forest (Peninsular Malaysia) is located in the most developed (among resource-rich countries) economy of the region. For the past years, the rural sector work force exhibited a decline corresponding to increased urbanisation. Economic development has led to higher wages and to a commodity-based agricultural sector. As a result, the forest is not used for subsistence activities. Part of it is still logged while the rest is mostly used for educational purposes.

Similar to Pasoh, *Khao Chong* (Peninsular Thailand) is set in an economy dominated by commodity production (e.g. rubber), but wage levels are lower than Malaysian ones. While Khao Chong is primarily a recreation and wildlife conservation area, forests nearby are still used by the local rural population, for example for hunting. In an even poorer region, the *Huai Kha Khaeng* (Thailand) plot is located in a World Heritage Sanctuary, but the surrounding forests are heavily used by local communities for a variety of uses, including, traditioanlly, logging. In a similarly poor rural setting is the Indian site of *Mudumalai*, interesting for its primary use as an eco-tourism reserve. Also in an economically disadvantaged situation is the site of *Palanan* (Philippines). What makes Palanan interesting from a socio-economic view point is the combination of a highly fragile ecosystem (the area is frequently hit by typhoons) and heavy forest exploitation.

The plot at *Lambir* (East Malaysia) is set in a rapidly developing rural economy, fueled by heavy resource exploitation (logging) and oil palm plantations. Intermittent rural wages make local populations still dependent on forest resources for various uses, including hunting, rattan extraction, and collection of other NTFPs. Its vicinity to the city of Miri makes Lambir a site where potential conflict of interests may arise in the near future between recreational uses demanded by city dwellers (Lambir already has the highest visitation rate of all Sarawakian National Parks) and consumptive uses still important to the rural population.

Finally, the site at *Sinharaja* (Sri Lanka) is located in a rural economy based on rice and paddy cultivation and home gardens. In recent years, government subsidies have promoted the conversion of home gardens into tea plantations. The communities living around Sinharaja still rely significantly on the forest for various products (home construction, food and medicines) and on tourism. The site is also an interesting experiment of collaboration between the Forestry Department and the rural communities living around the forest.
Figure 1. Centre for tropical forest science collaborative sites network
Table 1. Summary of activities at CTFS sites in Asia

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<tr>
<th>Social and economic research</th>
<th>Sites</th>
<th>Pasadena</th>
<th>Lambir</th>
<th>Khao Chong</th>
<th>Palanai</th>
<th>Sinharaja</th>
<th>Bukit Timah</th>
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Activities: X = Initiated, P = Proposed, D = Desired.

NB: D takes into account appropriateness and practicality of implementation, and avoidance of unnecessary replication. Mudumalai, in a strict preserve, is established for specific purposes only.

* All stations will have a standard automatic meteorological station: Rainfall, temperature, humidity, wind speed.
The rainfall seasonality gradient

This is represented by four plots on adult yellow sandy clay soils:

*Pasoh Research Forest*, Negeri Sembilan, Peninsular Malaysia; an initiative of the Forest Research Institute Malaysia under N. Manokaran. A 50-ha plot experiencing relatively low but evenly distributed rainfall, nevertheless with almost annual, but seasonally only weakly predictable, droughts. Topography is gentle, of low hills and flat land. Canopy disturbance is erratic, predominantly through squalls. Three censuses have been completed. Other Asian sites in the same climate, at Lambir and Sinharaja, differ in other respects. A replicate plot is under construction at Yasuni, on a tributary of the Napo River in the Ecuadorian Amazon. Soils there are similar, but the rainfall is higher (3500 mm) and the topography somewhat steeper.

*Khao Chong National Park*, Trang, Peninsular Thailand, sponsored by the Royal Thai forest Department and led by Sarayudh Bunyavejchewin as in the next case, with the collaboration of the National Institute of Environmental Sciences (NIES) of Japan. A 16-ha plot under much higher mean annual rainfall than Pasoh, but with a regular two month albeit not intense dry season. The first census is in process. This site was chosen in part to replicate the B.C.I. site but it is on steeper land, the dry season is slightly shorter, and the area experiences occasional typhoons. Secure forest on undulating land under this rainfall regime may no longer exist in the Asian tropics. B.C.I. conditions are also replicated at a plot being installed at Korup National Park, Cameroon, West Africa. Another island site in this rainfall climate exists in Asia at Palanan.

*Huai Kha Khaeng World Heritage Sanctuary*, west centre Thailand. At the driest, most seasonal limits in the distribution of lowland evergreen forest in Asia. Undulating land including an ecotone between dry evergreen dipterocarp forest and mixed deciduous forest. The first census is completed, the second scheduled for 1999. The site is as yet unreplicated.

*Mudumalai Wildlife Sanctuary*, Tamil Nadu, India, a site under R. Sukumar maintained by the Indian Institute of Science, Bangalore. The 50-ha plot of this associate site is in dry deciduous forest and experiences six dry months. Sukumar established it primarily to document the influence of overstocking of elephants and man-made fire on the vegetation. It is strictly outside the terms of reference of the network, but provides an invaluable test of trends along the rainfall gradient.

The soil nutrient gradient

The influence of mineral soil nutrient concentrations has been best documented in northwest Borneo (Baillie & Ashton 1983, Baillie *et al.* 1987, Ashton & Hall 1992), but similar relationships are expected to occur, on floristic evidence, throughout the climatic range of lowland rain forest (Ashton 1991). Much of the range of mineral soil nutrient concentrations on yellow-red soils in lowland mixed dipterocarp forests of Asia can be captured within one site.
Lambir Hills National Park, Sarawak, Malaysia, a project of the Sarawak Forest Department under Abang Abdul Hamid Karim, in association with T. Yamakura, Osaka City University, and K. Ogino, Ehime University. In this high annual rainfall aseasonal site, a 52-ha plot has been laid across the ecotone from sandy humult to clay udult ultisols. The extraordinary species richness reflects the high species turnover across the ecotone. The ecotone overlies a change in substrate, and crosses a ridge. Catenary gradients in soil water economy are therefore partially independent of the main nutrient gradient in this sample, permitting separate analysis of their influence on forest structure and function. Two censuses are completed. No replicate is yet installed, but weaker, covarying catenary gradients in soil nutrients and water occur in the Sinharaja plot.

Canopy disturbance

A regional gradient is captured by a site at Palanan, 8 ha, on the windward lower slopes of the Sierra Madre, Luzon, Philippines, which is led by the College of Forestry at Isabela State University, sited on a low ridge running perpendicular to the predominant track of frequent typhoons, the last of which hit in 1995. On red clay loam udult ultisols. The forest is distinguished by its even canopy, rarity of windthrow and high diameter/height ratio of canopy trees. The canopy experiences leaf and twig shredding during typhoons, and the species have high capacity for shoot reiteration. Once censused, it will be expanded to 16 ha. Palanan is replicated by a plot of the same size and climatic conditions at Luquillo National Park, Puerto Rico.

Khao Chong, Pasoh, and possibly Sinharaja serve as sites with occasional, more catastrophic canopy disturbance by wind. Lambir has no recorded history of killing winds, but the ridge within the plot is a cuesta, with a backslope which experiences periodic catastrophic landslips following exceptional rain. These landslips occur on both udult clay and humult sandy soils, and are set in slopes which are otherwise undisturbed.

Island biogeography

This is addressed by the Sinharaja plot, Sri Lanka, under C.V.S. and I. A. U. N. Gunatilleke of the University of Parideniya in association with the Sri Lanka Forest Department, B.M.P. Singakumara of Sri Jayawardenepura University and P.M.S. Ashton and his students at Yale University. This 25-ha plot is set across the catena of a steep slope and narrow ridge on pre-Cambrian metamorphic rocks bearing udult clay ultisols. The site is more heterogenous and the rainfall almost double that of Pasoh with no recorded droughts, yet the flora is only one quarter as rich. With the exception of Palanan whose historical biogeography is complex, all other plots are continental.

For educational purposes and as an experiment in conservation management, though, the Nanyang Technological University has placed a 2-ha plot, using the same protocols, within the c. 30 ha of residual primary forest remaining in the
Bukit Timah Forest Reserve, now a nature park within the City of Singapore. The aim of this residual fragment of lowland and hill dipterocarp forest on udult sandy clay ultisol soils, whose history is well-known, is to monitor tree species extinction, and also immigration rates.

**Accomplishments and first results from Asia**

The core site network in Asia has been identified, and plot establishment has been initiated throughout the network. Nevertheless recensus, and therefore dynamic data, are only available from two sites: Pasoh forest, where three recensuses, and Lambir and Bukit Timah, where one, are now complete. Published plot results are overwhelmingly concentrated on the Pasoh site. This is not the place to publish research results, which we therefore present in summary, in order to indicate the scope of what is now possible. Furthermore, there is a wealth of work currently in progress, to which only brief mention is appropriate. The advanced state of research at Barro Colorado Island, where a 50-ha plot, installed in 1982, has undergone three censuses, provides the primary yardstick for all current comparisons.

**Valuing non-timber forest goods**

One important objective of the CTFS programme is the quantification of the economic value of tropical forests, together with the study of the factors that influence these values. Addressing these issues is critical to understand how tropical forest values change as a response to economic development. They are also important in the design of appropriate policies and development programmes\(^1\). For example, as Wells and Brandon (1992) and Kramer *et al.* (1997) point out, many projects aiming at the dual objectives of conservation and rural development (e.g. Integrated Conservation and Development Projects or ICDPs) performed quite poorly (from a conservation standpoint), partly because of a poor understanding of the linkages between ecosystem productivity and human behaviour in a changing economic environment. Such linkages, in many cases, were ignored altogether in the project planning phases.

Initial work conducted in Pasoh Research Forest, Malaysia, to assess the non-timber riches of this forest revealed a large amount of species that are known to bear edible fruits and that, therefore, could potentially have economic value (Saw *et al.* 1991). The value of many NTFPs at Pasoh has been later quantified by Lim and Jamaluddin (1994). Their current economic value is concentrated in few species with an overall value that is quite limited especially if one considers the high extraction costs. The situation is not so in Sinharaja, Sri Lanka, where Gunatilleke (1998) estimates that,

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\(^1\)Of course, as many have noted (e.g. Common & Perrings 1992, Pearce 1996) valuation alone will not guarantee that forest resources will be managed more sustainably. The ability of resource users to "capture" those values is at least as important. Value capture, in turn, requires proper institutional arrangements (e.g. clearly defined property, use, and access rights).
on average, more than a quarter of household income comes from the collection of NTFPs. Such percentages may be close to zero for a few wealthy households and as high as 80% for many poor ones. Interestingly, household dependency seems to be influenced not only by the socio-economic characteristics of the household, but also by the availability of substitutes, and by other social and gender related considerations yet to be untangled (Lubowski in preparation). Anecdotal observations also suggest that the presence of the Forestry Department (extraction of timber and non-timber products from the forest is prohibited) has influenced villagers’ subsistence and commercial use of the forest.

This work has been complemented by research that meanwhile related forest use to size of land holdings and other socio-economic parameters (Caron 1995, Ekanayake & Abeygunawardena 1995, Senaratne & Abegunawardena 1995). This work is being continued and expanded by K. Dayanandan of the Sri Lanka Forest Department.

Other service values (amenity benefits) have been examined at Sinharaja by Abeygunawardena and Seranatne (1993).

Forest management and economics

Clearly, studies that focus on the importance of various forest goods and services are of extreme importance and demand further research attention. However, to take them into account in management and policy decisions requires another piece of information: how these values are influenced by other activities, in other words the degree to which management for one value enhances, or compromises, the use of another value (opportunity cost). Decisions often involve trade-offs, and tools that would aid in their quantification are also critical. Plot data have proved valuable in guiding silvicultural experiments and in the quantification of these trade-offs.

One of the first practical uses for the plot data was to identify merchantable species with promising growth rates that could be tested in plantations. This has been done in Panama (Condit et al. 1993a,b), and in Sri Lanka, where timber, and non-timber species important in the village economy have been line-planted experimentally following removal of varying numbers of lines in a maturing Pinus caribaea plantation within the Sinharaja buffer zone. The results proved excellent, and are currently being applied in practice and at larger scales (Singhakumara et al. 1996, Ashton et al. 1997 b, 1998).

Another use of the plot data was to develop simulation models that could be used to address tropical forest management and policy questions. In fact, although tropical forests occupy 51.5% of the world’s forested area (Borota 1991) and host the majority of the world biodiversity, relatively few tools are available to guide their management (see Liu & Ashton 1995 for a review). This is in contrast with the hundreds of models built for forests in temperate (e.g. Shugart 1984, Ek et al. 1988) and boreal regions (e.g. Leemans & Prentice 1987, Bonan et al. 1990). Furthermore, the majority of the existing tropical forest models are stand models (e.g. Vanclay 1989), mainly developed for predicting timber growth/yield, and thus less apt to consider other forest outputs (e.g. stand diversity, carbon storage, species
However, to deal with questions related to species richness requires the explicit recognition of tree species distribution and population dynamics and the influence of surrounding areas on forest dynamics (Liu & Ashton 1995).

Such ecological interactions have been considered in FORMOSAIC, a forest simulation model which considers not only ecological conditions within a focal forest but also the influences from adjacent areas (Liu & Ashton 1998a). The model is individual-based (it tracks the characteristics of every tree over time), spatially explicit, and hierarchically structured. It integrates information of tree position, regeneration, growth, death, spatial interaction, and environmental factors. Data for parameterising FORMOSAIC were obtained mainly from the 50-ha plot in the Pasoh Forest. Model simulation results agreed well with independent field census data in terms of species richness, species composition, tree abundance, and basal area.

Model behaviour was examined through sensitivity analysis and uncertainty analysis. Sensitivity analysis — used to test how model output responds to small changes in parameters of interest (Jørgensen 1986, Turner et al. 1994) — indicated minimum harvest size was the most sensitive parameter in influencing species richness (Liu & Ashton 1998a). Species richness was also extremely sensitive to the duration of seed immigration from species-rich surrounding forests.

Through uncertainty analysis — employed to identify how model results vary with large variances in parameters (i.e. when the parameter values have too much uncertainty or management parameters have a wide value range) — we found that species richness had scale-dependent and nonlinear relationships with many environmental (e.g. windthrows) and management (e.g. timber harvesting) factors.

We have also applied FORMOSAIC to evaluate the influence of adjacent non-forest on the fate of the species richness of the focal forest (Liu et al. 1998). We expect a surrounding area comprising non-indigenous species to impact species diversity within a primary forest in two important ways. First, it may contain animals or plants that may invade the indigenous forest and alter its dynamics.

Pasoh is partially surrounded with oil palm plantations. The fruit crop of African oil palm (Elaeis guineensis) provides an excellent food source for wild pigs (Sus scrofa), allowing the local pig population to increase in density by an order of magnitude. These wild pigs build breeding nests in the adjacent primary forest by harvesting numerous small trees and piling them up to create a dome-shaped nest. Simulations indicate that, if our hypotheses are correct, tree species diversity in the primary forest may change dramatically in response to the interactions among types of surroundings, timber harvesting, and pig damage. The effect of the above variables on species diversity was found dependent on the dimension of the focal forest. There were also strong and complex interactive effects of parameters related to pig damage on species richness.

So far, FORMOSAIC has been used to generate research hypotheses and to simulate long-term effects of hypothetical scenarios regarding timber harvesting in a landscape context. The model needs to be refined through collecting more empirical data, including seed dispersal, regeneration, growth, and survival of recruits < 1 cm in dbh. We expect that FORMOSAIC can be used to address other
important issues such as fragmentation and forest remnant dynamics and to assist in balancing forest management for species diversity and timber production from a landscape perspective.

In another research effort, we have utilised the data from Pasoh to build a model that would aid in the evaluation of the potential productivity of a lowland dipterocarp forest in Peninsular Malaysia with respect to timber, and other environmental indicators such as carbon storage and stand structural diversity. This set of studies was partially motivated by the fact that global environmental issues such as global climate change have increasingly taken the centre stage of international environmental debates and tropical regions can play a substantial role in addressing this issue.

Questions of interest included: What is the productive potential of these forests in both economic and environmental terms? What are the feasible and desirable ways to manage tropical forests for multiple uses? If certain environmental values could be internalised (for example through the Clean Development Mechanism established in 1997 by the third Conference of the Party of the Framework Convention on Climate Change) what alternatives do managers and policy makers have to maximise the value of these resources? What forest policy instruments (e.g. terms of concession agreements) are effective in defending the principles that underlie sustainable forest management?

To begin addressing these questions we developed a simple model where the hundreds of tree species present in the plot were grouped in a limited number of species and size groups (Boscolo et al. 1997). The model could represent the timber potential of the stand, its diameter and species group distribution, biomass changes, and the financial implications of alternative management schemes. The selection of model specification represented a compromise between management relevant detail, ease in results interpretation, and ability to integrate the model structure in optimisation modules so that searches for maximum carbon storage or maximum stand diversity subject to a minimum economic performance could be performed (Boscolo & Buongiorno 1997).

A first application of this model revealed that carbon emissions from logging activities could be reduced through lengthening of the felling cycle, through an increase of the diameter cutting limits, or through the adoption of less damaging harvesting practices. However, the extent to which each practice would be effective (in terms of carbon emissions saved, and its cost) was largely unknown. Using the model, Boscolo et al. (1997) simulated the outcome of logging a natural forest stand on timber revenues and carbon storage. By varying the frequency of harvests, the size of the trees cut, and the logging technology adopted, they were able to compute the carbon storage of the virgin stand, to identify the most profitable practices, and to estimate the trade-offs between financial returns from timber production and carbon sequestration. For example, the model predicted that, compared to conventional logging practices, the adoption of reduced-impact logging (RIL) could significantly reduce the amount of carbon release while improving the profitability of future harvests. Carbon savings could be attained at a cost of $3 to $5 per ton of carbon.
In another application, the forest growth model was integrated in an economic framework to study the desirability of alternative designs for forest concession contracts (Boscolo & Vincent 1998).

The rationale for such study was that, in absence of regulation, loggers can be expected to ignore the negative environmental impacts of logging and that appropriate concession contracts could play a potentially important role in providing loggers with the adequate incentives. The study tested the empirical significance of several common recommendations for promoting better logging practices: making concession agreements longer, linking renewal of those agreements to logging practices, and using performance bonds to encourage compliance with logging regulations. The findings of Boscolo and Vincent challenged some of the conventional wisdom. For example, they found that long concession periods by themselves do not induce less damaging logging practices, and that even short term concession periods, if their renewal is linked to observable performance indicators, may secure compliance with forest regulations. Vincent and colleagues are currently attempting to test these findings empirically. We expect that these models, and their future refinements, will become increasingly useful in the future. Further practical applications may include the development of baselines and project scenarios in forestry-based carbon offset projects.

**Forest structure and floristic composition**

Documentation of overall forest structure and floristic composition at Pasoh is already advanced (Kochummen et al. 1991, Manokaran et al. 1991, 1992, Kochummen 1997), and has been summarised at Lambir by the group of T. Yamakura, Osaka City University (Yamakura et al. 1995, 1996). A florula, a basic research tool required for each site, has been published for Pasoh (Kochummen 1997). A field guide to the common trees and shrubs of Sri Lanka, an associated project, has recently appeared (Ashton et al. 1997a).

Reports are being published containing a tree species list for each plot, and a map and information on the population structure of each species. This has appeared for Pasoh (Manokaran et al. 1992), is in draft for Huai Kha Khaeng and Bukit Timah, and in preparation for Lambir and Sinharaja.

These summary data are invaluable for identifying questions for analysis or further research. In particular, they provide preliminary data on the relationship between species distributions and abiotic factors, notably topography and soil. These relationships have been examined in detail for the three species of *Scaphium* in the Lambir plot (Yamada et al. 1997). The Pasoh maps assist in resolving differing interpretations of floristic variation (Wong & Whitmore 1970, Ashton 1976.) The Lambir maps show that, though species invade across ecotones onto soils beyond their normal edaphic range, they are mostly represented by juveniles there, implying higher mortality. The dynamic relationships underlying this pattern have been examined in elegant detail, by observation and experiment, in a continuing study of *Dryobalanops lanceolata* and *D. aromatica*, closely related dominant emergents occurring on either side of the ecotone at Lambir, by A. Itoh...
Liu and Ashton (1998a) also found that individuals of species whose populations have concentrated in swamp at Pasoh declined in average growth rate, the further they grow from swamp. Both observations are consistent with the source-sink hypothesis of Pulliam (1988).

There appears to be a consistent decline in stand density in the three sites censused, which varies little within plots at 6800–7500 individuals > 1 cm dbh ha\(^{-1}\) in the aseasonal lowlands, to 2400 ha\(^{-1}\) at Huai Kha Khaeng at the seasonal margin of evergreen forest, and 400 ha\(^{-1}\) in heavily browsed dry deciduous forest at Mudumalai. It has been assumed by foresters and ecologists in the past that this decline is due to increasing juvenile mortality in the dry season (e.g. Chengappa 1934, 1937). At Huai Kha Khaeng, Patrick Baker (in preparation) found little evidence of juvenile mortality due to drought, instead inferring that mortality is due to periodic incursions of ground fires from adjacent deciduous forest.

Evidence from population structure of certain canopy trees of both deciduous and evergreen forest at Huai Kha Khaeng suggests that conditions for their successful regeneration are periodic, apparently due to more or less long term shifts in the position of the deciduous-evergreen forest ecotone due to fire, a factor that is amenable to management.

Species diversity and its maintenance: testing theory

Research at the B.C.I. plot has focussed on identification of factors which may maintain species diversity. Mean annual rainfall has steadily declined there since records began in 1924. There was a severe drought in 1983, just after the first census, which led to increased mortality and decreased growth rates with consequent major changes in the rank order of species abundance. This implies that stochastic forces, in this case catastrophic drought, are influential in determining floristic structure, and that forest composition is not in equilibrium. Hubbell, on the basis of research at Guanacaste Province, Costa Rica and B.C.I., has held that deterministic influences are subordinate to the random effects of limited seed dispersal and irregular seed-set among species whose ecological ranges broadly overlap (Hubbell & Foster 1983, 1986).

Hubbell (1997) has also shown that accumulation of species richness follows the expectations of the theory of island biogeography from local plot to regional scales once speciation is taken into consideration, and that there is little predictability in local species composition. Pasoh and Peninsular Malaysian data (Condit et al. 1998) more closely followed his predictions than data from Panama.

Nevertheless this does not preclude the existence of equilibrating forces within communities, notably density dependent mortality and performance, which is particularly attributable to more or less host specific fungal pathogens. Gilbert et al. (1996) and Wills et al. (1997) are finding higher intensities of density dependent mortality at B.C.I. than had previously been revealed. Preliminary results from the more species-rich Pasoh plot indicate weaker intensities of density-dependent mortality there (Okuda et al. 1995, Wills in preparation). A further equilibrating force is habitat specificity. Only 40% of species each, at
B.C.I. and Pasoh, appear to have habitat-restricted distributions within the plots. But the dramatic biodiversity at Lambir, where we estimate that there is 65% turnover in the species composition across the edaphic ecotone, may limit the role of non-equilibrium models in explaining the level of species richness or the predictability of composition.

Wildlife

Animals play a critical role in forest function (e.g. Terborgh 1992). Now that the sites and plots are censused, animals will become a major focus of research particularly concerning their influence on tree species composition and diversity. How is plant species diversity, relatively easy to survey, related to overall diversity which overwhelmingly comprises insects? No-one yet knows.

Currently, K. Ickes is examining the impact of the indigenous pig (Sus scrofa) on forest regeneration within the Pasoh plot. Pigs have greatly increased following the conversion of adjacent forest to oil palm plantation. The sows use very large numbers of saplings, apparently selected at random, for nest building. The effect of this on sapling density and composition remains unknown, but it is being examined using simulation modeling (Liu et al. 1998).

In a second wildlife study at Sinharaja, Sarath Kotagama censused bird fauna in unlogged and freshly logged stands in the seventies; Eben Goodale currently assists Kotagama’s recensus. Here, where adjacent natural forest remains, nearly all bird species and the former community structure has returned after twenty years; the subcanopy species take longest to return.

Comparative ecology

Comparative observational and experimental studies of seedlings of species occurring in ecologically sympatric congeneric clades have been a major theme at the Asian sites. Two studies have included cladistic phylogenetic analysis. The objective has been both to throw light on the level of differentiation in life history characteristics which might permit these species series to cooccur through competitive differentiation in resource use; and to establish whether ecologically similar species are closely related, or whether life history characteristics have evolved many times more or less independently. These studies, each more comprehensive than its predecessor, started with that of Rogstad (1990) on the hypoleuca group of six species of Polyaltheia (Annonaceae), mainly subcanopy trees, which was focussed on Pasoh. More extensive studies of the nine species of Shorea section Doona (Dipterocarpaceae), climax canopy trees focused on Sinharaja (Dayanandan et al. 1990, Ashton 1995, Ashton et al. 1995, C.V.S. Gunatilleke et al. 1996, 1997, I.A.U.N. Gunatilleke & Gunatilleke 1996), and twelve species of the pioneer group Macaranga section Pachystemon at Lambir (Davies 1996, Davies et al. 1998) have followed. Each study confirmed that closely related species differ notably from one another when a range of life-history characteristics is compared.
This result has been further supported by Thomas (1996a-c) who demonstrated at Pasoh that related subcanopy tree species each reach a unique maximum height, and that maximum height is related to other characteristics including size at first flowering, light saturation point, and growth rates.

Closely related species do appear to share a range of life history characteristics (Dayanandan et al. 1990, Davies 1996, Davies et al. 1998), but many characteristics also seem to have evolved more than once in Macaranga (Davies et al. in press).

Reproductive biology and population genetics

Long term phenological observations have been carried out at Pasoh (Chan & Appanah 1980, Chan 1981), Sinharaja (Dayanandan et al. 1990), Lambir (Sakai et al. 1993) and Huai Kha Khaeng (Bunyavejchevwin et al. unpublished). Of these, those at Sinharaja have been continued consistently since 1985, but have been restricted to certain Dipterocarpaceae. The most comprehensive are those carried out at Lambir by the University of Kyoto group under the late T. Inoue since 1992, and which include quantitative monitoring of canopy insect numbers (Momose et al. 1996 and in press), in what is the most extensive study of flowering biology of the rain forest canopy ever undertaken.

This work at Pasoh has permitted understanding of the environmental cue to the mass flowering of canopy trees in Far Eastern tropical forests (Ashton et al. 1988) and has been further elucidated at Lambir (Sakai et al. 1998). Mass flowering and mast fruiting of canopy trees is unique to this region, and its understanding and possible manipulation fundamental to silviculture. Work in Sri Lanka (Dayanandan et al. 1990) demonstrated that it occurs there albeit on a reduced scale. But there is no mast in the seasonal tropics of Asia. Though dipterocarps and other canopy species may not flower annually there, they seldom or never fruit in synchrony. The absence of mast fruiting, previously unrecorded, may support higher frugivore numbers by allowing a more continuous supply of fruit. Higher seed predation may therefore be an additional or alternative reason why sapling density is low in the forests of monsoon Asia.

The first studies of rain forest breeding systems (Chan & Appanah 1980, Appanah 1981, Chan 1981) and population genetics (Gan et al. 1977) were carried out at Pasoh. These, together with recent work at Sinharaja (Murawski et al. 1994) demonstrate, as elsewhere in the tropics, that outbreeding is the rule, though apomixis through adventive embryony has been found to be quite widespread in Asia (Kaur et al. 1978, 1986). Recent work has confirmed the pattern among dipterocarps in the relatively species-poor rain forests at Sinharaja. There, comparisons of the breeding system of Shorea megistophylla in primary and logged forest, and in a solitary specimen tree showed increase in self-pollination, and in the solitary tree evidence of both apomixis and hybridisation (Murawski et al. 1994).
Research priorities for the future

- The immediate priority now is to generate dynamic data from all sites, and to clean and manage them so that our original objective, comparability, is met. Within a year it is intended that static, first census data will be complete for all sites in Asia except Palanan and Khao Chong, and dynamic data will be complete for Pasoh, Mudumalai, and Bukit Timah which are all already available, and Huai Kha Khaeng and Lambir. The task of data management is rapidly exceeding our combined capabilities. A full time data manager is under discussion between CTFS and NIES.

- Several studies world-wide have already documented the impact of logging on soil erosion and wildlife, but the impact on tree species diversity and on non-timber species of economic value remains unknown. The next research priority therefore is to test predictions of the consequences of different logging regimes on timber productivity and other forest values including diversity. In a pioneer study, C.V.S. and I.A.U.N. Gunatilleke with N. de Zoysa in the 1970s put in plots along the catena in selectively logged forest at Sinharaja in which rattan and other non-timber producers were recorded; monitoring continues. The opportunity has recently arisen for CTFS to join FRIM in a similar study in lowland dipterocarp forest in the peninsular state of Terengganu. Here, it is planned to census before logging, and to carry out logging experiments, as well as to document the effects of conventional logging. Spatially explicit data will be generated, essential for recording changes in interspecific interactions, and thereby infer causes of changes in species diversity. Eventually, these experiments should be replicated under other site and socio-economic conditions. With data generated by such experiments, we would hope to use simulation modelling to create hypotheses for site-specific management protocols.

- The problem of estimating non-market values needs continuing attention. Understanding the extent of these values and their determinants is a critical element in the design of credible, effective, and efficient conservation initiatives. There is a surge of interest in carbon offset projects, some of which are based on initiatives to slow, or reverse, current rates of deforestation. Yet, much is to be learned on the intricate linkages between resource uses, and environmental, economic, policy, and social considerations. Neglect to understand these linkages, or to take them into account, may lead to enormous waste of precious resources and energies, and to further tropical forests' deterioration. Also, critical attention needs to be given to the so called "non-use values," widely recognised by most as being very important. Yet, their recognition and consideration are still plagued by conflicting views regarding their identification and measurement. Our research agenda includes attempts to assess the roots of these values and to clarify the limits (and strengths) of economic analysis to account for them. Non-consumptive uses become the dominant values of forests in urbanised and economically developed societies.
Comparisons of the relative and total values, in services and goods, of Pasoh in the almost developed economy of Peninsular Malaysia, compared with Lambir in a region undergoing rapid development, and Sinharaja in a more traditional economy, all three sharing the same climate, would be particularly informative. In the medium term, research needs to be dedicated not only at the valuation of forest services but also at appropriate mechanisms for their "capture." Recent attempts in Sri Lanka to benefit local villagers through the development of local industries (e.g. eco-tourism) may provide interesting lessons for the future in these regards. Furthermore, development within the climate change debate, for instance the recognition of the value of forests as carbon sinks in an international binding agreement, may be another such opportunity.

Optimal management practices will have to take account of local variation in site conditions. Timber stocking on nutrient-poor humic and zonal udult clay ultisols differs qualitatively as well as quantitatively (Ashton 1964). Growth rates of regenerating forest, and therefore lengths of felling cycles will differ also (Ashton & Hall 1992). An early priority is to identify the soil variables that most influence species composition and stand performance. Early studies of forest flora-soil relationships by Gunatilleke and Ashton (1987) in Sri Lanka have been expanded into transplant experiments along the catena at Sinharaja (Gunatilleke et al. 1996). David Burslem proposes to critically analyse the influence of soil nutrients on species composition and performance along the Sinharaja catena. His student, Juliana Ahmad, is currently analysing the influences of soil on species distributions within the Pasoh plot, while Akira Itoh and Peter Palmiotto are examining the performance of selected canopy species in relation to the contrasting soil conditions at Lambir. This work must be expanded, especially to the seasonal tropics. Comparisons at stand level using spatially explicit data will assist in developing site-specific silvicultural protocols. Comparisons of species performance and interspecific interactions across ecotones and between plots, using spatially explicit data and seedling experiments may also help to explain differences in species composition and diversity.

Demographic information for the complete life cycle of selected tropical forest trees would facilitate identification of critical stages limiting survival and growth, thereby assisting management. Data as yet does not exist for the construction of a complete life table, but the current research on reproduction and establishment by A. Itoh and others, combined with data on survivorship and growth during stand development becoming available from the plots, will provide it. Priority might be given to species representative of the dynamic phases of the forest, pioneers, and successional and mature phase climax species; and species of economic value.

There is unexpectedly high persistence of climax tree species in the forest fragment of Bukit Timah in Singapore, and the evidence from the plot (Ercelawn 1997) is that population structures of the vast majority remain normal, despite local extinction of important seed dispersers such as pri-
mates and hornbills. This implies low host-specificity of such mobile links, and replacement of the original forest species by generalist species of secondary vegetation such as mynahs and macaques. Understanding the interdependence between plants and animals in the forest canopy is critical to forest management, especially the conservation management of small areas, yet it is still poorly understood. The important programme of canopy research established by the late T. Inoue and his colleagues of Kyoto University at Lambir promises to fill this gap.

- Seed and seedling predators, and relatively host-specific pathogens at all stages of the life cycle, are now known to be important in causing density-dependent reduction in plant fitness, and mortality in tropical forests (Janzen 1970, Augsperger 1983a, b, Clark & Clark 1984, Gilbert et al. 1996, Wills et al. 1997). Tree pathogen interactions may be critical in sustaining species diversity. They obviously also have important implications for the design of plantations of indigenous species, including enrichment planting. T. Okuda (Okuda et al. 1995) has initiated such research at Pasoh, where C. Wills and M. Potts are also using the plot data to this end; but this is a large and important subject meriting greater future emphasis.

It should also be noted that, during the past few years, many ecologists and government agencies have recognised a need for ecosystem management beyond ecological, political and ownership boundaries (e.g. Christensen et al. 1996). Ecosystem management requires a better understanding of how human disturbances (e.g. timber harvesting) influence biodiversity dynamics and how focal ecosystems interact with adjacent areas. Research on focal ecosystems alone is usually not easy, and the study of ecological impacts across boundaries is even more challenging because more variables must be considered. The interactive effects of numerous variables involved in studying landscape scale phenomena are difficult to measure through conventional experiments or field observations.

Spatially explicit models provide a vital and complementary tool (e.g. Dunning et al. 1995, Turner et al. 1995). Central to improved management of biodiverse tropical forests is an understanding of the predictability of forest and species dynamics in space and over time. This requires study of interactions at individual, population and stand scales, necessitating spatially explicit information from large plots. Experimental research at large plots can thereby provide evidence of the limits to which generalities concerning forest function can be inferred from site based field data.

Epilogue

The CTFS programme in Asia is off to a good start. The results to date have been promising, and the level of current activity, particularly when the work of associated researchers sharing the same sites is taken into account, is encouraging. Up to now, the project has progressed at a remarkably modest level of expenditure, and a salutary sharing of costs among all participants.
To achieve the research now regarded as of highest priority the team will require a major increase in funding. This may be achieved through joint participation and sponsorship of the CTFS Asia programme by NIES, presently under discussion.

Further, as key plot data now increasingly become available, it is critical that those who generated them share in the production of results. Workshops and research exchanges must be greatly increased. Our objective is to create a regional community of interacting forest scientists held together by the intellectual stimulus of a shared challenge.

Acknowledgements

The programme described here represents an ambitious effort by a dedicated group of collaborating field researchers in several countries. The leaders are mentioned by us, but there are so many more whom we have not been able to name. Their energy and commitment are the lifeblood of the enterprise, and are respected by us all. We also thank Ruben Lubowski and Elizabeth Losos, CTFS Director, for their helpful comments.

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