

Discussion for Yamada's paper

Losos How do you compare the people in the Amazon and the people in Borneo in terms of their attitude towards the forest.?

Yamada Unfortunately I was not able to venture deep into the Amazon to assess their attitude towards the forest. In one area in the Amazon though I did observe that some of the people have adapted themselves to the ecotourism operation. They have their own routes to the forest and normally bring tourists to the forest using their own route. In the Amazon communication is very difficult. This is not the case in Borneo or Southeast Asia as a whole where the villages live very close to one another and the forest areas being linked by rivers.

Hirai I find the system of land use where you have home gardens, shifting cultivation and virgin forest in differing altitudes rather interesting. Can you tell us the acreage of each and whether the system can be transferred to other areas.

Yamada The land use is already widespread all over Borneo and particularly in Central Kalimantan. I do not have actual figures of the size of each, but generally they are not very big.

Ashton The system of land use in Kalimantan is certainly an interesting one where the low-lying areas or low valleys which are frequently flooded are being used for irrigated rice crop or annual crop, the lower hill for villages with their home gardens, areas higher up still for shifting or Sweden agriculture and the ridge top kept under forest, sometimes modified, sometimes close to natural forest rich in natural species. Kahat? and Sri Lanka and certainly not confined to Kalimantan. In the current situation, what is interesting now is to see how the system adapts to changing economy and communication. In Sri Lanka, socio-economic and biological research on species being conducted. The poorer people are still practising the system which is a rather intensive system although their land holding or home garden or woodlot is rather small, half a hectare or so compared to Kalimantan. What happens now with better communication and higher commodity prices, is that it is more profitable to grow single crops and sell them for cash rather than to grow mixed species. Cinnamon and tea are two popular crops in this respect. So there is a massive change from mixed species garden to one or two species. Some products are still being harvested from the forest, for instance palm sugar. But there is greater pressures on forest areas than ever before. Tea gardens are slowly encroaching on to forest reserves. Massive deforestation is now occurring. Evidence of increased prosperity is apparently not leading to a decline in the social pressure on the forest. In due course we can expect something similar to happen in Kalimantan.

Yamada I agree. My impression is that the people are very adaptable. When new influence comes in they will adapt and form new systems, some of which are destructive, but nonetheless they adapt well to changing conditions.

What can be learned from a 50 ha plot which cannot be learned any other way?

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ABSTRACT

Tropical forests are rich in species because they contain exceptional numbers of species in very low density populations. In order to understand how these species are maintained in these forests over time, and how they are affected by human activities such as logging and forest fragmentation, research on their demography is needed. This requires samples of at least one hundred individuals of a species, which for big species mandates big plots. Besides this, big plots serve a variety of other useful purposes. They permit the precise mapping of individuals in species populations in relation to habitat changes. They also permit analysis of the various optimum plot sizes for different objectives, including reliable estimates of standing volume, and of growth. Most important, they permit predictive computer models of forest growth, and response to manipulation, to be constructed which are based on spatially explicit information concerning individual trees.

WHY LARGE PLOTS?

In 1992, Stephen Hubbell of Princeton University and I met for the first time and discussed our then differing views as to how tree species richness is maintained in tropical forests. We both agreed that Hubbell's approach, to analyse the spatial interactions between individuals and population samples of species over time, was the way forward; and that we would need the means to examine the demography of the majority of species which are those occurring in low population densities. Knowing that population samples of at least one hundred individuals would be needed for statistical analysis, very large plots would clearly be needed. Hubbell had by this time already established a plot of 50 ha. on Barro Colorado Island, the long-term research site of the Smithsonian Tropical Research Institute in Panama. The area of the plot was essentially decided on practical grounds but, in event, over half the species in it were represented by samples of more than one hundred individuals.

There is nothing mystical about fifty hectares. The samples being compared are the species populations, not the plots themselves, so smaller plots can be used in less species rich forest and a minimum area of 16 ha. has been adopted (Fig. 1). A lower size limit for inclusion of 1 cm. dbh was decided on because of the need to test for the presence of distance-related growth and mortality of juveniles from conspecific adults, predicted to be a factor favoring low species richness by D.H. Janzen (1970). In light of subsequent research, it now appears that such effects, if they are general, are

concentrated on seedlings and young saplings which therefore require subsampling, which we would eventually like to do in all plots for silvicultural reasons also.

A central question is whether performance and mortality is largely influenced by unpredictable, catastrophic events such as hurricanes, droughts or landslides, or whether they are mainly determined in a predictable manner by competition. Another is whether the high species diversity noted in heterogeneous habitats is caused by the combination of several assemblages of habitat-specific species within a single sample, or the opportunities for invasion and chance establishment of species into adjacent, normally alien habitats. To address such questions, it was agreed that several sites sharing a common biogeographical region would be needed, variously differing in rainfall seasonality, soil nutrients and proneness to wind-damage and landslides; and that to meet statistical requirements for independent replication similar sets of sites would need to be repeated in the three main tropical regions.

To foresters, these concerns may sound abstruse and irrelevant, but they are not! Our questions address the predictability of forest species composition in space and time: To what extent and how must site conditions be taken into account in the search for prescriptions for optimizing regeneration and stand development of production forest? In what way, if at all, does logging influence the survival of rare species, and the maintenance of biodiversity -- is logging in national parks a legitimate activity? Also, the theory of Island Biogeography (MacArthur and Wilson 1967), now well tested, predicts that extinction rates on islands are proportional to their area: When a habitat island is reduced in area by ninety percent, in due course its biodiversity will be reduced by fifty percent. This has obvious implications for the planning of national parks, such as Lambir, in a landscape in which the rest of the forest will be converted to agriculture and other development. But if the original forest already consists of an archipelago of habitat islands because the species in it are habitat specialists, then reduction of the total area may have relatively little impact on the extinction rates of these species. Only large demographic plots can address these questions in respect of tree species, or monitor the impact of change on all but the most abundant tree species populations.

EXAMPLES OF WHAT LARGE PLOTS CAN DO

A great limitation of scientific forestry in the tropics has been its inability to make quantitative generalizations at more than the broadest level, that is, at levels too broad to be useful in management protocols which take account of varying site conditions. This is because there have been no generally accepted standard procedures for sampling forests: Not only have sample sizes, which influence estimates of species diversity for instance, not been uniform but the ranges of sizes, and particularly the minimum size -- usually diameter -- of tree measured has varied. The large plots enable researchers to overcome this problem in two ways. From the outset, standard and rigorous protocols for surveying the plots, and measuring, mapping, tagging, and identifying the trees have been agreed to. Second, by adopting a very large plot size and a rather small (1 c. dbh) minimum size for census, and by mapping tree positions, it is possible to select data representing a wide range of subsamples from within the plot data for comparisons with data collected in a variety of ways in smaller plots at other

locations. As one example, earlier 1 1/2 acre (0.6 ha.) permanent plots, in which trees above 12 in. girth (9.7 cm dbh) were censused by the Sarawak Forest Department research section in the nineteen sixties are now included within the boundaries of the 50 ha. plot at Lambir.

GLOBAL COMPARISON AND GENERALISATION

Particularly, the large plots will permit global comparisons and generalisations for the first time. This is not yet possible because only two environmentally dissimilar plots, in Panama (BCI) and Peninsular Malaysia (Pasoh), are yet completed, with no replicates under similar habitat conditions. But they already indicate fascinating differences which early results elsewhere suggest may be general to the site conditions in which they are set. Both sites (Table 1) were chosen for their edaphic and topographic uniformity, and both are principally on sedimentary rocks and alluvium; both are undulating. Mean annual rainfall is similar, though it is somewhat higher at BCI, which is nevertheless markedly seasonal. The two sampled stands (Table 2) are remarkably similar in total basal area, even though the BCI at least partly represents old secondary forest. They markedly differ in other respects though: Pasoh has 2.7 times as many species and 1.5 times as many individuals, and this is mainly due to the much larger number of trees in the smallest size classes. This difference appears to be due to higher mortality rates in the smaller size classes at BCI, which exhibit high between-census variability there associated with variability in the length of the dry season (Hubbell and Foster 1990).

This pattern of declining stand density and tree species diversity with increasing seasonality is strengthened by initial results from the Royal Thai Forest Department plot at Huai Kha Khaeng, Thailand and also from the Indian Institute of Science plot at Mundumalai, Tamil Nadu, India (Sukhumar et al. 1992), which have c. 1500 and c. 1200 mm. mean annual rainfall, and five and six month dry seasons, respectively. In these two 50 ha. plots the number of species respectively declines to an estimated 300 (in a combination of evergreen and deciduous forest) and 71 (in deciduous forest), and the number of individuals to about 3000, and 520 per ha., with fire as well as drought a probable cause of mortality.

RELATIONS BETWEEN HABITATS AND SPECIES

The degree to which site heterogeneity influences species richness can be examined by correlating habitat diversity with species distributions and performance within plots. At Pasoh, distinctive habitats include swamp and stream sites, but these only occupy small areas and a relatively small proportion of species are confined to either (e.g. Fig. 2b). The vast majority of species are not confined to any habitat, although about half are significantly more abundant in one habitat, such as the hills, than another such as the alluvium (Fig. 2 c, d). Preliminary results from the Lambir plot (Fig. 3), which was chosen for its heterogeneity of soils and of disturbance rates (see Palmiotto, Ohkubo in this volume) and from Huai Kha Khaeng where water deficits during the dry season may vary dramatically in relation to topography, indicate

that many species there are confined to specific habitats, and most occur more abundantly in some habitats than others.

The maps of the two *Dryobalanops* at Lambir (Fig. 3) well illustrate the power of the plot data. Both *D. beccarii* and *D. aromatica* were identified by the field teams from the plot, but the plot indicates that identifications of *D. aromatica* occur mainly (though not always) in lines following the short axis of the plot, where *D. beccarii* is absent. The field teams censused along such lines, and the map provides clear evidence that the two species are either confused, or actually one; leaf samples from a proportion of the individuals have now confirmed that indeed this is one species, *D. aromatica*. Both maps indicate that smaller, presumably younger trees have wider distributions than larger trees although there are some aggregations of larger *D. aromatica* individuals where there are few accompanying small trees. Yamakura's contour map and Palmiotto's soils map indicate that larger trees of *D. lanceolata* are mostly confined to adult loamy soils on slopes, while large *D. aromatica* are completely confined to humult soils, with dramatic concentrations on crests. Such striking distributions appear to be shared by every one of the ninety other dipterocarp species in the plot although not, it seems, such a high proportion in other families. Small trees of both *Dryobalanops* species apparently do occur in each others' habitats, and there is one curious aggregation of larger *D. lanceolata* (circled, Fig. 3b) in one area of predominantly humult soils. Here again, the identity of trees with apparently anomalous distributions must be checked. But it does seem likely that juveniles can establish and survive for some time outside the edaphic ranges of reproductive adults. This interpretation, supported by the exciting researches of A. Itoh on seeds and germinants, and under study in seedlings by P. Palmiotto, will be further elucidated once comparative data on growth and mortality on the different soils is available. Together with the research into population genetics and reproductive biology which is being advanced by the Inoue group, the *Dryobalanops* work provides an impressive example of the way in which large plots provide previously unavailable opportunities for demographic research into tropical trees, which in this case may throw important light on the mechanisms of competition and niche specificity. When combined with phylogenetic analysis the opportunity exists to examine the evolution of ecological niches, a subject being addressed by S. Davies in a clade of pioneer *Macaranga* (Euphorbiaceae), also partly based at Lambir.

WHY 50 HA? WHY A RECTANGLE?

The original reason for choosing 50 hectares was to ensure that at least half the species, that is even the rare but widespread species within the plot, are represented by samples large enough for demographic analysis. This goal may not be reached at Lambir where at least two distinct habitats are represented. P. Hall has been using the Pasoh data to examine the effects of plot size and shape on the reliability of estimates of ecological and silvicultural variables, and the number of replicates therefore required to meet acceptable statistical confidence limits, by comparing subsamples within the 50 ha. plot.

Tree species diversity does not at first decline with reduction in area in the homogeneous plots; a 15 ha. sample contains, on average, over 90% of the 807 species

in the whole plot (Fig. 4). Further, the distribution of abundances remains the same (Figs. 5 a, b), with an unexpectedly high proportion of species in very low abundance as demonstrated already for the BCI plot by Hubbell and Foster (1986). Hall (in press) similarly found that the coefficient of variation between plots in the number of species contained in them declined to acceptable levels at about 1 ha. Plot shape, however, did not significantly influence estimates of species richness in the uniform terrain of Pasoh. But the size of population samples, particularly of the more abundant species differs radically, with less than one quarter being represented by 100 individuals in 15 ha plots. This forcibly demonstrates that such large plots are not necessary for classifying plant communities, or for comparing species richness, but are essential for examining the demographic processes which sustain their structure, species relative abundances and diversity. They are essential therefore for research aimed at optimising management protocols; for instance, for developing and refining silvicultural interventions which can optimise production both of timber and other forest products of value such as rattan or gaharu.

Hall has further found that the coefficient of variation in the stand variables density and basal area are minimized at c. 5 ha., and basal growth and mortality at c. 10 ha. From these calculations, the number of samples required to estimate means of a given confidence limit can be estimated.

STAND DEVELOPMENT AND PREDICTION OF LENGTH OF FELLING CYCLE

In a separate study currently in progress, Hall is developing means to predict length of felling cycles under different management including harvesting practices. The population samples of the more abundant species are large enough to exhibit the full range of growth rates which can occur in nature under the site conditions of the plot. Predictions can then be made of the number of years to reach a given minimum basal area, or number of merchantable stems above a given minimum diameter, assuming that maximum growth rates do not exceed those observed in the plot, but with a given rate, duration and distribution of 'release' (increase in growth rate in the residual stand following logging); and assuming a given percentage of the stand destroyed by logging damage. Preliminary results (e.g., Figs. 6, 7) appear to be realistic, but must be tested against field data.

We plan to test and refine these techniques, then use them to generate more precise predictions of basal area (and eventual volume), and length of felling cycle based on simple assays of forest structure and growth rates prior to felling. Finally, user-friendly software for these models will be written, suitable for forest staff in the sections.

INTERACTIONS BETWEEN LOGGING AND BIODIVERSITY

Biodiversity consists mainly of insects which are the least known of all groups of organisms, especially in the tropics. In this respect, the larger demographic tree plots serve an indirect role, as controls and as natural arboreta (like Semengoh but on a

larger scale) with large tree population samples tagged and identified for pollination and other studies of plant-animal interactions. The presence and accomplishments at Lambir of the group associated with Dr. T. Inoue serve as testimony to this function, though they have so far used adjacent forest, in part to minimize disturbance. At other sites, the large plots have attracted research on organisms as diverse as vertebrates (Pasoh, Huai Kha Khaeng), insects (Pasoh), soil fauna (Pasoh) and lichens (Huai Kha Khaeng).

A central and continuing issue in forest management remains the impact of logging on biodiversity, including tree species diversity. Work elsewhere (e.g. Johns and Skorupa 1987, Johns 1988, 1992) suggests that some birds and mammals may return to logged forest within a few years, although others may take much longer. The impact of logging on tree species diversity remains controversial, substantially because of the difficulties of rigorously studying it. Small sample plots have indicated an increase in species numbers following logging (D.I. Nicholson pers. comm.), but this should be viewed with suspicion, unless the additional species are exotics, because it indicates greater diversity within the sample rather than within the forest under examination as a whole. This is because gaps occupy less than 10% of most forests and their associated flora is therefore unlikely to be fully if at all represented in small primary forest plots; but logging, by increasing the area of gaps, will increase the likelihood that small plots will contain good representation of both gap and mature phase floras. Larger plots can overcome this artificial distortion of tree biodiversity assessment. The other reason why large plots are required to examine the impact of logging on tree species diversity is, as mentioned, that they provide the only means to capture adequate samples of the majority of species which are in low population densities, in order to monitor fluctuations in their numbers and performance consequent on logging.

The best direct means to monitor the effects of logging on biodiversity would be to establish a large demographic lot in primary forest, recensus it at least twice over ten years to establish trends in mortality and growth and their variability, then log it and continue to recensus thereafter. We cannot wait for this, but a good proxy is to monitor subsamples of logged forest of known history within the same forest in which a large primary forest is set, and compare both the changes in overall biodiversity in the logged forest (if any), as well as demographic changes within the rare species. The presence of logged forest adjacent to Lambir National Park provides such an opportunity, which we are keen to take in the near future. Because most rare species in the 50 ha. plot at Lambir appear to be clumped in populations of high local density rather than spread evenly across the plot, establishment of smaller plots, totaling 8-16 ha., as transects across the mosaic of roads, skid trails and the residual stand in the logged forest should provide an adequate means to monitor changes both in total tree diversity, and in the demography of representative rare species.

In the meantime, Jianguo Liu, a mathematical ecologist from China in our group who was unable to be here at this meeting, is developing computer models using the Pasoh recensus data which will be able, given certain assumptions, to generate testable hypotheses of the impact of logging on biodiversity (Liu and Ashton, in press). It is our eventual hope to further refine these models using recensus data from Lambir.

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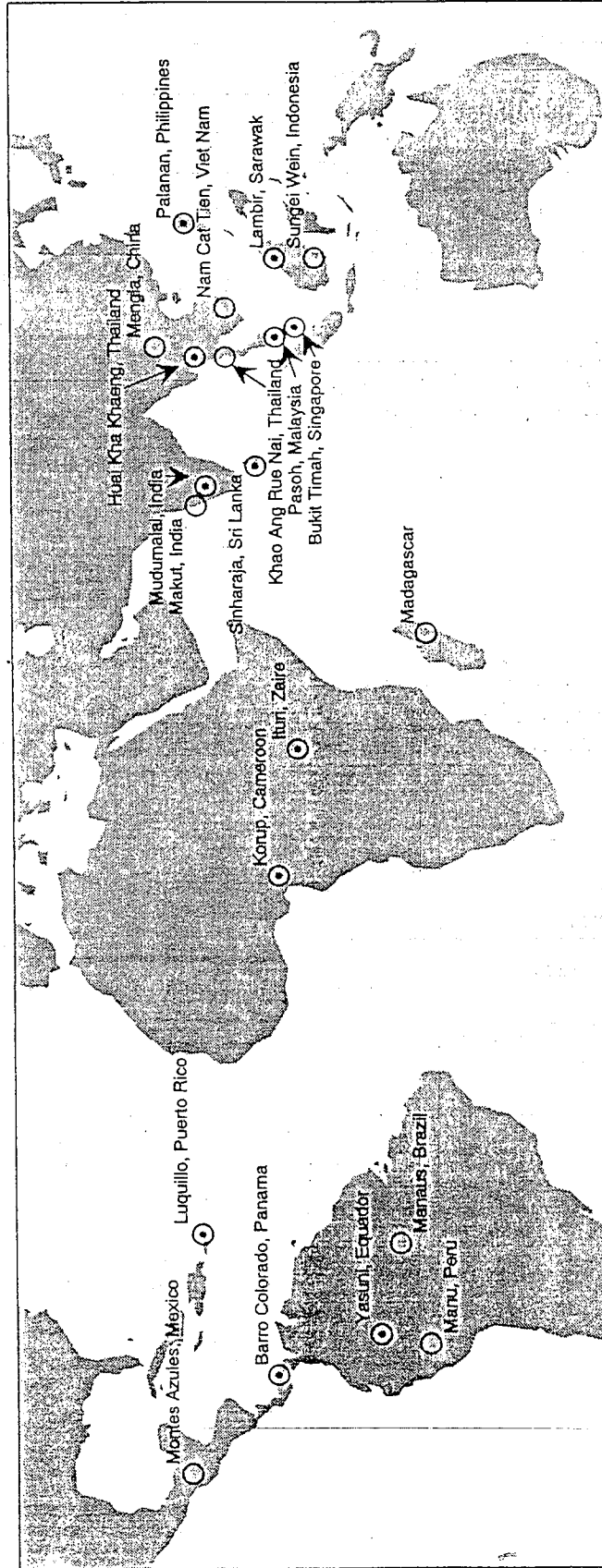
Discussion for Ashton's paper

- Yamakura** I am concerned that plots of such a size cannot sample the variations in the forest.
- Ashton** I share your concern about the coefficient of variation, but we have to accept that as the size of a samples increases, the number of samples that can be established decreases.
- Chai** Can you tell us about recruitment in the BCI plot, for instance, how many trees have moved into the 10 cm size class between enumerations.
- Ashton** I can't tell offhand as these have not been calculated.
- Palmiotto** I think what Ernest is concerned about is ingrowth, which may be of interest to know before the next census. Thus how trees have moved into the next size class between censuses.
- Ashton** Oh you mean ingrowths, in that case trees moving into the 1 cm diameter class not the 10 cm class. The number of recruits was less than 2.5% of the total number of trees. The number is not too extreme although they are quite difficult to identify at the juvenile stage.
- Losos** Between the two censuses we have carried out, we ended up with about 244,000 individuals, so about 60,000 individuals have disappeared or died over a 10 year period. In each census something of the order of 30,000 trees are added.

	BCI	PASOH
Location	Panama	Malaysia
Forest type	Lowland seasonal evergreen	Lowland mixed (dipterocarp)
Annual rainfall (mm.)	2600, 3 month dry season	2400, aseasonal
Substrate	Tertiary sediments	Cretaceous sediments, granite, alluvium
Plot established	1982	1987

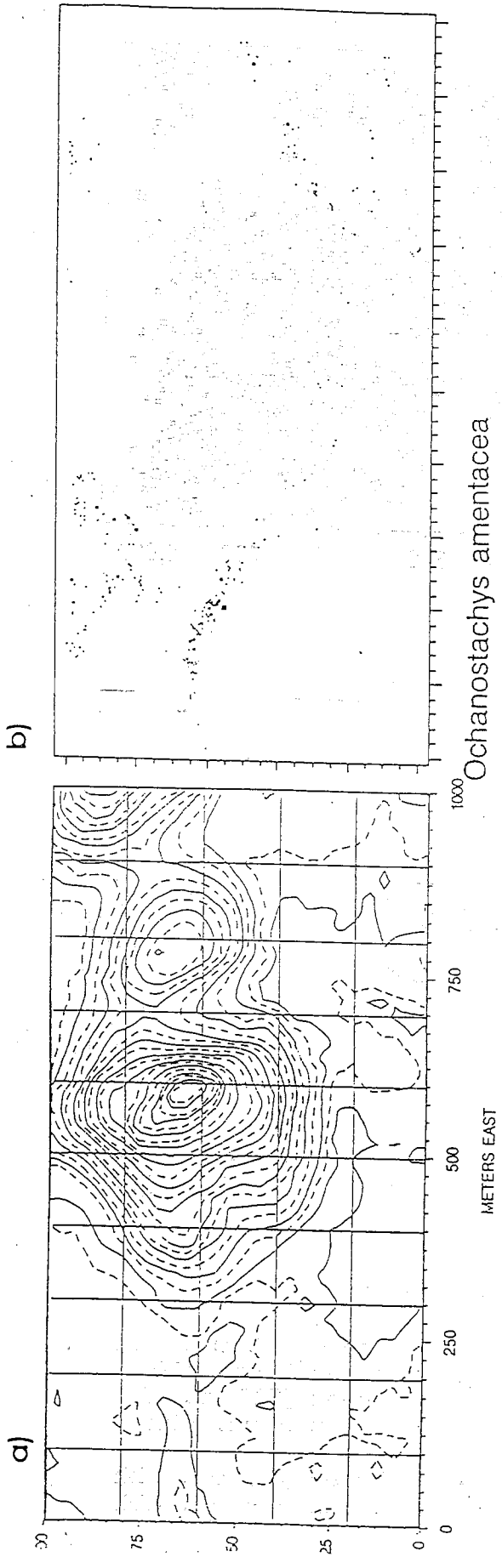
	BCI	PASOH
	<i>Trees ≥ 1 cm. dbh</i>	
Species in 50 ha.	314	807
Individuals per ha.	4426	6532
Basal area per ha.	29.4	29.7
Mortality (% per annum)	-2.26	-1.25
	<i>Trees ≥ 10 cm. dbh</i>	
Species	237	666
Individuals	415	517
Basal area	25.8	24.6
Mortality	-1.98	-1.23

Center for Tropical Forest Science Collaborative Sites Network



⊙ Established Sites ⊕ Proposed Sites

Fig. 1. World map of long-term sites for tropical tree demography and forest research, in association with CTFS.



Topographic map of the pFR 50 ha plot, at 1 m contour intervals, and gridded at 1 ha units.

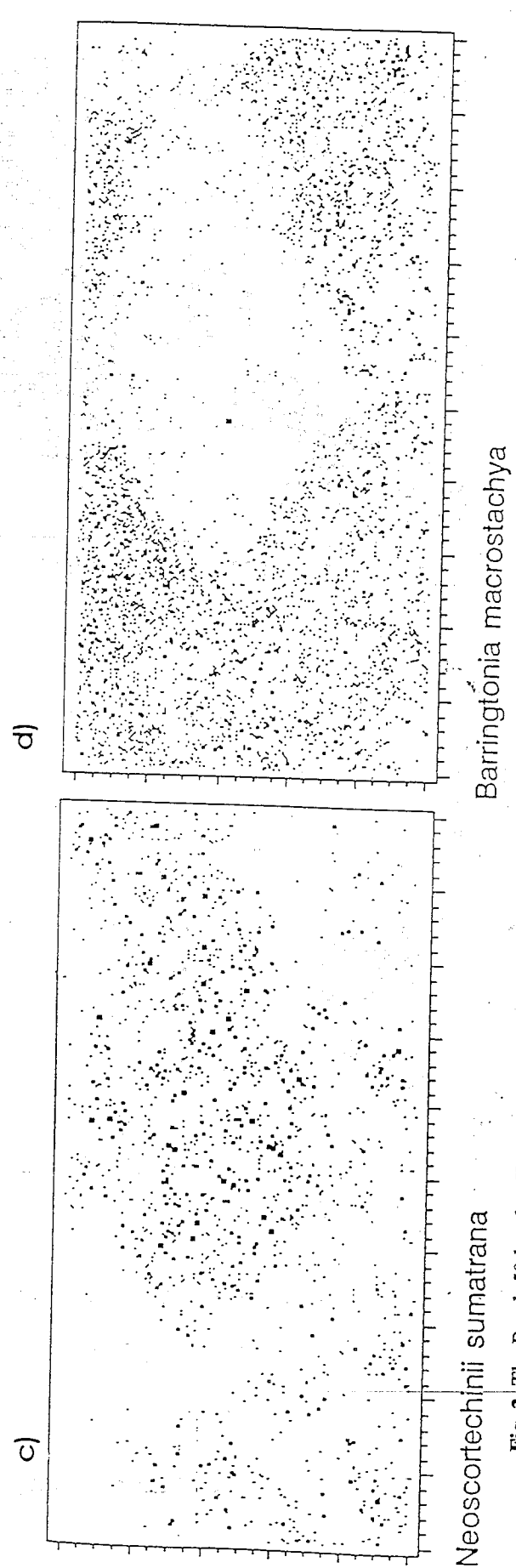


Fig. 2. The Pasoh 50 ha plot. Topography (a) and examples of species; of swamps and streams (b); mainly of hills (c); mainly of alluvium (d).

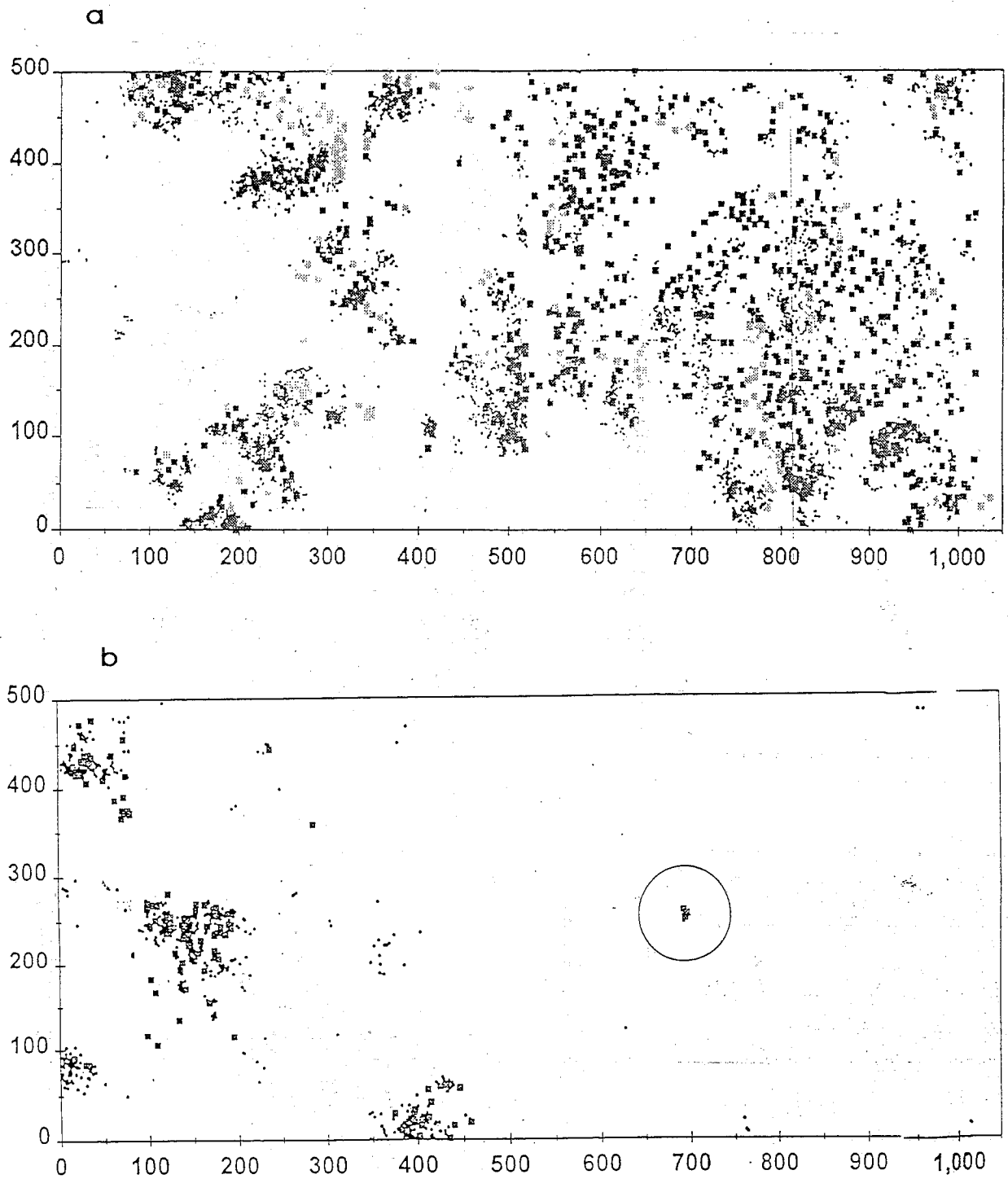


Fig. 3. Lambir N. P. Map of *Dryobalanops* within the 50 ha plot.

- | | | | |
|---|--------------------------|---|------------------------|
| a | <i>D. cf. beccarii</i> , | • | trees \leq 5 cm. dbh |
| | | ▣ | trees > 5 cm. dbh |
| | <i>D. aromatica</i> , | • | trees \leq 5 cm. dbh |
| | | ▣ | trees > 5 cm. dbh |
| b | <i>D. lanceolata</i> , | • | trees \leq 5 cm. dbh |
| | | ▣ | trees > 5 cm. dbh |

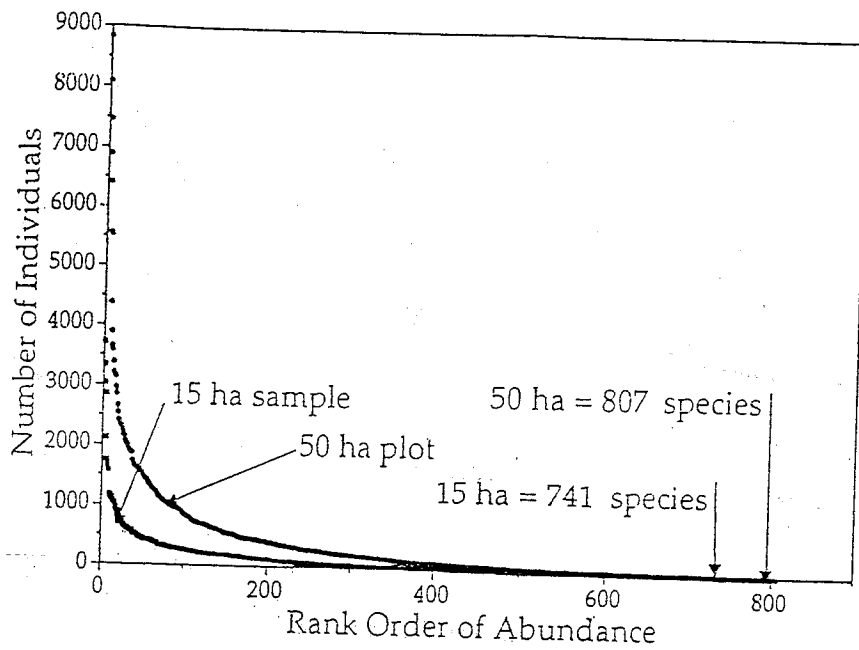


Fig. 4. The "tail" of rare species, Pasoh Forest Reserve, Malaysia.

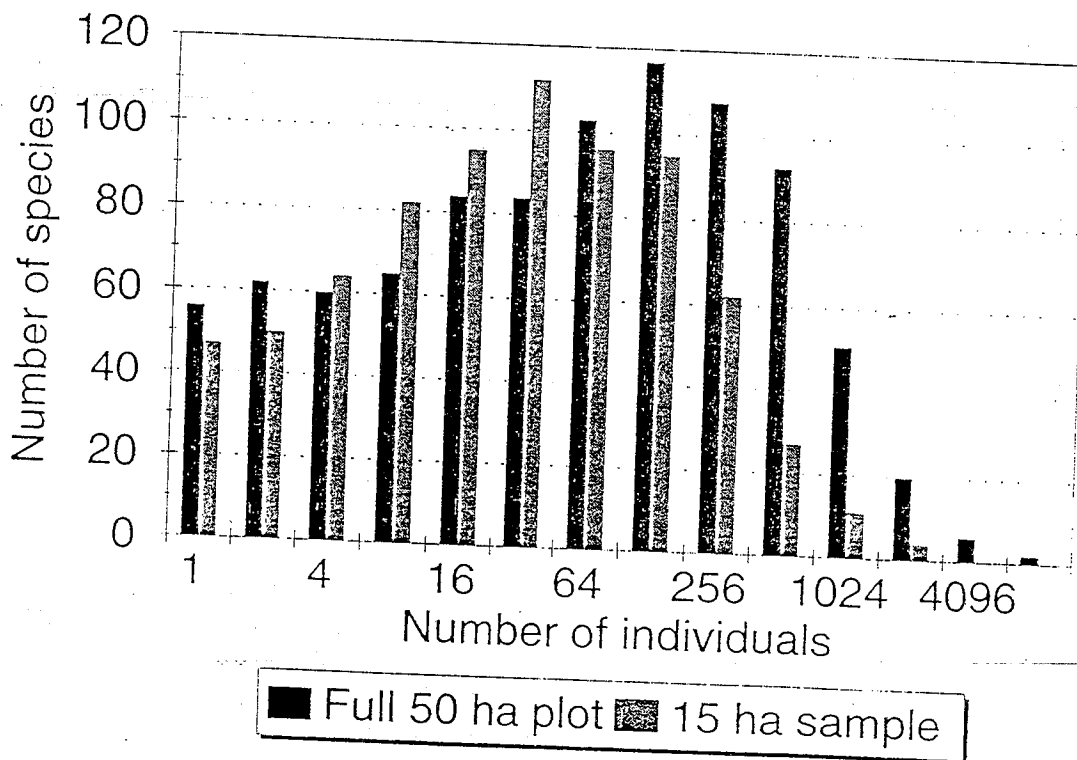


Fig. 5. Distribution of species abundances at Pasoh.

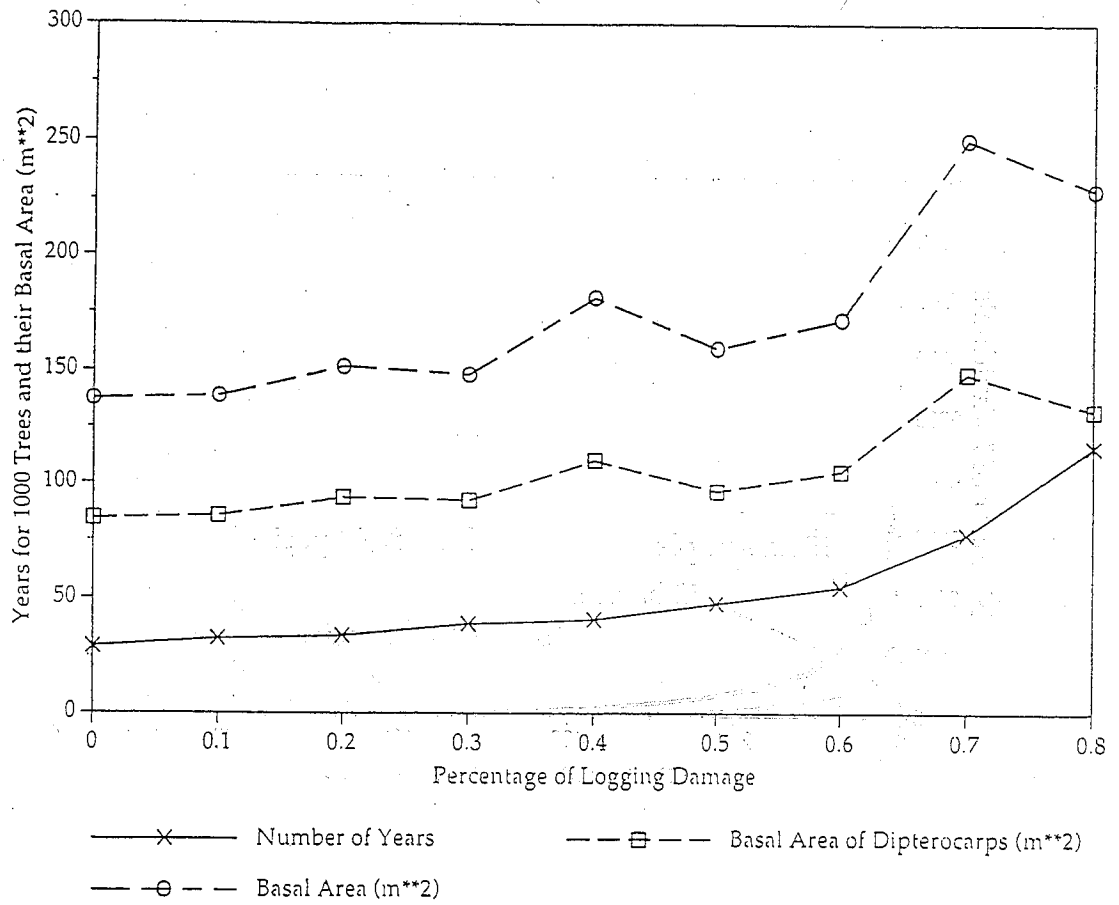
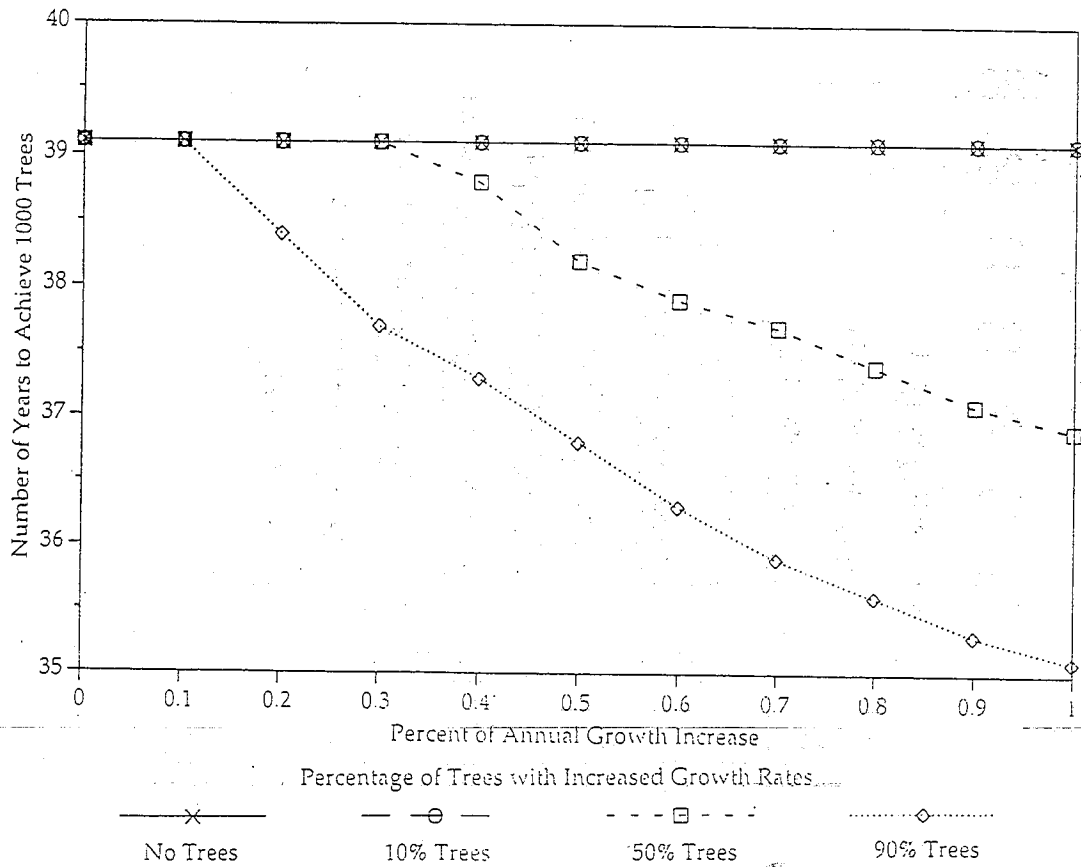


Fig. 6. Effect of logging damage on subsequent change of basal area over time of 1000 trees exceeding 30 cm dbh in a 50 ha plot (20/ha), following felling down to that diameter; basal area using natural mortality and no growth release.



Concluding Remarks