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Award number DPE-5542-G-~~SS~~-8023-00

Understanding the Maintenance of Tree Species Richness for Silvicultural and Conservation Management.

Final Report

The objectives of this grant were threefold: To test the hypothesis that the ten members of a group of dipterocarp trees endemic to Sri Lanka are ecologically diversified, each occupying a separate niche which may explain their occurrence in mixture; to extend phenological observations of flowering, fruiting and leaf change in the same species, initiated with some species by 1985, in order to document the details of mast fruiting among average dipterocarp species in South Asia; and to examine their phylogeny through isozyme and DNA analysis, and thereby to relate genetic and ecological similarity. The first hypothesis implies that different species associations and their associated site conditions will require different silvicultural management. The third provides base-line information for conservation management of genetic diversity. All objectives have been implemented in the field, although some field experiments are not yet completed. Professors C.V.S. and I.A.U.N. Gunatilleke are currently on sabbatical leave at Harvard, where they are analysing the results in collaboration with U.S. project participants.

1.Comparative seedling ecology.

Methods. Fruit became available for nine of the ten species over the 3½ year period of the grant, allowing most or all of these to be included in the following experiments:

1. Transplant experiments in which species were grown at middle altitude (400 m.) in the middle and edge of forest gaps, and in adjacent understory, on ridges, upper slopes and lower slopes at Sinharaja forest. This experiment had been initiated two years previously, using four species only, by M.J.S. Ashton in collaboration with C.V.S. Gunatilleke. (8 species included).

2. Companion experiments in which species were grown across forest gaps at low altitude (Waga Forest Reserve, 150 m.) and high altitude (Suriyakande, Sinharaja, 650 m.), so that comparative performance was evaluated at mean annual temperatures of 26°c, 24°c and c. 21°c. (8 species included).

3. The effects of water, light and soil nutrients have been examined independently in shade house pot experiments in which, all 9 species have been subjected to three watering regimes, three times a week, once a week, and once in two weeks; and five light

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regimes, 2000, 350 and 50 minutes in mols m^{-2} s^{-1} PAR, and 6 and 2 hours full sunlight per day; b) 8 species have been subjected to different concentrations of phosphorous (250 - 350 ppm) and magnesium (500 - 2000 ppm) in combination, elements found to correlate with species distribution in nature; and c) 8 species were grown in pots in soils from the plots in ridge, upper slope and lower slope and in pine plantation soil, whose mineral content has been analysed.

In each above experiment, total height and number of leaves of every individual were initially measured at 6 week intervals for 4 1/2 months, and 3 month intervals thereafter; and a subsample was dug, oven dried and weighed to estimate stem, leaf, tap root and fine root components.

4. Seedlings of 7 species were planted in mixture in the center of the gaps on ridge, and upper and lower slopes at Sinharaja, in a design such that individuals of each species were equidistant from those of the remaining six, and their above-ground competition was monitored (this was the only locality at which more than one species (in fact eight) co-occurred in nature).

Results. Species have shown marked differentials in relation to light, topography and watering regimes, and altitude/temperature. Preliminary analysis suggests that all species responded similarly in above ground performance to different levels of Mg and P, and to soils collected from different habitats, but the proportion of dry weight allocated to fine roots differed. Phosphorous affected performance more than magnesium though this differed among species. All species performed best on lower slope and pine plantation soils. Results are currently under statistical analysis by C.V.S. Gunatilleke and M.J.S. Ashton.

Preliminary Conclusions. The species examined show unique combinations of responses to light, temperature and topography (water regime) consistent with their individual distributions in nature. Variation in soil nutrient concentrations was correlated with variation in performance of all the species, and served more to increase the differences in above-ground performance between them than to reverse relative performances. Increased nutrients will therefore tend to accentuate differences in other niche characteristics and thereby increase habitat-specific dominance, perhaps reducing species diversity.

The competition experiment is continuing, above-ground interspecies interactions having only started early this year.

Further work. The Professors Gunatilleke are on sabbatical leave at Harvard during August 1992 - March 1993, in order to analyse results of data and prepare for publication.

A grant from the John D. and Catherine T. MacArthur Foundation to the Professors Gunatilleke is allowing continued monitoring of all experiments in the field; further analyses and publications will follow.

Publication to date.
Gunatilleke, C.V.S., Perera, G.A.D., Ashton P.M.S. Ashton, P.S. and Gunatilleke, I.A.U.N. In press. Seedling growth of Shorea section Doona (Dipterocarpacae) in soils from different forest sites of Southwest Sri Lanka. In M. Swaine and I. Alexander, eds. Ecology of Tropical Forest Tree Seedlings.

2. Phenology.

Methods. At least thirty individuals of eight species in the group are monitored for phenological activity at about one week intervals year round and three day intervals during flowering, at the middle altitude, Sinharaja site; four other dipterocarp species in four genera are similarly monitored.

The observations made during tenure of Award DPE 5542-G-55-4073-00 and initiated in 1985, were confirmed, elaborated in further detail, and added to during the present grant.

The eight species in Shorea section Doona are pollinated by honey bees, as is one of the other species under observation. The other three each have different pollinators. The field data provide the following:

a) Degrees of phenological synchrony within populations.

b) Degree of synchrony between species, particularly
   -- evidence for mast fruiting;
   -- evidence for sequential flowering among species sharing the same pollinators;
   -- the relationship between reproduction and leaf change, in other dipterocarps found to be important in influencing tree growth and wood production in flowering years.

Results. 2.1 Shorea trapezifolia (Thw.) Ashton and its near relative S. congestiflora (Thw.) Ashton are unique among dipterocarps examined to date in that inflorescences do not displace leafy shoots, leading to a six month hiatus in leaf area, but arise simultaneously with new leaves. Also, these species and S. affinis (Thw.) Ashton flush intermittently throughout the year. These imply that, unlike other dipterocarps observed, reproduction should not occur at the cost of timber production, and years to harvest should not be affected by the need to ensure adequate regeneration before harvesting. This

hypothesis, based on the phenological results, needs to be tested with growth measurements on reproductive trees.

2.2 Mast fruiting occurs among dipterocarps of SW Sri Lanka, but more frequently and not necessarily in the same years as in the Far East. Mast years during the period of observation have occurred in 1985, 1989, 1991 (weak) and 1992. (At Pasoh Forest, Malaysia, mast fruiting during this period occurred only in 1989). This means that seedling recruitment is more frequent in Sri Lanka, and the danger of seedling absence during timber harvesting less. In addition, four species at Sinharaja, S. congestiflora, S. trapezifolia, S. affinis and S. zeylanica (Thw.) Ashton, known collectively as Tiniya Dun, did not conform to the masting pattern. Specifically, their fruit fall did not occur synchronously with the other four species, known as Beraliya Dun, in which fruit fall is synchronous and concentrated into mast years. Of the four, the first three flowered and fruited most years, out of synchrony both with each other and with other species. The fourth did not flower as frequently as other species at Sinharaja.

2.3 It was discovered that, whereas fruit of the four mast fruiting species are heavily predated by rodents, and are also collected by villagers as a carbohydrate source, fruit of S. congestiflora, S. trapezifolia and S. affinis are not predated or collected. This can explain why they can survive with fruiting out of synchrony. It also identifies these species, on account of their leaf phenology as well as frequent fruiting, as particularly promising for enrichment planting and plantation, both in Sri Lanka and elsewhere.

2.4 Analysis of sequential flowering is being carried out by P.S. Ashton with T. Givnish, University of Wisconsin. The four mast fruiting species flower sequentially, consistently in the same order. The behavior of the other species is more complex, and will be subject of further analysis.

Further work. Demographic research is now planned, in which growth of numbered trees will be monitored in relation to flowering and fruiting.

Publications to date.

S. Dayanandan, D.N.C. Attygalla, A.W.W.L. Abeygunasekera, I.A.U.N. Gunatilleke and C.V.S. Gunatilleke. 1990. Phenology and floral morphology in relation to pollination of some Sri Lankan dipterocarps. In K.S. Bawa and M. Hadley (eds.) Reproductive Ecology of Tropical Forest Plants. Parthenon and UNESCO, pp. 103-133.

Yankadawela, K. Gunatilleke, I.A.U.N. and Gunatilleke, C.V.S. 1991. Phenology of Shorea spp. (Dipterocarpaceae) in the Sinharaja forest. Proceedings of the Sri Lankan

Association for the Advancement of Science. 47th Annual Session (Abstract).

3. Population genetics and phylogeny.

Methods. Two studies have been undertaken. In one, a Sri Lankan masters student, Bama Dayanandan, under supervision of Co-Investigator K.S. Bawa, University of Massachusetts, has examined the mating systems and population genetics of the Tiniya Dun, S. trapezifolia, by means of isozyme electrophoresis. Dr. Darlyne Murawski has examined the mating system of the related S. congestiflora using the same methods. Material for a comparative study of a Beraliya Dun, S. megistophylla Ashton, was collected and is currently under electrophoretic analysis jointly by I.A.U.N. Gunatilleke (University of Peradeniya) and Dr. Darlyne Murawski, in Dr. Bawa's lab.

In a second study, S. Dayanandan, a Fulbright Scholar at Boston University under R.B. Primack and Scott Williams, has been examining phylogenetic relationships within Shorea section Doona, and also the phylogeny of the Asian Dipterocarps as a whole, using chloroplast DNA.

Results and Further work. Shorea trapezifolia is the second dipterocarp to be subject to analysis of population genetic variation. As with the first, the Malaysian Shorea leprosula Miq. genetic variability within populations, although not exceptional, is greater than between them. One of the three populations sampled was characterized by an unique allele. S. trapezefolia nevertheless has a lower level of outcrossing, at 60%, than has generally been found among dipterocarps. S. congestiflora had an outcrossing rate of 87%. There was no evidence for apomixis in either species. A masters thesis is being completed.

Preliminary analysis of S. megistophylla indicates presence of facultative apomixis, through agamospermy, in that species.

All species of Shorea section Doona have been collected for DNA analysis. Chloroplast DNA analysis is completed, and cladistic analysis of results is in progress. Ribosomal DNA and restriction site analysis will be carried out early in 1993. This research is planned to be complete in late 1993 or early 1994.

In 1991 an isozyme electrophoresis laboratory facility was acquired and established at the University of Peradeniya Botany Department as requested in the proposal. This will be jointly used by B. and S. Dayanandan on their return, and also by I.A.U.N. Gunatilleke who is currently on sabbatical leave in Dr. Bawa's lab in order to learn techniques.

No publications have yet been prepared from this component of the research.

General Conclusions. So far, this research has demonstrated that the species examined are ecophysiologically unique, and this explains the consistently different combinations of species which occur in different habitats. The results on ecophysiology, reproduction and genetics provide basic information for modeling flexible silvicultural systems for natural forests and enrichment planting schedules aimed at optimizing performance of young stands in timber production forests under different site conditions. This will be the first time that such a refinement has been used in biodiverse tropical evergreen forest. It is a practical proposition in Sri Lanka, which has a well trained forest service and, now, legislation which mandates timber harvesting by elephant which is recognized as least harmful to regeneration. A further phase in the research, under Dr. P. Singhekumara and M.J.S. Ashton, is planned in which these models will be tested by full scale experimental forest manipulations.

The results of phylogenetic research, which may assist in active management of conservation forests, will start to become available next year.

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Review of Final Report:
Award number DPE-5542-G-55-8023-00

Understanding the Maintenance of Tree Species Richness for Silvicultural and Conservation Management

The Final Report successfully summarises work so far undertaken and that continuing for completion of the investigations towards understanding the maintenance of tree species richness for silvicultural and conservation management.

The results are obtained following carefully designed experiments, and the preliminary conclusions appear consistent with the results.

The further work planned on the growth of numbered trees is appropriate, and will be essential to develop silvicultural refinements for the forests in the region.

Never before, as far as I know, has there been a study on biodiverse tropical rain forests where such a large suite of related species have been examined for their ecophysiology, reproduction and genetics, all of which will be directly used for refining silvicultural and conservation practices. Simultaneouly the project aims to answer a primary question, whether the forests are in equilibrium dynamics and if so, are the management practices in cognizance with such a feature?

The results and conclusions of this work are critical, and apply to other forests in Southeast Asia as well. Therefore, the success of this project will depend on the speed with which the results can be translated into practical management guidelines. Above that, I urge the authors to come up with simple research protocols based on their experience, which can be rapidly tried out with key timber species in other dipterocarp forests in Southeast Asia.

Finally, some remarks on the draft itself are given in the next page.

Reviewed by:

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&
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NOV 17 1992

Remarks on draft:

Page 1, Line 6: "initiated with some species by 1985" should be "since 1985"

Page 1, Para 1: The first and third hypothesis/objective are explained; But nothing about the second?

Page 1, Line 12: The (capital)

Page 2, Last line: "results to data" should be "results of data"

Prof. Peter Ashton
Charles Bullard Professor of Forestry
Boston, Massachusetts

Ref. : Award number DPE-5542-G-55-8023-00

Dear Peter,

It was good to have you at our seminar, however pity it was you had to leave early for your CIFOR meeting in Washington. I hope the trip proved useful to you. I enclose some articles on the conference that appeared in some Indonesian news papers. Once again thank you very much for your participation.

Also thank you very much for the draft final report of the above mentioned award. The type of results here described are very important. Please find attached some of my notes. Our 500 hectare experimental planting may provide you with some comparison data from Kalimantan. We planted Shorea leprosula, S. parvifolia, S. pauciflora, S. seminis on tops of ridges, middle slopes and lower slopes as well as in four different light conditions comparable to the conditions described in the report for the gaps. In addition we included different provenances as well as different ectomycorrhizal fungi. Because of the fairly large number of plants involved in the now two to three year old plantings (some 170.000 plants surviving) I hope we will be capable of discerning similar trends as the ones found by Mark. Our aim is the same, to get better stress resistant plantings of dipterocarps either by correct species site matching as well as through manipulation of mycorrhizal symbionts.

I am looking forward to meeting with you on 12 december (any more information on date, time and place ?) in Jakarta and receiving your comments on the part of my thesis you took along.

Salam hangat untuk Mary dan Mark juga dari Syennie dan anak-anak.

Willie Smits
Team Leader Tropenbos-Kalimantan

cc. arsip

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