Tree Distribution Patterns in the Bukit Timah Nature Reserve, Singapore.

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Abstract

All living stems > = 2 cm dbh were marked, identified and mapped at a scale of 1 cm to 1 m in two 0.24-ha plots in the Bukit Timah Nature Reserve, Republic of Singapore. The Fern Valley plot was V-shaped in cross-section and contained a small area of exposed bedrock and several boulders along an ephemeral stream channel; the Jungle Fall Valley plot had no stream channel and neither exposed bedrock nor boulders. In both plots combined (0.48 ha), there were over 290 species representing 53 families. The two plots shared 95 species, while 76 were unique to the Fern Valley plot and 119 to the Jungle Fall Valley plot. Fern Valley had 20% fewer species, 44% fewer stems, 23% less total basal area and 40% fewer woody climbers > = 1.4 m tall than Jungle Fall Valley. Shallower depth to granitic bedrock in Fern Valley is hypothesized to be a contributing factor for this difference. In both plots, the Dipterocarpaceae had the greatest basal area and the Euphorbiaceae the greatest density and number of species. The distributions of *Shorea curtisii* and *Pimelodendron griffithianum* along slopes in these small plots conformed to their observed ecological preferences on a larger scale in the Malay Peninsula. The presence of a few old trees of pioneer species with little regeneration indicated an on-going process of recovery from disturbance during and prior to World War II.

Introduction

The purposes of this study were to compare the vegetation of two plots in the Bukit Timah Forest Reserve, Singapore, and to analyze the distribution patterns of woody species along elevational gradients. Because the two plots were only 250 m apart and presumably shared a similar vegetational history, I set out to discover how similar they would be in species composition, stem density, total basal area and size distributions of the stems of those species represented by more than five stems or contributing more than 0.5% of each plot's basal area. Answers to these questions should provide a better understanding of the natural variability of the vegetation within the reserve and a basis for prediction of future changes in species composition.

The Bukit Timah Nature Reserve was established in 1883 and covers an area of 71 ha but lacked governmental protection between 1930 and 1937 and during World War II (Corlett 1988). The highest point on Singapore Island is located within the reserve and has an elevation of 162.5 m. Bedrock is granite probably of post-lower Jurassic age (Wong 1969, Hill 1973, Nature Reserves Board 1975). Ives (1977) described the soils of Bukit Timah as belonging to the Rengam series, which is well-drained and characterised by a dark, greyish-brown topsoil 10–20 cm deep; there is a yellowish brown subsoil, which grades to a yellowish-red, firm horizon below 1.5 m.

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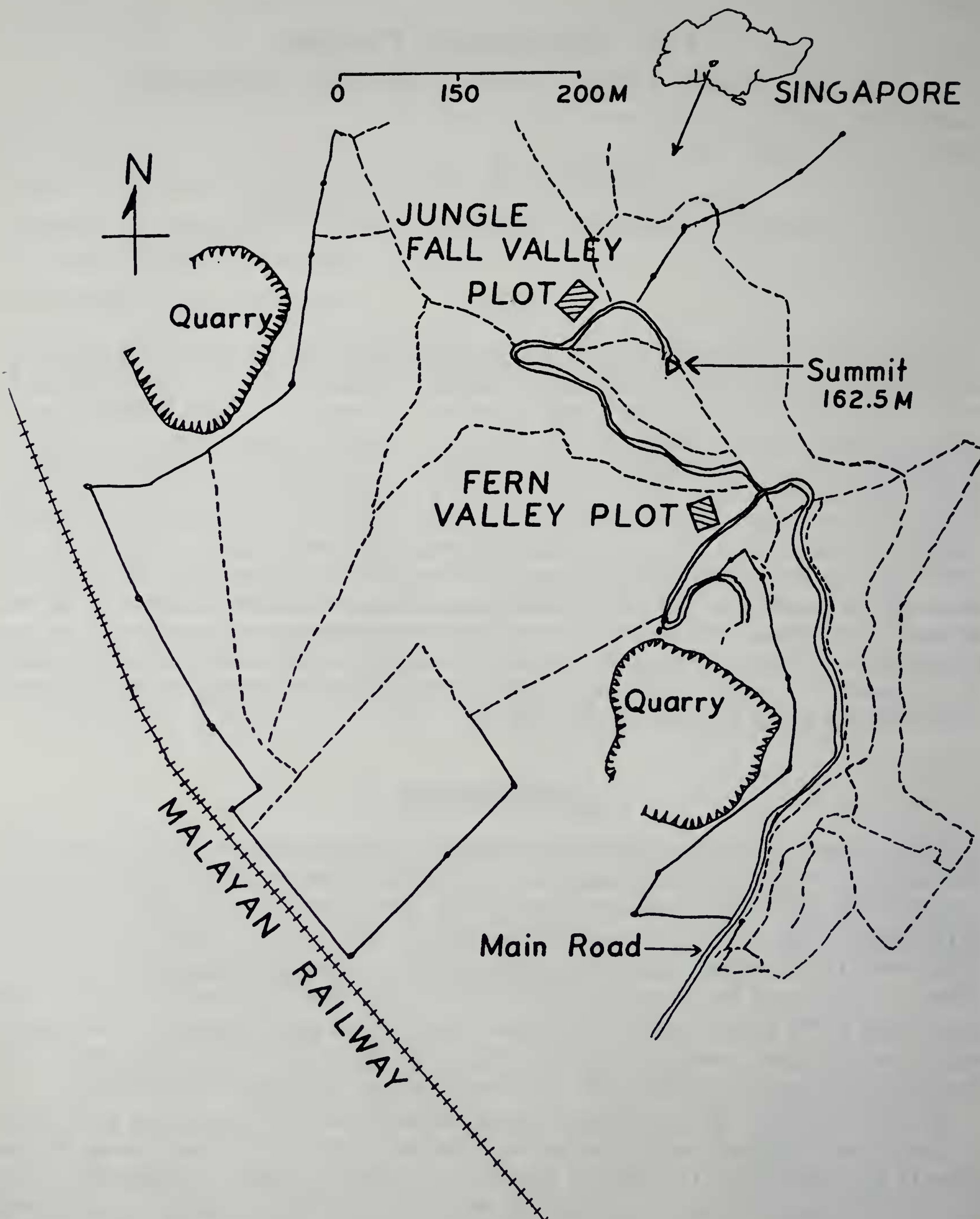

Fig. 1: Map of the Bukit Timah Forest Reserve showing the locations of the two 0.24 ha plots.

The flora of the reserve has been intensively studied and is the source of type specimens of many species. Hill (1977) constructed a vegetation map of Singapore and reported the presence of 99 tree species at the Bukit Timah Forest Reserve. Wong (1987) sampled 687 trees > = 24 inches in girth in the reserve. He reported tree densities of 57 to 137 stems per acre and postulated that past harvesting of smaller stems by residents of nearby villages could account for areas of low tree density. His total sample of 849 trees represented 212 species, 111 genera and 44 families. Whitmore (1984) concluded that the vegetation of the Bukit Timah Forest Reserve was an isolated relict of dipterocarp forest with fewer species that would normally be present in typical lowland tropical moist forest on the nearby Malay Peninsula. He also described the lowland dipterocarp forests on ridges of the Malay Peninsula as being dominated by *Shorea curtisii*, which forms an edaphic climax there as it does at Bukit Timah.

The following animals were observed during sampling: Long-tailed Macaque (*Macaca fasicularis*), Flying Lemur (*Cynocephalus variegatus*), Red-bellied Squirrel (*Callosciurus notatus*), and Great Racquet-Tailed Drongo (*Dicrurus paradiseus*).

Materials and Methods

Design and Layout

I selected one 0.24 ha plot in Fern Valley (Fig. 1) and one about 250 m away in Jungle Fall Valley on the bases of minimal slope, lack of excessive disturbance from tree falls, width of more than 60 m across each valley, and absence of roads and foot paths. Each plot was 60 by 40 m and was oriented so that the long axis was perpendicular to the path of water drainage. Fern Valley drains to the west and Jungle Fall Valley to the north-northeast. The vegetation of each plot was sampled by use of six contiguous quadrats (in two rows of three quadrats) 20 m square (400 m^2). In Fern Valley, two of these quadrats were on the north side of the valley and had slopes of 25° towards the southwest (220°). The valley bottom was on the southern edge of these quadrats. Four quadrats were on the south side of the valley and had slopes of 18° or less towards the northwest (320°). In Jungle Fall Valley, all six quadrats had slopes of 12° to 28° to the north.

Stem Measurement, Labeling and Identification

In each plot, the diameters at 1.4 m height (dbh) of all living stems > = 2 cm dbh were measured, and a numbered aluminium tag was attached to each. I estimated stem heights and mapped the positions of all living and dead stems > = 2 cm dbh and fallen stems > = 20 cm in diameter at a scale of 1 cm equal to 1 m (Figs. 2 & 3). The following plant growth forms were defined in terms of a species' potential adult stem diameter as follows: a species described as a treelet or shrub had stems < = 5 cm dbh; small trees, 6–15 cm; trees, 16–30 cm; and large trees, >30 cm. Samples of leaves and fruits were collected for later identification at the Singapore Botanic Gardens Herbarium. Scientific nomenclature of plant species follows Keng (1973, 1974, 1976, 1978, 1980, 1982).

Plant specimens collected from the study plots were deposited at the Department of Botany, National University of Singapore, and their identification was verified by Dr R.T. Corlett, a faculty member in the department. A partial set of specimens is stored in the herbarium of the Department of Biology, West Liberty State College, West Liberty, West Virginia 26074, USA. Copies of my field notes and maps of the two plots are on file at the Department of Botany, National University of Singapore. Species names with authorities are listed by family in the Appendix.

Pattern Analysis

To determine whether or not species with four or more stems per plot differed from each other in distribution patterns along valley slopes, I used the map of each plot to measure the distances from each stem perpendicular to the valley bottom or drainage path (D-S) and to the point of lowest elevation (DLP). The Jungle Fall Valley plot did not have a clearly defined valley bottom while the Fern Valley plot did. I estimated the valley bottom in Jungle Fall Valley to be along a line from the lowest point perpendicular to the long axis of the plot. To study other aspects of distribution patterns, the distance of each stem was measured to the nearest conspecific (NNSS), to the nearest neighbour (NN), and to the nearest fallen stem (DNFT) > = 20 cm in diameter.

To perform regression and correlation analyses, the Daisy statistics software for the Apple Computer, Rainbow Computing Inc., 9718 Pagoda Blvd., Pasedena, California, USA, was used.

Results and Discussions

Differences in the Vegetation of the Two Plots

The vegetation of the Fern Valley plot was simpler in composition and structure than that of the Jungle Fall Valley plot. While the two plots shared 95 species, 76 were unique to Fern Valley and 119 to Jungle Fall Valley. The Fern Valley plot had 20% fewer species, 44% fewer stems > = 2 cm dbh, 23% less total basal area, and 40% fewer woody climbers > = 1.4 m tall (Table 1). A comparison of the species area curves for the two plots (Fig. 4) shows the curve for Jungle Fall Valley (bivariate normal correlation coefficient, r = 0.9838, cumulative number of species versus number of 10 by 10 m quadrats) to be consistently higher than that for Fern Valley (r = 0.9768) with the gap between the two widening after ten 100-m^2 quadrats (Connor and McCoy 1979). In both plots, the Dipterocarpaceae had the greatest basal area and the Euphorbiaceae the greatest density and number of species (see Appendix).

The differing characteristics of the vegetation in the two plots may be due to chance or may indicate that there are environmental differences between them. Soil depth is a possible cause of the observed differences. Physical evidence for less soil depth in Fern Valley includes exposed bedrock near the upper end of the plot's stream channel and large boulders one to two metres in largest dimension lying exposed toward the lower end of the channel (Fig. 2). About 50 m west of the Fern Valley plot, I observed several large cracks in the soil perhaps caused by soil slippage during exceptionally heavy rains. In contrast, the Jungle Fall Valley plot contained neither rock exposures nor soil cracks. About 2 m from the southeast corner of the Jungle Fall Valley plot there was a circular hole of unknown origin and age, 1.3 m in diameter and 3-4 m deep with no sign of bedrock along its sides.

Shorea curtisii (Dipterocarpaceae) had a greater basal area than any other species in each plot (Tables 2 and 3). Of the dicotyledonous tree species capable of attaining great size, it also had the most individuals in the 2-10 cm dbh size class. In Fern Valley its stems grew at the highest average elevation (#20, Fig. 5), and in Jungle Fall Valley at the ninth highest elevation (#6, Fig. 6). I assume that the elevational gradients depicted in Figs. 5 and 6 may reflect not only water relations (with the driest end being at the upper right corner) but also differences in soil depth, texture, chemical composition, and a tendency for soil slippage. Whitmore (1984) noted that *Shorea curtisii* characteristically grows along ridge crests between 225 and 750 m on inland

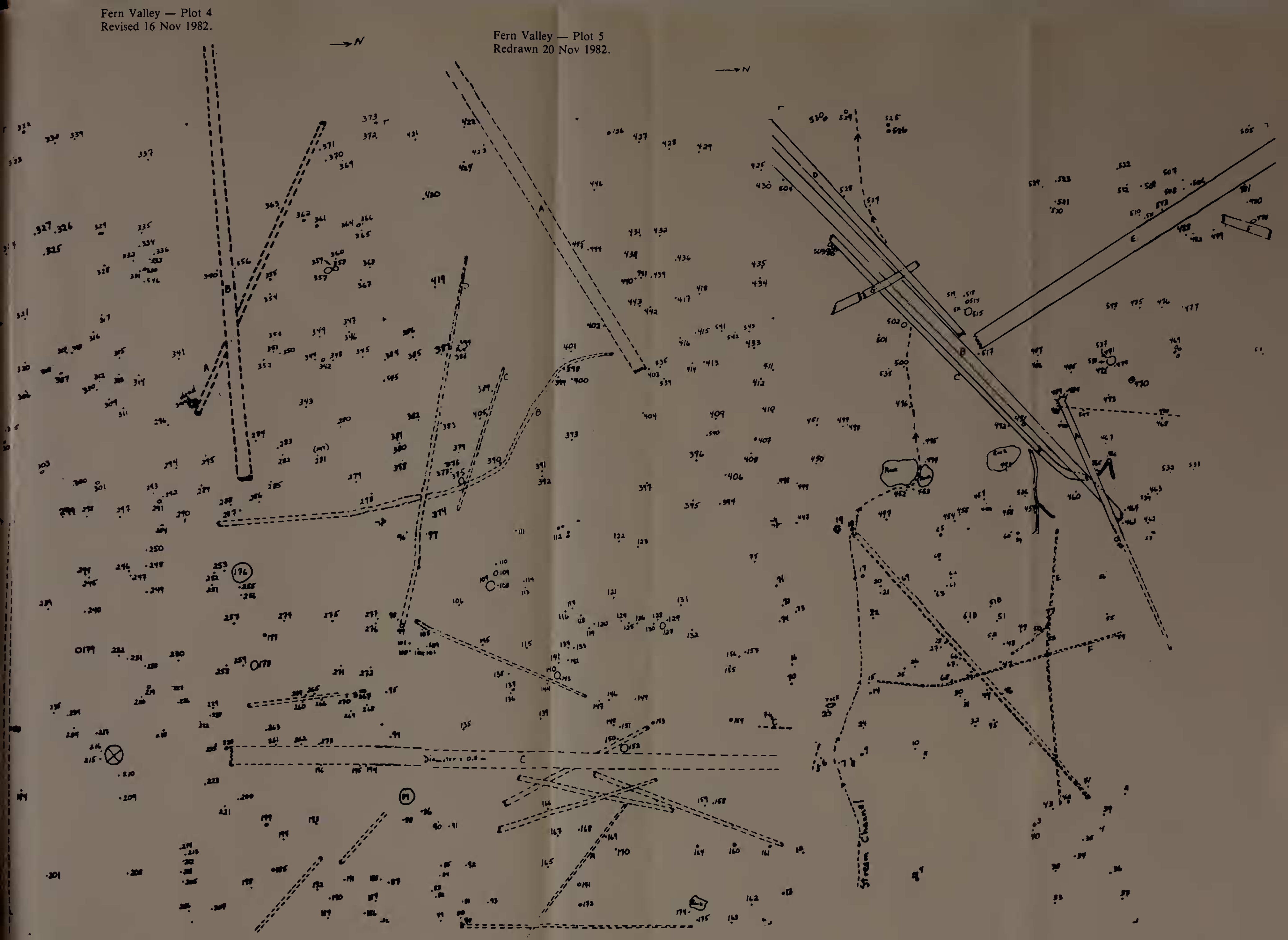

Fig. 2: Map of the Fern Valley plot showing the locations of all living stems > = 2 cm dbh and fallen stems > = 20 cm in diameter. The plot is 40 by 60 m as measured on the south and east sides respectively. The west side measures slightly more than 60 m.

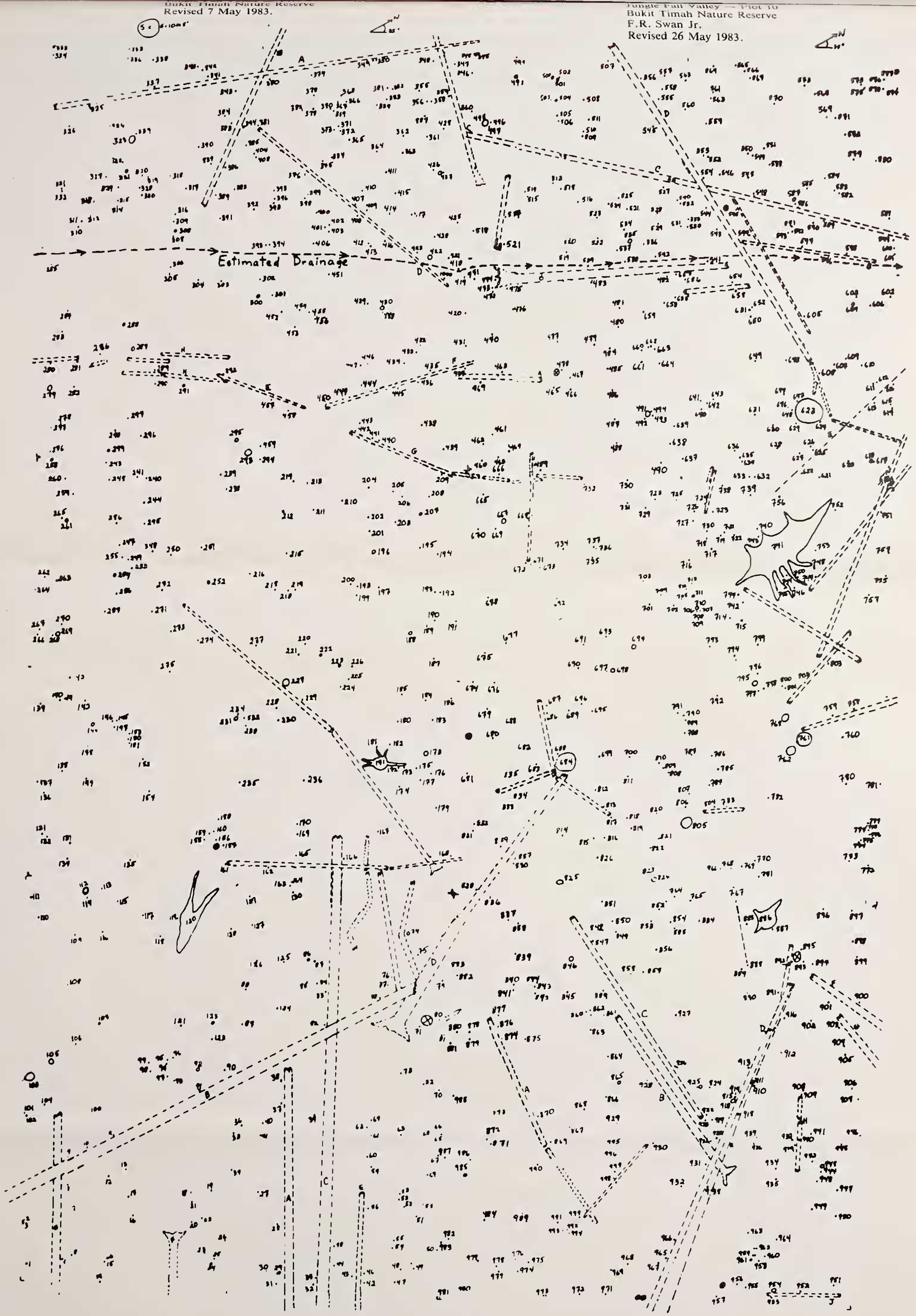

Fig. 3: Map of the Jungle Fall Valley plot showing the location of all living stems > = 2 cm dbh and fallen stems > = 20 cm in diameter. The plot is 40 by 60 m.

Table 1
A comparison of the major features of the vegetation and soils in the Fern Valley and Jungle Fall Valley plots.

	Fern Valley	Jungle Fall
Number of species >= 2 cm dbh	171	214
Number of families	39	49
Number of individuals >= 2 cm dbh	564	1000
Total basal area (m^2/ha)	22.3	28.9
% stems >= 2 cm dbh with attached climbers >= 1.4 m tall	25.1	39.7
Number of climbers >= 2 cm dbh	55	47
Number of climbers <2 cm dbh & >= 1.4 m tall	334	938
Total climbers per stem >= 2 cm dbh	0.71	0.46
Number of woody climbers >= 2 cm dbh	27	45
Number of monocot climbers >= 2 cm dbh (Palmae)	28	2
Number of monocot climbers <2 cm dbh & >= 1.4 m tall	11	214

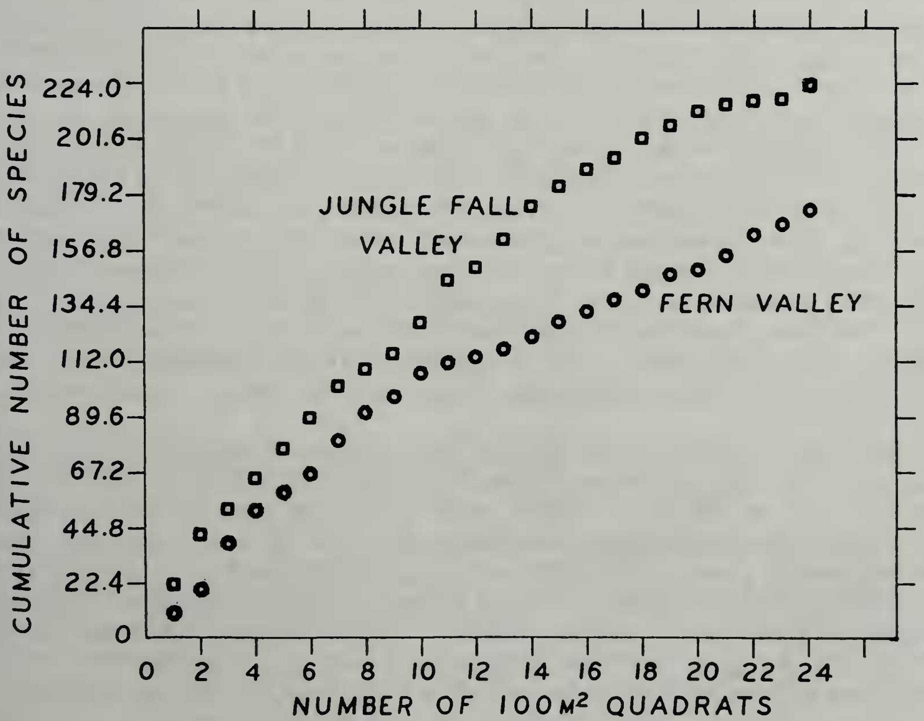

Fig. 4: Species area curves for the Fern Valley (plot F) and Jungle Fall Valley (plot J) plots.

mountain ranges of the Malay Peninsula and nearly down to sea level on coastal hills. Its canopy leaves are hard and waxy and have a high albedo, giving it some drought resistance.

Of the 25 species of greatest basal area in the Fern Valley plot (Table 2), 15 had one or more stems > = 20 cm dbh but zero or one individual in the 2–10 cm dbh size class. Comparable values in the Jungle Fall Valley plot were nine of 24 species (Table 3). A study of larger plot sizes is needed to determine whether reproduction of these species is taking place anywhere in the forest reserve under current environmental conditions.

Gironniera parvifolia (Ulmaceae) was the most numerous woody species in Jungle Fall Valley (43 stems, Table 5) and was the eighth most numerous species in Fern Valley (9 stems, Table 4). The largest individuals were 13 cm dbh in Jungle Fall Valley and 79 percent of the stems were in the 2–10 cm dbh size class. In Fern Valley, the largest stem was 17 cm dbh, and 67 percent of the stems were in the 2–10 cm dbh size class. It occupied a central position along the elevational gradient in Fern Valley (#8, Fig. 5) and a slightly higher position in Jungle Fall Valley (#1, Fig. 6). Because of its abundance under current conditions, I postulate that it is a shade tolerant species that has increased under conditions of minimal disturbance. The same explanation may apply to *Santiria apiculata* (Burseraceae), the third most abundant woody species in Jungle Fall Valley.

Urophyllum hirsutum was the most numerous species of sapling-size woody plant (treelet) in both plots and showed highly significant clumping by the test of Clark and Evans (1954) (Tables 4–7). It occupied a high average slope position in both plots (#1, Fig. 5 and #2, Fig. 6), indicating greater reproductive success than other species under upper elevational soil conditions.

The arborescent palm, *Oncosperma horridum*, and at least two species of climbing palms or rattans (*Calamus* sp. and *Daemonorops* sp.) were the next most numerous stems in Fern Valley (Table 4). *Oncosperma* was not present in Jungle Fall Valley or its vicinity. Historical accident could have played a part in the absence of *Oncosperma* from Jungle Fall Valley as well as different soil conditions.

More frequent tree falls in Fern Valley than in Jungle Fall Valley may be a factor that has aided the growth of rattans, which were especially dense in the northwest portion of the Fern Valley plot around three fallen trees. During the 11 months of this study, three tree falls occurred in the Fern Valley plot (one standing dead *Shorea curtisii* from outside the plot and two live trees within the plot belonging to the species *Ixonanthes icosandra* and *Eugenia duthieana*). No tree falls occurred in the Jungle Fall Valley plot. There was no significant difference between the two plots in total length of fallen dead stems > = 20 cm in diameter. If soils are thinner in Fern Valley than Jungle Fall Valley, a higher rate of uprooting of live trees could be expected to continue there.

There were large differences between the two plots in numbers of both woody (lianes) and herbaceous climbing plants. The Jungle Fall Valley plot had 67% more lianes > = 2 cm dbh (45 or 188/ha vs. 27 or 112/ha) and 181% more climbers <2 cm dbh (woody and herbaceous stems = 938) than the Fern Valley plot (woody and herbaceous stems = 334). While the Fern Valley plot had 28 climbing palms (*Calamus* and *Daemonorops*) > = 2 cm dbh and 11 Araceous climbers <2 cm dbh, Jungle Fall Valley had two climbing palms > = 2 cm dbh but 214 Araceous climbers <2 cm dbh. I suggest that these differences in numbers of climbers may indicate significant differences between the two plots in available moisture as influenced by soil depth. Putz and Chai (1987) found 164 and 348 woody vines/ha >2 cm dbh in hilltop and valley study plots respectively within primary dipterocarp forest in Lambir National Park, Sarawak, Malaysia.

Table 2
Distribution by size class of plant species with stems contributing the most basal area in the Fern Valley plot.

Species	Basal Area	Distribution by dbh size classes (cm)				
	(cm^2)	2–10	10–20	20–30	30–40	40+
Shorea curtisii	9,164	5	0	0	0	1
Pertusadina eurhyncha	7,235	0	0	0	0	1
Oncosperma horridum	5,174	9	21	2	0	0
Pellacalyx saccardianus	3,494	7	1	0	1	1
Artocarpus lanceifolius	2,952	0	0	0	0	1
Dipterocarpus penangianus	1,913	4	3	1	1	0
Meiogyne virgata	1,507	0	0	0	0	1
Gluta wallichii	1,265	1	0	0	1	0
Castanopsis lucida	1,251	0	0	0	0	1
Adenanthera bicolor	1,226	0	0	0	0	1
Litsea castanea	1,140	0	0	0	0	1
Licania splendens	1,123	0	0	0	0	1
Dalbergia parviflora	759	1	1	1	0	0
Artocarpus lowii	755	0	0	0	1	0
Myristica cinnamomea	743	3	2	1	0	0
Ixonanthes icosandra	660	0	0	1	0	0
Calophyllum ferrugineum	651	1	0	1	0	0
Gironniera parvifolia	580	6	3	0	0	0
Santiria sp.	491	0	0	1	0	0
Eugenia longiflora	491	0	0	1	0	0
Polyalthia angustissima	469	1	0	1	0	0
Santiria apiculata	439	5	0	1	0	0
Macaranga triloba	419	7	2	0	0	0
Tabernaemontana peduncularis	410	7	1	0	0	0
Eugenia densiflora	394	3	0	1	0	0
146 other species	8,829	445 stems in all size classes				
Totals	53,534	564 stems in all size classes				

Table 3
Distribution by size class of plant species with stems contributing the most basal area in the Jungle Fall Valley plot.

Species	Basal Area	Distribution by dbh size classes (cm)				
	(cm^2)	2–10	10–20	20–30	30–40	40+
Shorea curtisii	15,469	23	0	0	0	3
Shorea parvifolia	7,860	1	0	0	0	1
Shorea macroptera	7,405	2	1	1	1	1
Gluta wallichii	4,232	5	1	2	1	1
Santiria griffithii	3,087	2	0	0	1	1
Dillenia grandifolia	1,752	2	1	0	0	1
Crypteronia cumingii	1,603	2	0	0	0	1
Gironniera parvifolia	1,366	34	9	0	0	0
Ixonanthes icosandra	1,046	1	0	2	0	0
Dacryodes sp.	962	0	0	1	0	0
Adenanthera bicolor	908	0	0	1	0	0
Shorea gratissima	888	0	1	1	0	0
Aporusa benthamiana	836	7	1	1	0	0
Planchonella maingayi	707	0	0	1	0	0
Artocarpus rigidus	707	0	0	1	0	0
Strombosia ceylanica	651	20	3	0	0	0
Cyathocalyx remuliflorus	639	9	2	0	0	0
Garcinia griffithii	601	6	0	1	0	0
Euodia glabra	589	1	0	1	0	0
Eugenia duthieana	563	7	3	0	0	0
Xylopia malayana	549	3	2	0	0	0
Knema laurina	542	21	1	0	0	0
Memecylon megacarpum	504	4	2	0	0	0
Scorodocarpus borneensis	452	0	0	1	0	0
Unidentified climbers	425	34	0	0	0	0
190 other species	14,920	765 stems in all size classes				
Totals	69,263	1,000 stems in all size classes				

Table 4
Relative density and distribution by dbh size class of the most numerous species in the Fern Valley plot.

Species	Relative Density	Distribution by dbh size classes (cm)		
	(%)	2–10	10–20	20+
Urophyllum hirsutum	6.2	35	0	0
Oncosperma horridum	5.9	9	21	2
Calamus-Daemonorops	5.1	28	0	0
Ganua kingiana	4.0	22	0	0
Koilodepas wallichianum	3.5	19	0	0
Urophyllum streptopodium	2.6	14	0	0
Pellacalyx saccardianus	1.8	7	1	2
Dipterocarpus penangianus	1.6	4	3	2
Gironniera parvifolia	1.6	6	3	0
Streblus elongatus	1.6	8	1	0
Macaranga triloba	1.6	7	2	0
Urophyllum glabrum	1.5	8	0	0
Tabernaemontana peduncularis	1.5	7	1	0
Dacryodes rostrata	1.5	8	0	0
Knema laurina	1.5	7	1	0
Aporusa symplocoides	1.3	5	2	0
Blumeodendron tokbrai	1.1	6	0	0
Polyalthia sp.	1.1	5	1	0
Myristica cinnamomea	1.1	3	2	1
Shorea curtisii	1.1	5	0	1
Santiria apiculata	1.1	5	0	1
Hopea mengarawan	1.1	6	0	0
148 other species	296 stems in all size classes			
Total	564 stems in all size classes			

Table 5
Relative density and distribution by dbh size classes
of the most numerous species in the Jungle Fall Valley plot.

Species	Relative Density	Distribution by dbh size classes (cm)		
	(%)	2–10	10–20	20+
Gironniera parvifolia	4.3	34	9	0
Urophyllum hirsutum	4.2	42	0	0
Santiria apiculata	2.8	29	0	0
Koilodepas wallichianum	2.7	27	0	0
Santiria laevigata	2.7	27	0	0
Shorea curtisii	2.6	23	0	3
Dyera costulata	2.5	25	0	0
Buchanania sessilifolia	2.3	25	0	0
Strombosia ceylanica	2.3	20	3	0
Calamus-Daemonorops	2.2	22	0	0
Knema laurina	2.2	21	1	0
Baccaurea parviflora	2.0	20	0	0
Phaeanthus ophthalmicus	1.9	20	0	0
Ganua kingiana	1.8	18	0	0
Popowia fusca	1.4	17	0	0
Ardisia teysmanniana	1.3	14	0	0
Pimeleodendron griffithianum	1.2	11	1	0
Gcnystylus confusus	1.1	13	0	0
Glycosmis chlorosperma	1.1	12	0	0
Calophyllum tetrapterum	1.1	11	0	0
Cyathocalyx remuliflorus	1.1	9	2	0
Myristica cinnamomea	1.0	9	1	0
Gynotroches axillaris	1.0	9	1	0
Gluta wallichii	1.0	5	1	4
Eugenia duthieana	1.0	7	3	0
190 other species	530 stems in all size classes			
Total	1,000 stems in all size classes			

Table 6

Summary of clumping tests for woody species in Fern Valley with 5 or more stems. One asterisk indicates significance at P<0.05 and two asterisks, significance at P<0.01. Three indices of aggregation are compared: c — Clark and Evans (1954); I — Grieg-Smith (1982); and z — Johnson and Zimmer (1985). Significantly negative *c* values indicate positive skewness and thus clumping, while significantly positive values indicate nearest neighbour distances greater than expected by chance.

Species	n	c	z	I	Growth Form
1. Urophyllum hirsutum	32	−5.06**	−0.77	20.54	Treelet
2. Oncosperma horridum	32	—	−0.89	—	Tree palm
3. Ganua kingiana	22	−0.57	1.35	44.96**	Treelet
4. Koilodepas wallichianum	19	−1.07	3.09**	51.31**	Treelet
5. Urophyllum streptopodium	14	−9.19**	−0.56	16.59	Treelet
6. Pellacalyx saccardianus	10	0.87	−0.78	23.54**	Tree
7. Dipterocarpus penangianus	9	−0.44	0.93	39.12**	Large tree
8. Gironniera parvifolia	9	−0.32	—	14.65	Tree
9. Streblus elongatus	9	0.82	—	6.70	Large tree
10. Macaranga triloba	9	0.82	−0.63	75.10**	Small tree
11. Knema laurina	8	0.42	−0.74	48.95**	Tree
12. Urophyllum glabrum	8	−0.02	—	79.78**	Treelet
13. Tabernaemontana peduncularis	8	0.73	1.55	13.56	Treelet
14. Dacryodes rostrata	8	−2.31*	−0.04	7.93	Large tree
15. Aporusa symplocoides	7	0.27	—	48.65**	Treelet
16. Myristica cinnamomea	6	−1.00	2.72**	12.08	Tree
17. Blumeodendron tokbrai	6	1.75	−0.13	40.06**	Large tree
18. Santiria apiculata	6	2.08*	−0.76	10.48	Small tree
19. Hopea mengarawan	6	0.57	—	23.30**	Large tree
20. Shorea curtisii	6	−2.42*	−1.34	5.50	Large tree
21. Dehaasia sp.	5	−0.31	—	16.92**	Tree
22. Canarium sp.	5	−0.80	—	9.72	Tree
23. Xanthophyllum eurhynchum	5	−1.21	−0.35	6.48	Tree
24. Ardisia teysmanniana	5	−4.43**	—	2.13	Small tree
25. Medusanthera affinis	5	−1.05	—	7.51	Treelet
26. Horsfieldia sp.	5	−0.12	−0.39	18.50**	Large tree
Percentage clumped			12.5	48%	
+ Skewed		20%			
− Skewed		4%			
Randomly dispersed		76	87.5%	52%	

Table 7

Summary of clumping tests for woody species in Jungle Fall Valley with 5 or more stems. One asterisk indicates significance at $P<0.05$ and two asterisks, significance at $P<0.01$. Three indices of aggregation are compared: c — Clark and Evans (1954); I — Grieg-Smith (1982); and z — Johnson and Zimmer (1985). Significantly negative *c* values indicate positive skewness and thus clumping, while significantly positive values indicate nearest neighbour distances greater than expected by chance. Numbers may be slightly less than in Table 5 due to elimination of stems one metre or less from the edge of the plot.

Species	n	c	z	I	Growth Form
1. Gironniera parvifolia	43	3.46**	−1.57	78.49**	Tree
2. Urophyllum hirsutum	42	−7.56**	0.96	30.84	Treelet
3. Santiria apiculata	28	0.86	−0.40	36.78	Small tree
4. Santiria laevigata	27	1.14	−0.81	28.65	Large tree
5. Koilodepas wallichianum	27	−2.44**	−0.66	56.10**	Treelet
6. Shorea curtisii	26	−1.83	−0.36	21.32	Large tree
7. Dyera costulata	25	−1.61	−0.39	36.38	Large tree
8. Buchanania sessilifolia	23	−1.63	0.82	66.55*	Tree
9. Strombosia ceylanica	23	−0.80	0.8	47.14**	Small tree
10. Knema laurina	22	−0.54	0.14	55.10**	Tree
11. Baccaurea parviflora	20	−0.25	2.39*	21.90	Small tree
12. Phaeanthus ophthalmicus	19	−3.68**	3.60**	113.26*	Small tree
13. Ganua kingiana	18	−2.92**	0.14	13.19	Treelet
14. Popowia fusca	14	0.65	−0.02	16.67	Tree
15. Ardisia teysmanniana	13	0.92	0.19	93.02**	Small tree
16. Pimeleodendron griffithianum	12	−1.58	0.04	50.79**	Tree
17. Gonystylus confusus	11	−2.05*	0.90	5.33	Treelet
18. Glycosmis chlorosperma	11	1.16	—	46.76**	Treelet
19. Calophyllum tetrapterum	11	1.98*	−0.41	8.58	Tree
20. Cyathocalyx remuliflorus	11	−1.03	−1.23	52.10**	Tree
21. Myristica cinnamomea	10	0.24	—	38.1**	Tree
22. Gynotroches axillaris	10	−1.93*	0.68	43.42**	Tree
23. Gluta wallichii	10	0.29	0.11	42.46**	Large tree
24. Eugenia duthieana	10	1.79	0.69	32.3	Tree
25. Gomphandra quadrifida	9	0.16	−1.38	17.24	Treelet
26. Anisoptera megistocarpa	9	3.14**	—	21.02*	Large tree
27. Litsea accedens	9	1.65	—	62.31**	Tree
28. Aporusa benthamiana	9	1.27	—	5.10	Tree
29. Macaranga triloba	9	−3.57**	0.83	136.01**	Small tree

(Cont'd opposite page)

Table 7 *(Cont'd)*

Species	n	c	z	I	Growth Form
30. Payena lucida	8	3.16**	−0.15	11.38	Treelet
31. Palaquium microphyllum	8	2.18*	0.25	19.26**	Tree
32. Ardisia colorata	8	1.07	−1.07	22.97**	Small tree
33. Polyalthia sumatrana	8	0.28	0.30	51.71**	Tree
34. Unknown Meliaceae	7	−2.36**	−0.39	34.68**	Tree
35. Calophyllum ferrugineum	7	1.47	—	27.77**	Tree
36. Garcinia griffithii	7	−1.26	—	8.66	Tree
37. Randia densiflora	6	0.25	0.11	34.97**	Partial liana
38. Memecylon megacarpum	6	0.13	—	20.02**	Treelet
39. Shorea macroptera	6	−0.31	0.004	3.03	Large tree
40. Polyalthia angustissima	6	−0.66	—	37.06**	Small tree
41. Aporusa microstachya	6	1.54	−1.29	26.24**	Treelet
42. Gaertnera grisea	5	0.10	—	4.67	Shrub
43. Microcos blattaefolia	5	0.71	—	3.63	Small tree
44. Eugenia longiflora	5	2.22**	—	5.39	Tree
45. Hopea mengarawan	5	−1.45	—	0.29	Large tree
46. Archidendron sp.	5	1.00	—	18.19**	Small tree
47. Cnestis platantha	5	−2.91**	—	1.86	Liana
48. Prunus polystachya	5	0.34	—	60.90*	Tree
49. Actinodaphne malaccensis	5	−1.52	0.75	13.21*	Tree
Per cent clumped			6.1%	57.1%	
+ Skewed		18.4%			
− Skewed		12.2%			
Randomly dispersed		69.4%	93.9%	42.9%	

Tests of Dispersion

There are no records of major disturbances from fire, typhoons or earthquakes in the Bukit Timah Forest Reserve in the past 100 years. Therefore the degree of clumping should be high due to the presence of regeneration patches from tree falls (Pickett 1983), the most common form of disturbance (Armesto et al. 1986).

Three tests of dispersion were used to evaluate the degree of clumping in all species with > = 5 stems per plot [Clark and Evans (1954), Grieg-Smith (1983), and Johnson and Zimmer (1985)]. By use of that criterion, 26 species were analysed in Fern Valley (Table 6) and 49 in Jungle Fall Valley (Table 7). The test of Grieg-Smith (1983) declared more species to be significantly clumped than the other two methods (48 and 57.1% for Fern Valley and Jungle Fall Valley respectively.

Drought Deciduousness

Several species showed adaptations for deciduousness during the 1982–83 drought. I observed one large individual of each of four species of trees, *Parkia speciosa, Anisoptera megistocarpa, Parishia sp.,* and *Planchonella maingayi,* become leafless for a period of 3–6 weeks, and lianes also shedding many leaves. The large variation in annual rainfall from 1969 to 1983 (4007–1642 mm/yr) probably is typical of past variability. Holttum (1953) stated that over the previous 46 yr there had been 21 months with less than 6.2 cm of rain.

Future Trends in Forest Composition

The study plots and the reserve itself represent a mature phase rain forest (Whitmore 1984) in a ''state of structural and dynamic non-equilibrium'' (Ho et al. 1987: 51, Hartshorn 1980). Features of a mature phase rain forest include abundant seedlings and saplings of at least some tree species attaining the canopy, many tree, sapling and seedling size classes represented, low light intensities on the forest floor, a lack of disturbance from fire and domestic animals, and minimal disturbance from humans.

The small size of my study plots make it difficult to predict future changes in tree species composition on the two areas. Reproduction of the more important tree species must be studied over a larger area and longer period of time. *Shorea curtisii* dominated both plots in basal area and had some saplings in the smallest size class (Tables 2 and 3). However, eleven species in Fern Valley and five in Jungle Fall Valley were represented by one large individual and no representation in the two smallest size classes (Tables 2 and 3), while other species of mid-size and large trees were represented by seedlings and saplings but no mature individuals, such as *Pentace triptera* in Fern Valley and *Santiria laevigata* and *Dyera costulata* in Jungle Fall Valley. Wong (1987) reported finding 3, 8 and 1 individuals of these species respectively of gbh > = 12 inches in his sample of 889 trees in a 3.24 ha area of the reserve. *Dyera costulata* has been identified as a colonizer of gaps (Poore 1968) and a strong, light demanding species (Whitmore 1973).

A low number of adult individuals of other known light-demanding species persisted in the study plots without regeneration, such as *Macaranga triloba* (nine stems in each plot), and *Ixonanthes icosandra*, a long-lived pioneer according to Ho et al. (1987). According to Hartshorn (1978), such tree species with little or no regeneration may be gap species that are normally present in mature rain forest. Knight (1975) concluded that the tropical forest reserve on Barro Colorado Island, Panama, had not reached a climax equilibrium state after 130 yr of development and that in the older part of the forest several species of trees probably depended on wind-created canopy gaps for their persistence.

Evidence for Niche Differentiation

The graphs of slope position of 26 species in the Fern Valley plot and 49 in the Jungle Fall Valley plot (Figs. 5 & 6) provide some evidence for niche separation of woody species on hilly topography. These data support the position of Ashton (1976) regarding mixed dipterocarp forest in the Malayan lowlands ''that floristic variation is unequivocally and consistently correlated principally with environmental factors, among which physiography is clearly important.'' *Shorea curtisii*, a ridgetop species according to Whitmore (1984), occurred at a more extreme upper right position in the Fern Valley (#20, Fig. 5) than in the Jungle Fall Valley graph (#6, Fig. 6). The Fern Valley plot is more eroded and dissected than the Jungle Fall Valley plot and may offer an environment more like ridgetop conditions than Jungle Fall Valley would. Ashton (1978) described the differences between the canopy and sapling leaves of *Shorea curtisii* and suggested that the mature phase canopy trees had evolved characteristics to cope with moisture stress over a long lifetime. Dipterocarps in Sarawak and Brunei appear to have strong site-specificity (Ashton 1964, 1969 and Brunig 1973).

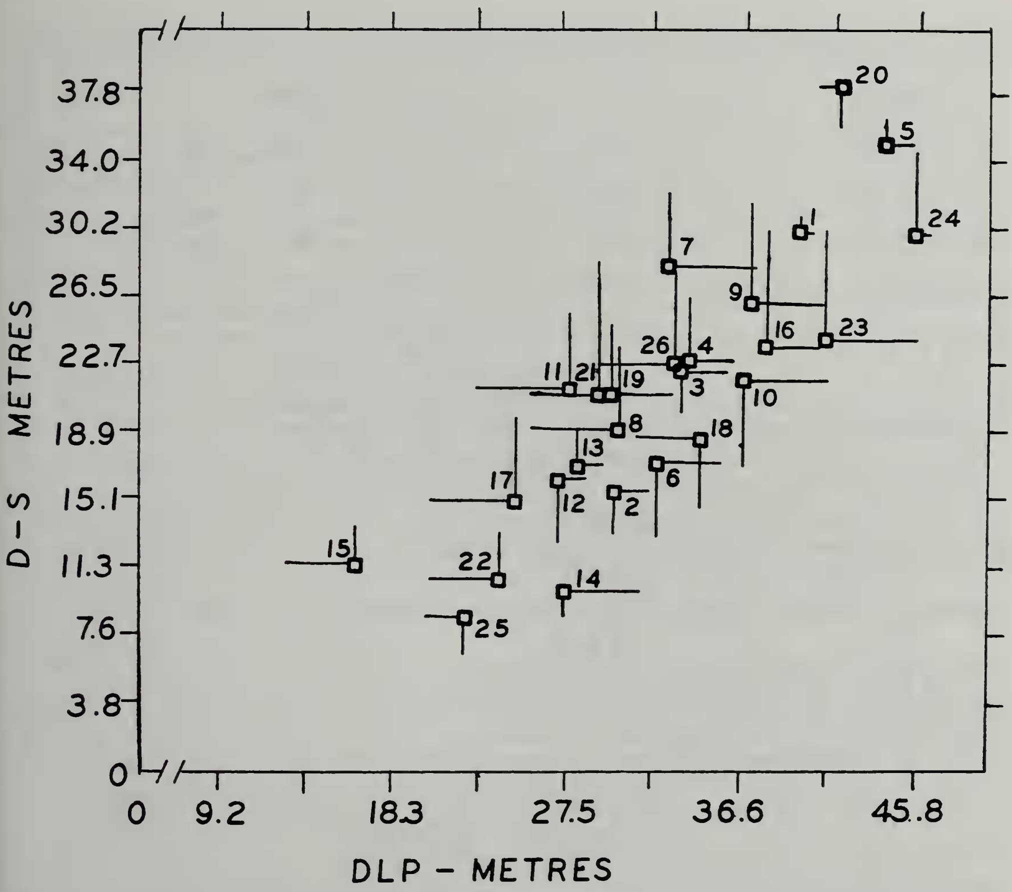

Fig. 5: Regression of the locations of stems of 26 woody species in the Fern Valley plot in which mean perpendicular distance to the drainage path (D-S) is plotted against mean distance to the lowest point in the plot (DLP). Single lines indicate one SE. Species numbers correspond to those in Table 6. Multiple $r = 0.85286$, $F = 32.015$, 1/12 DF, $P<0.002$, two-sided test.

Of those species that were numerous in both plots, some displayed similar mean elevational positions and some did not. *Gironierra parvifolia* (#8 in Fig. 5 and #1 in Fig. 6) occupied a similar mean elevational position to *Shorea curtisii* in the Jungle Fall Valley plot, but their positions were widely separated in Fern Valley. *Urophyllum hirsutum* occupied a high elevational position in both plots. *Knema laurina,* listed by Ho et al. (1987) as a common understory species of Malayan rain forests, occupied similar central positions in both plots (#11 in Fig. 5 and #10 in Fig. 6). On the other hand, *Ardisia teysmanniana,* a small tree, had a high position in Fern Valley (Fig. 5, #24) and a low position in Jungle Fall Valley (Fig. 6, #15). *Pimeleodendron griffithianum* occupied a low mean elevational position in Jungle Fall Valley (lower left corner of Fig. 6, #16), presumably the wettest location. Ho et al. (1987) listed it as a widely distributed species in lowland dipterocarp forest typically found in swampy soils.

Differences in behavioural characteristics and environmental requirements other than slope position may be especially important in reducing competition between two or more species in the same genus when these species are abundant in the same small

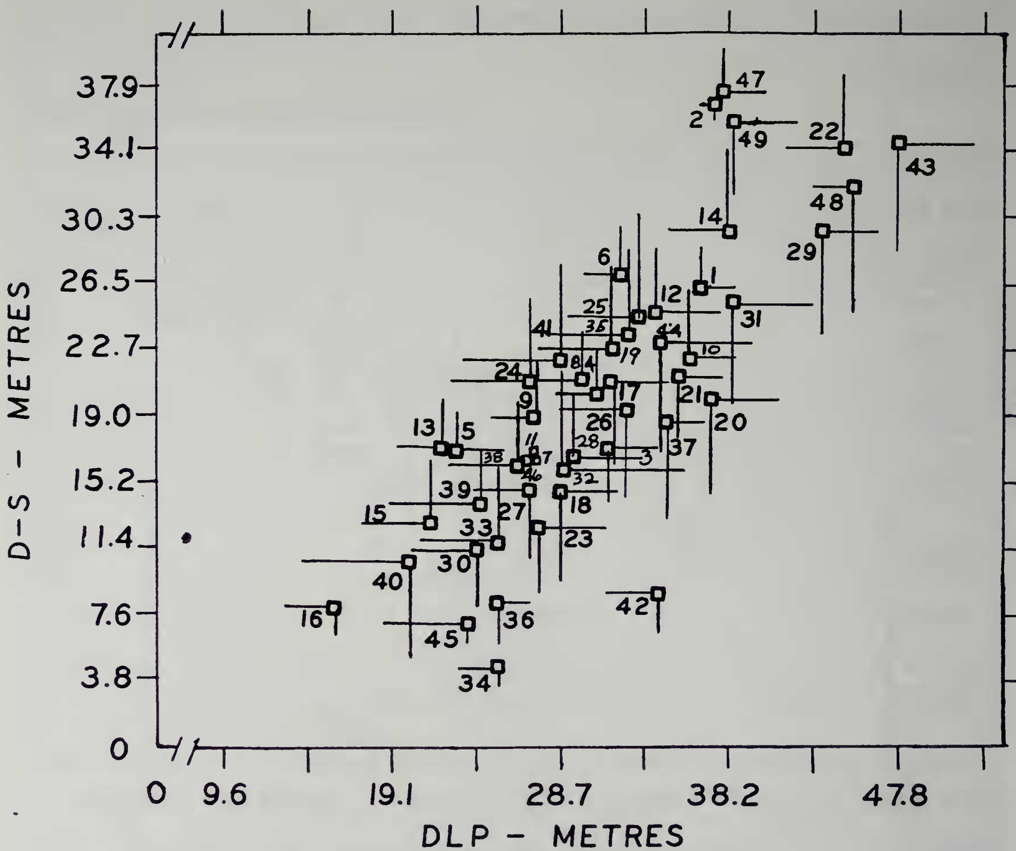

Fig. 6: Regression of the locations of stems of 49 woody species in the Jungle Fall Valley plot in which mean perpendicular distance to the estimated drainage path (D-S) is plotted against mean distance to the lowest point in the plot (DLP). Single lines indicate one SE. Species numbers correspond to those in Table 7. Multiple r = 0.65364, F = 8.9516, 1/12 DF, $P<0.05$, two-sided test.

area. In the Fern Valley plot (Fig. 5), three species of *Urophyllum,* all treelets, (*U. hirsutum*-#1, *U. streptopodium*-#5, and *U. glabrum*-#12) differed significantly in slope position. However, two other pairs of species in Jungle Fall Valley (*Eugenia longiflora*-#44, *E. duthieana*-#24, *Ardisia colorata,* #32 and *A. teysmanniana*-#15) did not differ significantly in slope position between species within a genus.

The Need for Forest Conservation

Based on the 11 months I spent studying the Bukit Timah Forest Reserve, I have become concerned that a nature reserve of only 71 ha would be in grave danger of gradually losing its rarer species because of accidents to one or a few remaining individuals or because of poor reproduction (Lovejoy et al. 1983). According to Lovejoy and Oren (1981), there is some support for the hypothesis that small fragments of ecosystems gradually become impoverished due to a predictable, sequential loss of species and possible invasion by weedy species. At Bukit Timah, the lack of the original complement of animal species, human encroachments on the reserve due to bull-dozing and quarrying of rock around its periphery, and intensive use as a city park all threaten the health of this valuable, small reserve. May (1986: 1121) stated, "in so far as any mathematical generalization exists, it is that randomly constructed ecosystems are likely to become less stable — more prone to fluctuation and less able to recover from disturbance — as they become more complex...."

The number of species of animals that once dispersed seeds in the Singapore area must be greatly reduced over that prior to 20,000 yr B.P. Absent species in the Holocene might well include gibbons, langurs, elephants, bovids, rhinoceros, tapirs, and pigs (Janzen 1978). Janzen (1970, 1974, 1975, 1978) has described the interaction of herbivores with tropical tree species, the irregular but abundant flowering and fruiting of the dipterocarps, and their chemical defences in the form of resins and gums. Putz (1979) stated that various animal species dispersed the seeds or fruits of 90% of the canopy tree species at the Bukit Lanjan study area 25 km northeast of Kuala Lumpur, Malaysia.

Ricklefs (1987) urged ecologists to study communities from a regional and historical point of view. Broad regional processes over more than 80 million yr have produced an unusually high diversity of flowering plant species in Southeast Asia (Fedorov 1966). Keng (1970) estimated that there are 8000 to 8500 plant species in the Malay Peninsula. Plant conservation in Southeast Asia will require much cooperation between Thailand, Malaysia, Singapore and Indonesia to establish a series of reserves, each including a continuum of communities from high to low elevations and thus to avoid the disastrous consequences of having only a small number of isolated fragments by the 21st century.

The Republic of Singapore is on the threshold of becoming a major biotechnology center of Southeast Asia. The more species of plants that can be grown in their natural setting with reproductively viable populations, the greater will be the opportunities for genetic manipulation of a vast treasure house of plant species and for future restoration of moist tropical forest to degraded land.

It would be prudent therefore to protect and upgrade the nature reserve by the following actions: establishment of 1) a stable buffer zone between the reserve and rock and earth-moving activities nearby and 2) special plantations to propagate rare species and others now extinct in Singapore so that plant species could be introduced into suitable habitats from which they have disappeared.

The great advances that have been made in tissue culture, cell hybridization, and genetic engineering have provided additional, urgent reasons for plant conservation and for understanding the processes that sustain plant communities. The Republic of Singapore has the scientific resources to capitalize on the enormous wealth of plant species for food crops, enzymes, hormones, medicinal drugs, timber, and ornamentals. Now is the time to act on the establishment, preservation and improvement of nature reserves.

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