The Ecology of a Semi-Evergreen Forest Community in Sri Lanka

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ABSTRACT

Semi-evergreen forests cover the dry zone plains of Sri Lanka and constitute four-fifths of the island's vegetation. In a sample area of 3 km^2, in the Polonnaruwa Sanctuary, 63 tree species were found; 46 were characteristic of other dry zone forests, and 17 occurred only under special edaphic and biotic conditions. As in other dry zone forests, *Drypetes sepiara* (Euphorbiaceae) prevailed with a relative density of 21.3 percent. The Shannon index of diversity was 4.23 bits per individual, of which 79.4 percent was attributable to evenness; most species had few individuals. Dominance was shared between species typical of the subcanopy and canopy. Measures of diversity and of dominance between species placed the semi-evergreen community in Polonnaruwa as a type intermediate between tropical rainforest and deciduous monsoon forest. Measures of diameters (DBH) and estimates of the height of trees indicated that all species with typically very large trees had few individuals that were distributed more or less evenly through all the size classes. Typically smaller species had large numerical representation. These facts are discussed in light of dominance relationships and regenerative patterns in the community, and are related to possible evolutionary trends. The distribution of most species was clumped, but that of certain rare species was random. Clumping at 2,500 m^2 plot size usually meant clumping at smaller-sized plots. Clumping on a large scale reflected local differences in species dominance.

Five shrub associations were distinguished by density and constitute dominant and co-dominant species. Differences were related to the amount of light penetrating through the tree canopy and to edaphic factors. *Glycosmis pentaphylla* (Rutaceae) was the dominant shrub species in the climax association which flourished under a fairly closed tree canopy and lacked an herbaceous layer.

ALTHOUGH EVERGREEN RAINFORESTS and monsoon forests of tropical Asia have received considerable attention from ecologists (e.g., Richards 1962, Ashton 1964, Ogawa *et al.* 1961, 1965), the semi-evergreen forests have been less intensely studied. In Sri Lanka the forests have been surveyed primarily from an economic perspective (e.g., Andrews 1961). This paper aims first, quantitatively to describe some structural features of a community of semi-evergreen forest in Sri Lanka; second, to examine the dominance relationships between species in this community. These relationships are briefly related to possible successional patterns in the dry zone of Sri Lanka, and to possible evolutionary trends among plants in general.

The semi-evergreen forest has been described by Walter (1971: 209) as one in which the "upper tree layer is defoliated for some of the year [during the drought],[1] while the lower tree layer retains its foliage." According to certain structural features, annual rainfall and drought duration, it is a type intermediate between tropical evergreen rainforest and deciduous monsoon forest.

The tropical island of Sri Lanka has a gradation of forests from lowland and montane rainforests to lowland scrub forests and savanna (fig. 1). The majority of the forests may be roughly classed as semi-evergreen, however. These cover the most extensive physiographic feature of Sri Lanka, the lowland plains in the dry zone.

[1] Brackets are mine.

Several classificatory schemes have been proposed for the vegetation of Sri Lanka (e.g., Koelmeyer 1958, Gaussen *et al.* 1964, Fernando 1968). Mueller-Dombois (1968) evaluates these schemes and offers an up-to-date reclassification according to long-term climatic information.

The community of forest described herein is located within the Polonnaruwa Sanctuary in the northwestern dry zone at 07° 56′ N and 81° 00′ E. Polonnaruwa was the capital of Sri Lanka for varying periods between the 8th and 13th centuries. It was completely abandoned by the end of the 13th century, and natural vegetation reclaimed the land for the next 700 years. The area was resettled only at the beginning of the 20th century. Most of the natural vegetation has been maintained within the Sanctuary, although the shrub layer has been removed in areas immediately surrounding archaeological sites. The cutting of trees is prohibited, but poaching, particularly of young trees of construction-pole size, is not completely prevented. Parts of the study area are completely devoid of young trees and shrubs. These areas have been largely omitted in the present sample. The study site encloses approximately 3 km^2, is bounded by water and cultivation, and is continuous with more extensive expanses of forest by a narrow connection.

The ecologically significant parameters of temperature and rainfall may be portrayed in a composite "climate diagram" (fig. 2). It was developed by Walter (1957), applied on a world-wide basis by

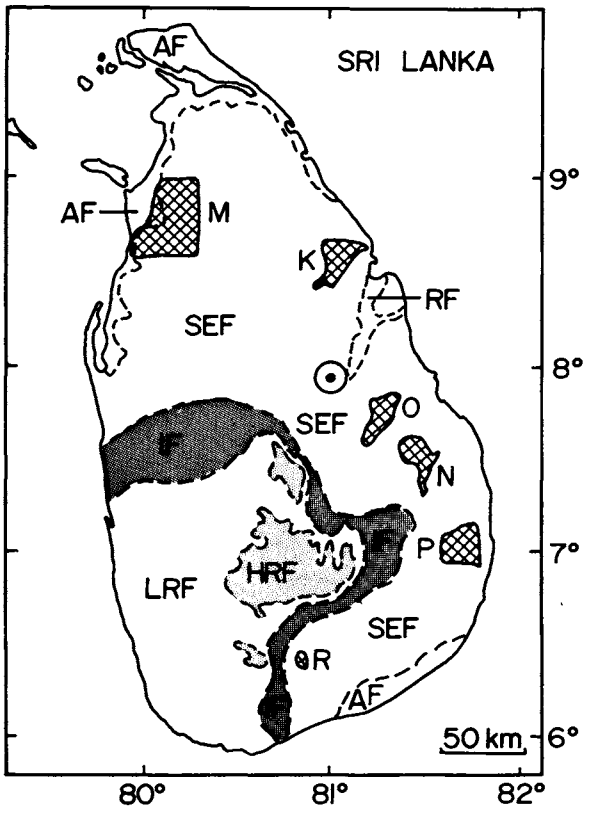

FIGURE 1. Map of the natural vegetation of Sri Lanka. AF = arid zone forest; HRF = highland rainforest; IF = intermediate forest; LRF = lowland rainforest; RF = riverine forest; SEF = semi-evergreen forest (modified after Fernando 1968). The location of the Polonnaruwa study site is encircled. Six forest reserves shown are: K = Kantalai; M = Madhu; N = Nuwaragala; O = Omunagala; P = Panama; and R = Ratkarawwa.

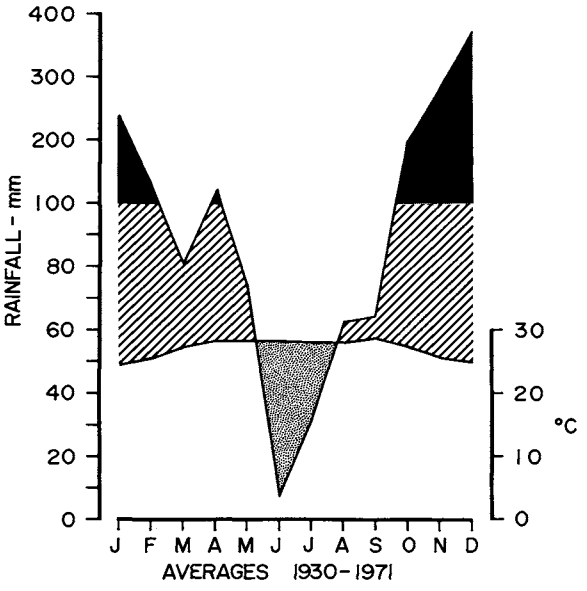

FIGURE 2. Climate diagram for Topaweva, Polonnaruwa, monthly averages 1930-1971. Superhumid periods are shaded dark, drought is light stippled; rainfall most significant for plant growth is indicated in diagonal lines. Temperature is indicated in degrees centigrade (C). See text for explanation of climate diagram.

Walter and Lieth (1960), and to Sri Lanka by Mueller-Dombois (1968). It is a convenient synopsis of monthly water relations plotted for one year. When plotting mean monthly temperatures (T) and precipitation (P) graphically, a scale of 10° C = 20 mm precipitation is used (Gaussen 1955). This scale (T: P = 1:2) follows empirical evidence (Walter 1957) that a period of stress or drought occurs for plants when the precipitation curve (P) cuts below the temperature curve (T). The stippled areas in figure 2 represent such a drought. Monthly rainfall in excess of 100 mm is of little importance to plant growth since much of it is lost as run-off *(ibid.)*. The diagram would become cumbersome if the same scale (T:P = 1:2) were retained when rainfall far exceeded 100 mm. Therefore, it is expedient to reduce the scale to one-fifth whenever monthly rainfall exceeds 100 mm. Such super-humid periods are shown in black in the climate diagrams. Rainfall most significant for plant growth is shown by the diagonal lines pattern. Mean annual rainfall over 42 years in Polonnaruwa is 1671 mm.

All rainfall information was obtained from the Meteorological Station of Topaweva, only 1 km from the study area. Temperature data were collected at the dry zone station of Maha Illuppallawa, 64 km WNW of Polonnaruwa. All data were taken from several reports of the Colombo Observatory (Ekanayake 1964, 1968, 1969, 1970) and through the kind cooperation of the Director of the Topaweva Meteorological Station and the Director of the Colombo Observatory.

Sri Lanka falls under an equatorial climatic regime modified by monsoons. Most rains in Polonnaruwa are brought by zenithal or convectional rains and cyclones from October to November. These foreshadow and grade into the NW monsoon which brings rainfall to a peak in December. Zenithal rains are again marked in April. The northern and eastern regions of Sri Lanka are shielded from SW monsoon rains by the montane region. Instead, the SW monsoon is a strong, dessicating wind which blows almost constantly between May and August. It has the effect of accentuating the drought conditions in the dry zone. Climatic conditions throughout most of

the lowland dry zone were similar to those in Polonnaruwa. For details of local variations, see Mueller-Dombois (1968).

The major factor influencing soil formation in Sri Lanka is climate, parent material being generally a subordinate factor; the boundaries of major soil groups follow closely the rainfall divisions of the island. Locally, however, appreciable differences may occur between soils on the crest of a ridge and those at the bottom of a slope (Cooray 1967). Reddish Brown Earths are one of the Great Soil Groups of Sri Lanka, occurring extensively in the lowland dry zone where annual rainfall is less than 1900 mm. Most of the parent material in these areas is relatively uniform consisting of biotite and hornblende bearing gneises of the metamorphic Vijayan Series of middle Paleozoic Age *(ibid)*. In these soils leaching occurs only partially. During the drought part of the leached materials are brought back to the surface by capillary action, and iron oxide remains in a hydrate state giving a uniformly reddish-brown color to these soils (Fernando 1968). The topography of the Polonnaruwa area is generally "flat," relief within the areas sampled being less than 10 meters. Based on soil maps *(ibid.)*, the geology and climate of Polonnaruwa, the soils there are typically Reddish Brown Earths, although they were not analyzed in this study.

METHODS OF VEGETATION ANALYSIS

The field data for the analysis of trees is based on the 10 percent strip method commonly used by foresters (Cain and Castro 1959). Detailed topographical maps were constructed from aerial photographs on the scale of approximately 1:2,380 (1 cm = 24 m). These and compass lines served for orientation. A series of 10-meter-wide swaths were taken every 100 meters until the entire study area was sampled. The swath was subdivided into contiguous 100 meter^2 plots. There were a total of 1825 100 m^2 plots. In each plot all trees above 5 m were identified, and their circumference at breast height and height were recorded. The circumferences were tape-measured and later converted to diameters (DBH). The heights were visually estimated by two persons.

Woody plants less than 5 m in height were considered as shrubs. In the shrub layer several more or less distinct associations were evident by the dominance or co-dominance of species. Each hectare of the study area was divided into nine equal-sized sub-plots. The dominant growth was recorded for each subplot. In parts of the area greater refinement was employed. Within each shrub association, several randomly selected plots of 100 m^2 were laid out; the total number of plots was 63. The number of shrubs per species was recorded for each plot.

Voucher specimens of all plant material surveyed in Polonnaruwa were collected. These are stored in the herbaria of the Peradeniya Royal Botanical Gardens (Sri Lanka), and in the collections of Dr. Raymond Fosberg at the United States National Museum of Natural History, Washington, D.C.

RESULTS

THE NUMBER OF TREE SPECIES.—An extensive inventory of the forests of Sri Lanka was carried out in 1955 by the Hunting Survey Corporation Limited, Toronto, Canada, under the auspices of the Canada-Colombo Plan. The object of this survey was purely economic; to assess marketable species and volume by forest types for the island. Our own results will be compared to this survey where relevant.

The dry zone forests constitute about 86.5 percent of the total forested area of Sri Lanka (Andrews 1961). The maximum number of tree species found here is approximately 111 *(ibid.)*, but there is much local variation according to climatic and edaphic factors. The number of species found in any one area, as in a forest reserve of several hundred km^2, varies between approximately 47 species in the very dry Madhu Reserve (Oudshoorn 1961) to 69 species in the moister Omunagala Reserve (McCormack and Pillai 1961a) for equivalent sample sizes. Even on a local scale, many of these tree species are not typical semi-evergreen forest species. Andrews (1961) lists 85 species as "dry zone species." A check of their distribution and characteristic habitat according to Worthington (1959) reveals that 28 of these species occur only under special conditions, mainly along river banks or in grasslands, and/or are typical of other climatic zones.

The total number of tree species found in the Polonnaruwa study area of 3 km^2 was 61, belonging to 50 genera and 25 families. The species, their densities, and relative densities are tabulated in table 1. The table includes species that were found in the study area, but that were either too rare to appear in the sample plots, or that appeared only under special edaphic and biotic conditions. The following species occurred exclusively on the periphery of the Parakrama Samudra lake, or along the banks of the irrigation channel that bordered the study area: *Morinda tinctoria, Azadirachta indica, Streblus asper, Madhuca longifolia, Eugenia bracteata, Lannea coromandelica,* and *Alstonia scholaris.*

This distributional pattern is in accord with Worthington's (1959) observations that most of these species are most common along the coastal areas of

TABLE 1. *The number and density of tree species.*

FAMILY Species	Number of trees	Density per hectare	Percent relative density Species	 Family
EUPHORBIACEAE				22.4
Drypetes sepiara	635	38.5	21.3	
Phyllanthus polyphyllus	15	0.9	0.5	
Bridelia retusa	10	0.6	0.4	
Croton lacciferus	6	0.4	0.2	
VERBENACEAE				14.5
Premna tomentosa	253	15.3	8.4	
Vitex pinnata	184	11.2	6.1	
LEGUMINOSAE				12.4
Cassia fistula	190	11.5	6.3	
Cassia roxburghii	158	9.6	5.2	
Bauhinia racemosa	21	1.3	0.7	
Tamarindus indica	4	0.2	0.1	
Peltophorum pterocarpum	1	0.1	0.1	
Erythrina variegata	0			
SAPINDACEAE				11.4
Schleichera oleosa	128	7.8	4.2	
Lepisanthes tetraphylla	110	6.7	3.6	
Gleniea unijuga	64	3.9	2.1	
Sapindus emarginatus	45	2.7	1.5	
TILIACEAE				9.3
Grewia polygama	278	16.8	9.2	
Grewia tiliaefolia	1	0.1	0.1	
Muntingia calabura	0			
RUBIACEAE				7.4
Ixora arborea	103	6.2	3.4	
Adina cordifolia	84	5.1	2.8	
Mitragyne parvifolia	21	1.3	0.7	
Canthium coromandelicum	14	0.8	0.5	
Morinda tinctoria	0			
LOGANIACEAE				4.7
Strychnos potatorum	142	8.6	4.7	
MELIACEAE				3.4
Walsura piscidia	81	4.9	2.6	
Chloroxylon swietenia	18	1.1	0.6	
Aglaia roxburghiana	7	0.4	0.2	
Azadirachta indica	0			
BORAGINACEAE				2.5
Cordia sp.	74	4.5	2.5	
MORACEAE				2.4
Ficus amplissima	49	3.0	1.6	
Ficus bengalensis	13	0.8	0.4	
Ficus retusa	5	0.3	0.2	
Ficus religiosa	2	0.1	0.1	
Ficus mollis) *Ficus racemosa*) *Ficus parasitica*)	1	0.1	0.1	
Streblus asper	0			
SAPOTACEAE				2.3
Manilkara hexandra	69	4.2	2.3	
Madhuca longifolia	0			
ANNONACEAE				1.8
Polyalthia longifolia	47	2.8	1.6	
Polyalthia korinthii	8	0.5	0.2	
Annona reticulata	0			
MYRTACEAE				1.6
Syzigium cumini	47	2.8	1.6	
Eugenia bracteata	0			
GUTTIFERAE				0.9
Garcinia spicata	28	1.7	0.9	
BIGNONIACEAE				0.8
Stereospermum personatum	24	1.5	0.8	
ULMACEAE				0.8
Holoptelea integrifolia	23	1.4	0.8	

TABLE 1. (Continued)

EBENACEAE				0.6
Diospyros ovalifolia)	10	0.6	0.3	
Diospyros montana)				
Diospyros ferrea	9	0.5	0.3	
CELASTRACEAE				0.4
Elaeodendron glaucum	13	0.8	0.4	
LAURACEAE				0.4
Alseodaphne semecarpifolia	13	0.8	0.4	
STERCULIACEAE				0.2
Sterculia foetida	5	0.3	0.2	
ALANGIACEAE				0.1
Alangium salviifolium	2	0.1	0.1	

the dry zone. *Alstonia scholaris* is typical of the wet zone (Andrews 1961). *Feronia limonia* occurs through most of the dry and arid zones, but preferentially where periodic flooding occurs (Eisenberg, pers. comm.). The palmyra palm, *Borassus flabellifer,* which occurs commonly in exposed places in the dry zone, was represented by only one tree in the study area; several grew on the lake bed.

Cocos nucifera, Mangifera indica, Annona reticulata, Erythrina variegata, and *Muntingia calabura* are naturalized or cultigens and were absent from the forest. Considering the aforementioned species as atypical of the forest, the tally reduces to 46 species, 36 genera, and 21 families. Two species, *Phyllanthus polyphyllus* and *Croton lacciferus,* were most common as shrubs, but some specimens exceeded 5 meters in height, hence their inclusion in the table.

GEOGRAPHIC VARIATIONS IN SPECIES COMPOSITION.—Comparisons in forest composition are made between five forest reserves that are climatically similar to Polonnaruwa (table 2). The Madhu Forest Reserve, however, is found in and towards the arid zone (fig. 1), where annual rainfall averages approximate-

TABLE 2. *Variations in species composition between six geographically separated forest reserves in the dry zone* (x = Species present in rank of abundance above 10).

	Percent relative density of tree species in forest reserve				
	Omunagala Nuwaragala Ratkarawwa		Kantalai	Panama	Madhu
Tree species	L[a] (1549 - 2133 mm)[c]	M[b]	L (1714 mm)	L (1701 mm)	L (1270 mm)
Drypetes sepiara	17.1	15.5	22.5	36.1	53.4
Diospyros ovalifolia	12.2	4.5	4.5	10.8	2.8
Pterospermum canescens	11.0	8.1	6.2	6.8	1.9
Nephelium longana	8.4	16.0	10.2	4.4	0.0
Memecylon spp.	8.1	7.6	13.4	7.3	4.7
Gleniea unijuga	5.0	3.4	4.4	3.9	2.4
Chloroxylon swietenia	4.0	x	x	2.7	5.5
Diospyros ebenum	3.2	6.0	2.7	x	4.2
Premna tomentosa	3.2	3.9	x	x	x
Vitex pinnata	2.6	1.8	x	x	2.8
Atlantia monophylla	x	2.9	3.8	0.0	x
Pityranthe verrucosa	x	x	10.8	x	x
Tricalysia dalzelli	x	x	3.6	3.2	x
Dimorphocalyx glabellus	x	x	x	3.6	x
Mischodon zeylanicus	x	x	x	3.5	x
Manilkara hexandra	x	x	x	x	4.5
Maba buxifolia	x	x	x	x	3.0
Total number of species	56	67	44	40	47

[a] L = low yield or dry forest.
[b] M = medium yield or moist forest (see text).
[c] Average annual rainfall over 30 years.

ly 1000 mm or less (Mueller-Dombois 1968), compared to 1140 to 1787 mm in the other forest reserves *(ibid.)*. Table 2 indicates the 10 most common tree species and their relative densities in each of the forests. An "x" indicates the presence of the tree species, but in a rank of abundance beyond 10. Information for the Madhu Forest Reserve was derived from Oudshoorn (1961), and for the other reserves from McCormack and Pillai (1961a, b and c). The latter authors combined their data from Nuwaragala, Omunagala, and Ratkarawwa Forest Reserves because of similarities in the incidence and distribution of tree species between these forests. Because of their economic interest, the aforementioned authors distinguished between Medium Yield (M) forests that were found only locally along streams or other places where ground moisture is plentiful, and Low Yield (L) forests that occupy the more extensive areas of the dry zone. Comparisons in table 2 are made primarily between dry or low yield forests.

Considerable uniformity in species composition is evident between these dry zone forests; *Drypetes* was the dominant growth in all of them. The Madhu Forest towards the arid zone shares a slightly lesser number of species with the others, and indicates the extreme preponderance of *Drypetes*. The medium-yield or moist forests generally showed a greater number of species, and a trend for the dominance of *Nephilium longana*.

The forest composition at Polonnaruwa differs somewhat from the rest of the dry zone forests in the prevalence of *Grewia polygama, Cassia fistula,* and *Ixora arborea*. The flowers from the latter two species are commonly used in religious offerings, and some *C. fistula* appear to have been planted near temple clearings for decorative purposes.

Discussions of relative abundance of tree species usually refer to the two-layered structure of the forest; an upper or canopy layer, and a second story or subcanopy layer. Shrubs constitute the undergrowth. Authors of the Hunting Survey consistently report that most variation in species composition occurs in the canopy layer on both the local and wider geographic scales. Table 3 lists the tree species most common in the canopy in different forests of the dry zone. The variations between the forests in the same climatic zone are attributed to local, edaphic, and biotic differences (Andrews 1961).

The relative abundance of species in the Polonnaruwa study area is portrayed in figure 3, by five equal interval classes of relative density. Raunkiaer (1934) gave such information according to frequency classes. Because of the non-random distribution of trees in our sample (see table 5), relative density is a more accurate measure. Figure 3 clearly illustrates that there were many more rare species than common ones.

A species-number diversity curve (fig. 4) and a species area curve (fig. 5) were constructed by numbering consecutive sample plots (100 m^2) in the field data and selecting plots according to the random numbers table. The cumulative sum of species is plotted arithmetically. The curves conform to the usual pattern and approach asymptote at approximately 40 tree species.

Estimates of species diversity by information content are given in table 4 according to 3 logarithmic bases. These estimates refer to the sample of 46 species and 3015 trees as a population or entity in itself, and not as a sample for a larger population (Pielou

TABLE 3. *Variations in the constituent tree species of the canopy and their relative densities (expressed in percent) between geographically separated reserves.*

Tree species typical of the canopy	Polonnaruwa (1671 mm)[a]	Omunagala (2133 mm)	Ratkarawwa (1549 mm)	Panama (1701 mm)	Kantalai (1714 mm)	Madhu (1270 mm)
Schleichera oleosa	4.2					
Vitex pinnata	6.1	2.6	X[b]	0.4		
Adina cordifolia	2.8				<0.1	
Manilkara hexandra	2.3				2.6	4.5
Stereospermum personatum	0.8	<0.1	X	<0.1		
Holoptelea integrifolia	0.8		X			
Mitragyne parvifolia	0.7		X			
Chloroxylon swietenia		4.0	X		1.1	5.5
Alseodaphne semecarpifolia		<0.1				
Berrya cordifolia		1.8		0.8		
Diospyros ebenum		3.2	X			
Syzigium cumini				<0.1		
Diospyros malabarica				<0.1		
Mesu ferrea				<0.1		
Albizzia odoratissima					<0.1	

[a] Average annual rainfall over 30 years.
[b] The species marked "X" were present, but their relative densities were unavailable.

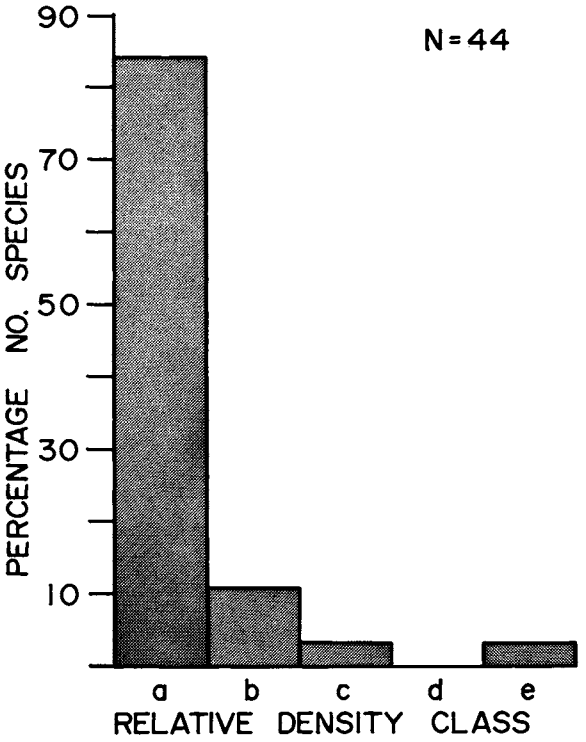

FIGURE 3. The relative abundance of 44 tree species. The percentage of the total number of species is shown per class of relative density: a = 0-20% of the sum of relative densities, b = 21-40%, c = 41-60%, d = 61-80%, e = 81-100%.

TABLE 4. *Indices of diversity of a sample population of 3015 trees, 46 species.*

Shannon Index of information content	Diversity (H) expressed in Bits ($\log_2 N$)	Nats ($\log_e N$)	Decits ($\log_{10} N$)
H	4.28591	2.97077	1.29019
H max	5.39788	3.74152	1.62492
J	79.40%	79.40%	79.40%

1969). The high evenness (J = 79.4%) reflects that much of the value of diversity (H) is attributable to evenness of abundances, or again that most species are relatively rare.

The probability that two trees drawn at random from the sample population (without replacement) are from the same species is 8.1 percent, or low. By Simpson's (1949) measure, diversity is therefore high (D = 91.9%).

THE ABUNDANCE OF TREES AND SPECIES ACCORDING TO SIZE CLASSES.—The number of trees according to size class as measured by the diameter at breast height (DBH) was tabulated for each species in table 4, chapter 2 of Dittus (1974). The same

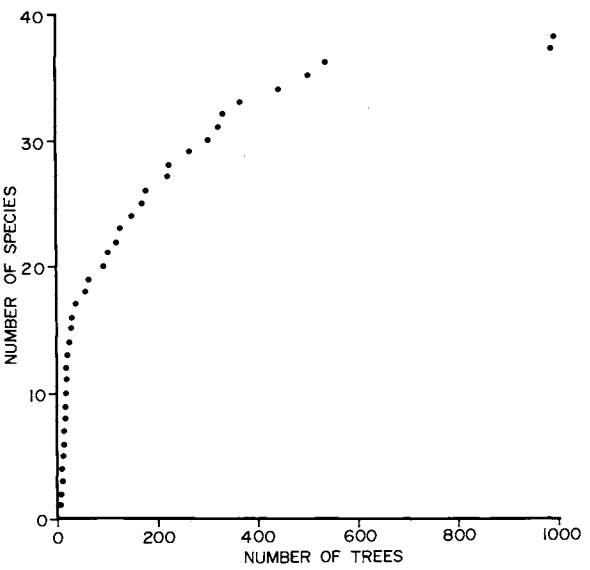

FIGURE 4. Species-number diversity curve for 3015 trees. The graph indicates the cumulative number of tree species encountered with increase in the number of trees sampled.

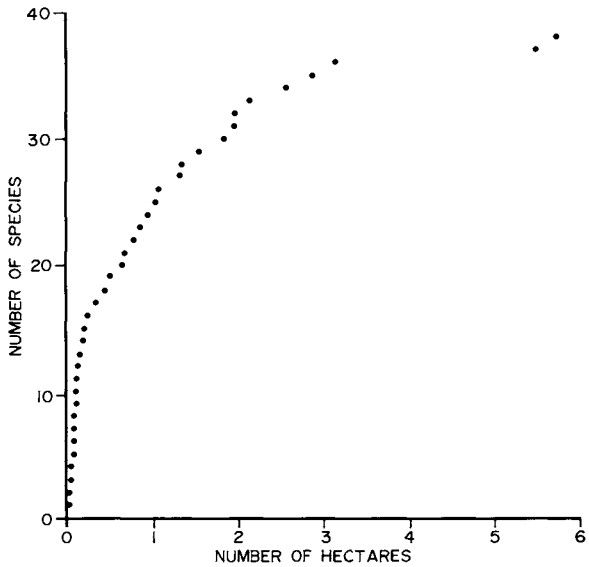

FIGURE 5. Species-area diversity curve for 571 plots of 100 m^2 area. The graph shows the cumulative number of tree species encountered with increase in the number of 100 m^2 plots sampled. The sample plots are summed cumulatively and expressed as the total area of hectares sampled.

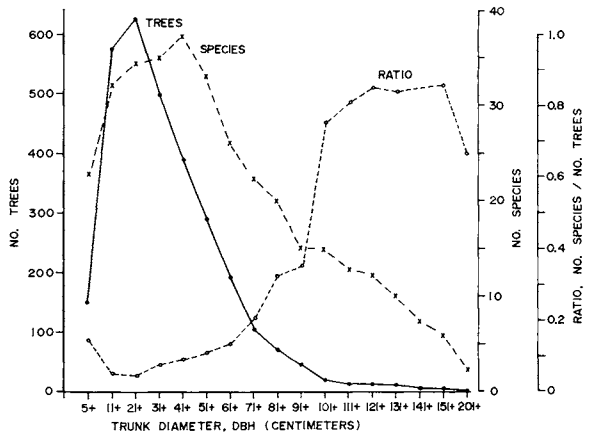

FIGURE 6. The number of individuals, species and the ratio of the number of species to number of individuals per size class of diameter at breast height (DBH). The curves for trees and species between size classes (11 to 20 cm and 141 to 150 cm) represent frequency polygons with equal class intervals of 10 cm.

information is summarized graphically here in figure 6. An examination of the data shows the following: (1) The trees of most species were of relatively small diameter. (2) There was a trend for species of typically small size (e.g., *Premna, Cassia* sp., *Cordia, Drypetes*) to have many individuals; for this reason the modal class of diameters for all trees was less than that for the numbers of species. (3) The numbers of trees and species decreased rapidly with increase in trunk diameter. (4) Many species had very large-sized individuals but extremely few of them. (5) Species that typically grew to largest size had few individuals in all size classes.

The smallest-diameter classes were not the modal classes. Partially, this finding might be a reflection of sampling technique; plants were included only if they were above 5 meters in height, the minimum diameter that corresponds to this height was 5 cm. Species with the fewest numbers in the small-diameter classes were those that typically grew to large size, indicating a dearth of young trees in these species. A similar distribution in the size-class representation of dominant trees was indicated for several forests in British Guiana by Davis and Richards (1933-34), quoted by Richards (1952). In Polonnaruwa this pattern may have been accentuated owing to illicit cutting of pole-sized trees in many parts of the study area. In certain areas, not included in the survey, trees of less than 15 to 20 cm were nearly absent.

The largest trees occurred by water holes, the size of some is likely a reflection of their old age; unlike the forest reserves, the Polonnaruwa Sanctuary is too small for economic exploitation such that very large-sized trees have remained. Growth form also contributes to a large diameter. In *Ficus bengalensis,* aerial roots fused engulfing the trunk of the host tree. Measures of diameter size for some species were somewhat overestimated. The trunks of *Drypetes sepiara* generally departed markedly from a regular cylindrical form. The trunk consisted of one or more smaller trunks fused. In species of *Ficus,* minor buttresses were occasionally unavoidable in the measures of diameter.

Figure 7 indicates the abundance of all forest trees according to height classes. The data concern species that are trees which are, by our definition, typically higher than 5 meters. Hence, the data point for the 5 to 7 meter class does not "fit" the smoothness of the curve. At these lower heights shrub species predominate. If these were incorporated, the curve would continue towards a tail to the right. Plotted in this fashion, no marked stratification is evident in the overall height distribution of trees. A better understanding of forest stratification is gained by considering the height and spatial distribution of each species.

The number of trees per height class for 20 of the more common species is shown in figure 8. Species of low stature tended to have many individuals, whereas the species with the tallest trees had relatively few individuals, and these were distributed

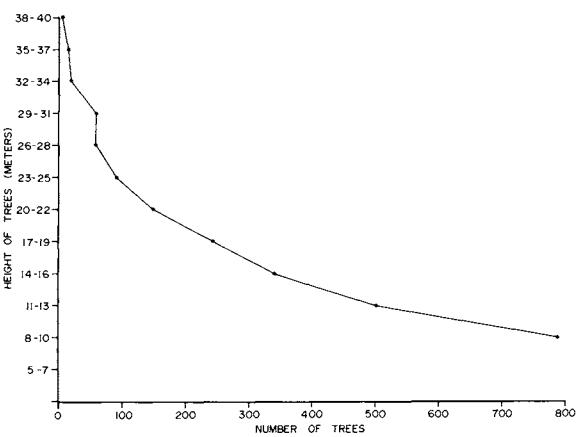

FIGURE 7. The number of forest trees per height class. The height of trees is indicated according to 3 m interval classes. The heights of 2738 trees are enumerated.

more or less evenly from the shortest to the tallest height class. Or, in species with very tall trees, representation by tall trees increased at the expense of many small ones.

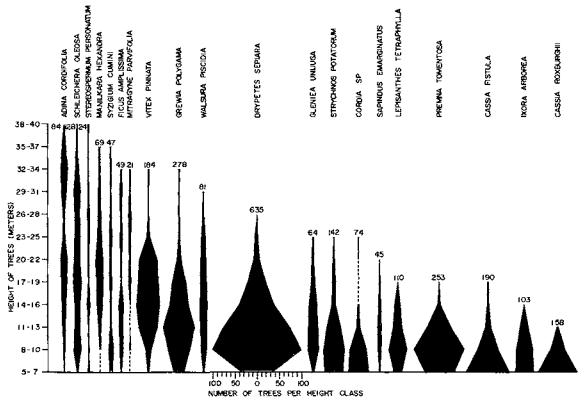

FIGURE 8. The number of trees per height class for 20 of the more common species. The total number of trees per species is written above each graph.

This effect is more accentuated than it appears. Keeping in mind that volume and hence biomass are roughly an exponential function of trunk diameter times height (Ogawa *et al.* 1961), the major concentration of biomass predictably would be in few very tall trees rather than in many short ones.

THE SPATIAL DISTRIBUTION OF TREE SPECIES.—The measure of frequency concerns the uniformity or regularity with which plants of a species are distributed throughout a community, and is expressed as the proportion of sample plots that contain a given species (Cain and Castro 1959). Frequency, therefore, depends on sample plot size. For purposes of community description, it is desirable to choose a sample plot size which has 95 percent frequency for at least one species (Archibald 1949, in Shimwell 1971). Figure 9 shows changes in the probability of finding one or more trees in sample plots of different size, for the most common species, *Drypetes sepiara.* Original sample plots were 100 m^2. In the data analysis larger plots were attained through addition of contiguous plots among the sample strip. This has been called the accumulated rectangular forest-plot method by Cain and Castro (1959).

The graph (fig. 9) indicates that a sample plot of 2500 m^2 (250 m x 10 m) is most suitable for comparisons of measures of frequency for the various species in the Polonnaruwa study community. These frequencies are tabulated in table 5. A high frequency indicates a trend towards a ubiquitous distribution of the species throughout the community.

The degree to which individuals of a species cluster spatially can be expressed through Morisita's (1959) "index of dispersion," (I_δ). It is the ratio of the probability that any two individuals chosen at random will be from the same sample plot to that same measure of probability, but assuming a completely random distribution of all trees in the population. A value of 1 indicates a random distribution. In a clumped pattern in which a high proportion of individuals is concentrated into only a few of the sample plots, I_δ is greater than 1. The significance of I_δ increases with sample size, an F-test is used to test its validity (Greig-Smith 1964). The values of I_δ, F, and the probability (P) that the difference of I_δ from 1 (random) arose by chance are tabulated in table 5. The conclusion as to the random or clumped distribution of trees per species using a 2500 m^2 plot size is given in the last column of table 5.

For some of the very rare species, the sum of the sample plots was insufficient to justify a mathematical conclusion, and I have substituted my subjective appraisal (marked with an asterisk) as to the pattern of distribution. (*Ficus religiosa* is the sacred Bo tree brought to Sri Lanka by Buddhists circa 228 B.C. (Worthington 1959). These trees were artificially clumped through planting about religious buildings. Only one tree appeared in the sample plots.)

From working in the habitat and examining the

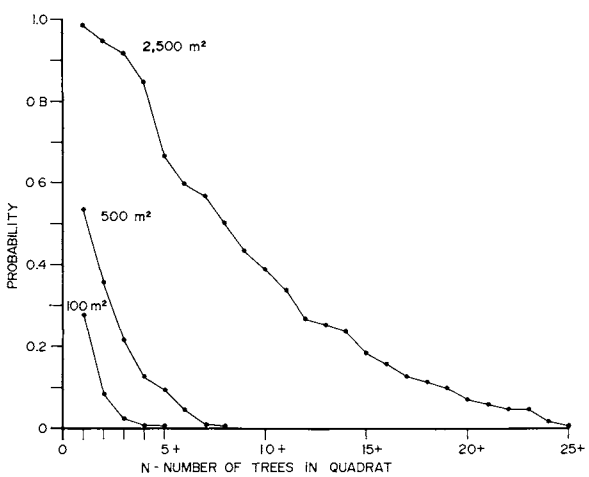

FIGURE 9. The probability of finding N or more trees of the most common species *(Drypetes sepiara),* with sample plot sizes 100 m^2, 500 m^2, and 2500 m^2.

TABLE 5. *The spatial distribution of tree species, indicating for each species the total number of trees in the sample area of 18.25 hectares; the frequency or the percentage of 73 sample plots of 2500 m² size that contain at least one tree of that species; the degree of clumping between trees (I_δ) (see text for explanation); the value of the statistic F; and the probability (P) that the difference between the degree of clumping (I_δ) and random distribution ($I_\delta = 1$) arose by chance.*

FAMILY Species	No. trees	Frequency per 2500 m²	Morisita's I_δ	F-test F	P	Conclusion
EUPHORBIACEAE						
Drypetes sepiara	635	98.6	1.20	3.12	<.01	clumped
Bridelia retusa	10	6.8				clumped*
VERBENACEA						
Premna tomentosa	253	86.3	1.39	2.36	<.01	clumped
Vitex pinnata	184	83.6	1.31	1.80	<.01	clumped
LEGUMINOSAE						
Cassia fistula	190	84.9	1.39	2.02	<.01	clumped
Cassia roxburghii	158	68.5	2.12	3.44	<.01	clumped
Bauhinia racemosa	21	24.7				random*
Tamarindus indica	4	2.7	3.65	2.47	<.01	clumped
SAPINDACEAE						
Schleichera oleosa	128	75.3	1.46	1.81	<.01	clumped
Lepisanthes tetraphylla	110	71.2	1.97	2.47	<.01	clumped
Gleniea unijuga	64	39.7	3.43	3.13	<.01	clumped
Sapindus emarginatus	45	30.0	3.08	2.28	<.01	clumped
TILIACEAE						
Grewia polygama	278	89.0	1.31	2.21	<.01	clumped
RUBIACEAE						
Ixora arborea	103	64.4	1.53	1.75	<.01	clumped
Adina cordifolia	84	52.1	2.70	2.96	<.01	clumped
Mitragyne parvifolia	21	19.2	5.18	2.16	<.01	clumped
Canthium coromandelicum	14	12.3	4.81	1.69	<.01	clumped
LOGANIACEAE						
Strychnos potatorum	142	54.8	3.58	6.05	<.01	clumped
MELIACEAE						
Walsura piscidia	81	49.3	1.85	1.90	<.01	clumped
Chloroxylon swietenia	18	19.5				random*
Aglaia roxburghiana	5	7.3				random*
BORAGINACEAE						
Cordia sp.	74	49.3	1.57	1.58	<.01	clumped
MORACEAE						
Fiscus amplissima	49	43.8	1.46	1.31	>.05	random
Fiscus bengalensis	13	16.4	0.95	0.99	>.05	random
Fiscus retusa	5	5.5	7.30	1.35	>.05	random
SAPOTACEAE						
Manilkara hexandra	69	53.4	1.90	1.85	<.01	clumped
ANNONACEAE						
Polyalthia longifolia	47	34.2	4.23	3.07	<.01	clumped
MYRTACEAE						
Syzigium cumini	47	43.8	1.83	1.53	<.01	clumped
GUTTIFERAE						
Garcinia spicata	28	28.8	3.87	2.08	<.01	clumped
BIGNONIACEAE						
Stereospermum personatum	24	23.3	1.58	1.12	>.05	random
UMLACEAE						
Holoptelea integrifolia	23	19.5	32.59	10.48	.01	clumped
CELASTRACEAE						
Elaeodendron glaucum	13	16.4				random*
LAURACEAE						
Alseodaphne semecarpifolia	13	12.3	2.81	1.30	.05	random
EBENACEAE						
Diospyros ovalifolia	10	13.7				random*
Diospyros ferrea	9	12.3				random*
STERCULIACEA						
Sterculia foetida	5	6.8				random*
ALANGIACEAE						
Alangium saliviifollum	2	2.6				clumped*

*Distribution patterns of species are based on subjective interpretation.

field data, it was my impression that all the species noted as gregarious, using 2500 m^2 plot size (table 5), were also clumped at 500 m^2 plot size. With the exception of very large-sized trees, such as *Schleichera oleosa, Holoptelea integrifolia,* and *Adina cordifolia,* where one tree alone might exclusively occupy 100 m^2, clumping occurred also at 100 m^2 plot size particularly for the more common, small-sized gregarious species in table 5.

On a larger scale, there were marked local differences in the relative abundance of species particularly in the canopy layer. This circumstance was especially true of *Holoptelea integrifolia* and *Stereospermum personatum,* which formed a dominant stand of a few hectares in one part of the study area only. *Adina cordifolia* was generally common in the canopy layer, but was also absent in some areas and formed locally dominant stands in many parts of the area.

The importance value index (IVI) of Curtis and McIntosh (1951) incorporates three measures into one value or index. These are the relative density, relative frequency, and relative dominance. The latter was calculated as the proportion of the basal area of a species to the community (sum of sample plots) as a whole. Values of IVI range up to 300, which is the sum of the three relative measures in percent. The desirability of this index lies in the fact that it attaches importance to those species that tend toward large size and ubiquitous distribution over those that do not. Hence, it is a more accurate measure of the degree of influence that a species has on the community than any one of the measures alone. Table 6 summarizes the three relative measures and gives the IVI for each species. Species are ranked according to their IVI values for the first 21 ranks in table 7. Changes in rank owing to tree size and distribution when compared to rank of numerical density only are also indicated. All gains in rank in table 7 concern

TABLE 6. *The Indices of Importance Value* (IVI) *for tree species.*

FAMILY Species	Relative density	Relative frequency	Relative dominance	IVI
EUPHORBIACEAE				
Drypetes sepiara	21.3	6.7	27.5	55.5
Phyllanthus polyphyllus	0.5	0.8	.1	1.4
Bridelia retusa	0.4	0.8	.8	2.0
Croton lacciferus	0.2	0.5	.02	.7
VERBENACEAE				
Premna tomentosa	8.4	5.9	5.7	20.0
Vitex pinnata	6.1	5.7	9.4	21.2
LEGUMINOSAE				
Cassia fistula	6.3	5.8	1.1	13.2
Cassia roxburghii	5.2	4.7	1.1	11.0
Bauhinia racemosa	0.7	1.7	0.9	3.3
Tamarindus indica	0.1	0.2	0.2	.5
Peltophorum pterocarpum	0.1	0.1	0.03	.2
Erythrina variegata	0.0			
SAPINDACEAE				
Schleichera oleosa	4.2	5.2	11.7	21.1
Lepisanthes tetraphylla	3.6	4.9	1.8	10.3
Gleniea unijuga	2.1	2.7	1.1	5.9
Sapindus emarginatus	1.5	2.1	1.0	4.6
TILIACEAE				
Grewia polygama	9.2	6.1	4.3	19.6
Grewia tiliaefolia	0.1	0.1	.01	.2
Muntingia calabura	0.0			
RUBIACEAE				
Ixora arborea	3.4	4.4	1.8	9.6
Adina cordifolia	2.8	3.6	6.4	12.8
Mitragyne parvifolia	0.7	1.3	1.3	3.3
Canthium coromandelicum	0.5	0.8	0.2	1.5
Morinda tinctoria	0.0			
LOGANIACEAE				
Strychnos potatorum	4.7	3.7	1.6	10.0
MELIACEAE				
Walsura piscidia	2.6	3.4	2.5	8.5
Chloroxylon swietenia	0.6	1.3	0.5	2.4
Aglaia roxburghiana	0.2	0.5	0.1	0.8
Azadirachta indica	0.0			
BORAGINACEAE				
Cordia sp.	2.5	3.4	0.7	6.6
MORACEAE				
Ficus amplissima	1.6	3.0	4.1	8.7
Ficus bengalensis	0.4	1.1	2.0	3.5
Ficus retusa	0.2	0.4	0.8	1.4
Ficus religiosa	0.1	0.2	0.6	0.9
Ficus mollis, *Ficus racemosa*, *Ficus parasitica*	0.1	0.1	0.1	0.3
Streblus asper	0.0			
SAPOTACEAE				
Manilkara hexandra	2.3	3.7	3.5	9.5
Madhuca longifolia	0.0			
ANNONACEAE				
Polyalthia longifolia	1.6	2.3		
Polyalthia korinthii	0.2	0.6	0.3	5.0
Annona reticulata	0.0			
MYRTACEAE				
Syzigium cumini	1.6	3.0	2.2	6.8
Eugenia bracteata	0.0			
GUTTIFERAE				
Garcinia spicata	0.9	2.0	0.5	3.4
BIGNONIACEAE				
Stereospermum personatum	0.8	1.6	0.6	3.0
ULMACEAE				
Holoptelea integrifolia	0.8	1.3	1.9	4.0
EBENACEAE				
Diospyros ovalifolia, *Diospyros montana*	0.3	0.9	0.2	1.4
Diospyros ferrea	0.3	0.8	0.1	1.2
CELASTRACEAE				
Elaeodendron glaucum	0.4	1.1	0.7	2.2
LAURACEAE				
Alseodaphne semecarpifolia	0.4	0.8	0.2	1.4
STERCULIACEAE				
Sterculia foetida	0.2	0.5	0.4	1.1
ALANGIACEAE				
Alangium salviifolium	0.1	0.2	0.02	0.3

TABLE 7. *Comparison of ranks of importance and abundance.*

Species	IVI	Rank Relative Density	Change
Drypetes sepiara	1	1	0
Vitex pinnata	2	5	+3
Schleichera oleosa	3	8	+5
Premna tomentosa	4	3	-1
Grewia polygama	5	2	-3
Cassia fistula	6	4	-2
Adina cordifolia	7	11	+4
Cassia roxburghii	8	6	-2
Lepisanthes tetraphylla	9	9	0
Strychnos potatorum	10	7	-3
Ixora arborea	11	10	-1
Manilkara hexandra	12	14	+2
Ficus amplissima	13	17	+4
Walsura piscidia	14	12	-2
Syzigium cumini	15	17	+2
Cordia sp.	16	13	-3
Gleniea unijuga	17	15	-2
Polyalthia korinthii	18	17	-1
Sapindus emarginatus	19	19	0
Holoptelea integrifolia	20	21	+1
Ficus bengalensis	21	30	+9

typically large-sized species. The largest trees (e.g., *Ficus bengalensis* and *Schleichera oleosa*) showed the largest gains.

THE NUMBER AND DENSITY OF SHRUB SPECIES.— There was considerable local variation in the abundance and composition of the shrub layer. Parts of the study area were almost devoid of shrubs owing to cutting, or edaphic and biotic conditions. The variation was patterned, however, such that several associations were recognized by differences in the dominant species or association of co-dominants. These associations and their composition are tabulated in table 8. Shrubs that generally grew to tree size are marked with an asterisk.

Each of the associations is characteristic of different edaphic and biotic conditions. The climax growth here and elsewhere in the dry zone was the *Glycosmis* association which thrives best under the shade of the closed forest subcanopy.

The *Randia-Carissa* association bordered the *Glycosmis* association, but was typical of a partly open forest subcanopy. Most of the plants were very thorny and constituted an almost impenetrable patch, owing not to its density of plants, which is about the same as for *Glycosmis* or *Phyllanthus* (table 8), but owing to the close intertwining of contiguous thorny branches and the interlacing of vines. In very open places the less dense *Randia-Canthium* association predominated as scrub. Plants were thorny and typically bordered the forest edge or formed a patch at the base of a cluster of trees in a discontinuous or open subcanopy. Shrubs of this association were the only ones that could be found in the most exposed areas. Open areas were rarely without a scattering of small clusters of *Randia dumetorum* and *Cassia roxburghii* shrubs, again preferentially at the base of isolated trees.

The *Phyllanthus-Randia* association occurred under similar conditions as the *Randia-Canthium* association, but was most typical of the forest border where shade and moisture were more available than in open areas. With increasing moisture, *Phyllanthus* especially increased in density and constituted about 50

TABLE 8. *Number and density of shrubs per association.*

FAMILY Species	*Glycosmis* N	D[a]	(19)[b] % D	*Randia-Carissa* N	D	(13) % D	*Randia-Canthium* N	D	(13) % D	Open N	D	(2) % D
EUPHORBIACEAE												
Phyllanthus polyphyllus	148	7.9	4.1	342	26.3	13.5	48	3.7	6.6	6	3.0	16.0
Croton lacciferus	376	19.8	10.3	93	7.2	3.7	18	1.4	2.5			
**Drypetes sepiara*	203	10.7	5.5	92	7.1	3.6	5	0.4	0.7	2	10.0	2.7
Breynia retusa				12	0.9	0.5	3	0.2	0.4			
RUTACEAE												
Glycosmis pentaphylla	1824	96.0	49.8	305	23.5	12.1	11	0.8	1.4			
Murraya koenigii)	141	7.4	3.8	87	6.7	3.4	25	1.9	3.4			
Micromelum minutum) ?	23	1.2	0.6	7	0.5	0.3						
Atalantia monophylla	1	0.1	0.1	1	0.1	0.1						
RUBIACEAE												
Randia dumetorum	51	2.7	1.4	691	53.2	27.3	315	24.2	43.3	17	8.5	22.7
Canthium coromandelicum	11	0.6	0.3	64	4.9	2.5	75	5.8	10.4	6	3.0	8.0
Randia malabarica	47	2.5	1.3	28	2.2	1.1	12	0.9	1.6	1	0.5	1.3
Tarenna asiatica	19	1.0	0.5	33	2.5	1.3						
**Ixora arborea*				10	0.8	0.4	2	0.2	0.4			
APOCYNACEAE												
Carissa (spinosum ?)	130	6.8	3.5	487	37.5	19.3	34	2.6	4.7	15	7.5	20.0

TABLE 8. (Continued)

EBENACEAE												
Diospyros ovalifolia	140	7.4	3.8	19	1.5	0.8	4	0.3	0.5			
Diospyros (montana?)	2	0.1	0.1	4	0.3	0.2						
**Diospyros ferrea*	3	0.2	0.1	2	0.2	0.1	1	0.1	0.2			
LEGUMINOSAE												
**Cassia roxburghii*	5	0.3	0.2	20	1.5	0.8	48	3.7	6.6	15	7.5	20.0
**Cassia fistula*	8	0.4	0.2	2	0.2	0.1	32	2.5	4.5			
**Bauhinia racemosa*	1	0.1	0.1	3	0.2	0.1	3	0.2	0.4			
Acacia caesia				1	0.1	0.1	2	0.2	0.4			
Flemingea strobilifera												
POLYGALACEAE												
Salomonia sp.	98	5.2	2.7	13	1.0	0.5	2	0.2	0.4			
SAPINDACEAE												
Allophyllus cobbe	6	0.3	0.2	42	3.2	1.6	2	0.2	0.4			
**Schleichera oleosa*	4	0.2	0.1	12	0.9	0.5	5	0.4	0.7	1	0.5	1.3
**Lepisanthes tetraphylla*	8	0.4	0.2									
**Gleniea unijuga*	10	0.5	0.3									
MELIACEAE												
**Aglaia roxburghiana*	94	4.9	2.5	9	0.7	0.4	2	0.2	0.4			
BORAGINACEAE												
Carmona microphylla	23	1.2	0.6	31	2.4	1.2	2	0.2	0.4			
Cordia sp.	1	0.1	0.1	3	0.2	0.1						
GUTTIFEREAE												
**Garcinia spicata*	69	3.6	1.9	1	0.1	0.1						
RHAMNACEAE												
Zizyphus mauritiana	2	0.1	0.1	28	2.2	1.1	29	2.2	3.9			
Scutia myrtina	4	0.2	0.1	7	0.5	0.3						
SAMYDACEAE												
Casearia zeylanica				20	1.5	0.8	7	0.5	0.9			
TILIACEAE												
**Grewia polygama*	40	2.1	1.1									
Grewia orientalis				3	0.2	0.1				3	1.5	4.0
ANNONACEAE												
Polyalthia korinthii	58	3.1	1.6									
**Polyalthia longifolia*	2	0.1	0.1									
CAPPARIDACEAE												
Capparis divaricata	32	1.7	0.9									
BIXACEAE												
Flacourtia indica				16	1.2	0.6	11	0.8	1.4	2	1.0	2.7
VERBENACEAE												
**Premna tomentosa*	3	0.2	0.1	11	0.8	0.4	1	0.1	0.2			
**Vitex pinnata*	4	0.2	0.1	1	0.1	0.1						
Lantana camara												
MYRTACEAE												
**Syzigium cumini*	2	0.1	0.1	6	0.5	0.3	3	0.2	0.4			
SAPOTACEAE												
**Manilkara hexandra*	5	0.3	0.2	9	0.7	0.4						
LOGANIACEAE												
**Strychnos potatorum*	1	0.1	0.1	2	0.2	0.1						
CELASTRACEAE												
**Elaeodendron glaucum*												
ANACARDIACEAE												
Lannea coromandelica				1	0.1	0.1						
UNIDENTIFIED												
Type 1	42	2.2	1.1	2	0.2	0.3	1	0.1	0.2			
Type 2	9	0.5	0.3	1	0.1	0.1	1	0.1	0.2			
Others	13	0.7	0.4	12	0.9	0.5	11	0.8	1.4	7	3.5	9.3
Totals	3663	192.8		2553	194.8		726	55.8		75	37.5	

* Species which commonly occurred as trees.
[a] Density (number of trees per hectare).
[b] The number of 100 m^2 plots sampled for that association.

Table 8 (Continued)

TABLE 8. *Number and Density of Shrubs per Association (Part 2).*

FAMILY Species	*Phyllanthus* (8)			*Phyllanthus-Randia* (5)			*Croton* (3)			*Total* (63)		
	N	D	% D	N	D	% D	N	D	% D	N	D	% D
EUPHORBIACEAE												28.1
Phyllanthus polyphyllus	796	99.5	50.6	244	48.8	38.7	51	17.0	12.4	1635	26.0	17.1
Croton lacciferus	92	11.5	5.9	51	10.2	8.1	111	37.0	27.1	741	11.8	7.7
**Drypetes sepiara*	31	3.9	2.0	11	2.2	1.7	13	4.3	3.1	357	5.7	3.7
Breynia retusa	24	3.0	1.5	13	2.6	2.1	2	0.7	0.5	54	0.9	0.6
RUTACEAE												27.5
Glycosmis pentaphylla	10	1.3	0.7	14	2.8	2.2	64	21.3	15.6	2228	35.4	23.2
Murraya koenigii)	89	11.1	5.6				8	2.7	4.3	350	5.6	3.7
Micromelum minutum)												
?	15	1.9	1.0	2	0.4	0.3	6	2.0	1.5	53	0.8	0.5
Atalantia monophylla	1	0.1	0.1							5	0.1	0.1
RUBIACEAE												17.5
Randia dumetorum	59	7.4	3.8	107	21.4	17.0	10	3.3	2.4	1250	19.8	13.0
Canthium coromandelicum	19	2.4	1.2	23	4.6	3.7	13	4.3	3.1	211	3.3	2.2
Randia malabarica	12	1.5	0.8	15	3.0	2.4	5	1.7	1.2	120	1.9	1.2
Tarenna asiatica				5	1.0	0.8				57	0.9	0.6
**Ixora arborea*	24	3.0	1.5	7	1.4	1.1	7	2.3	1.7	50	0.8	0.5
APOCYNACEAE												7.9
Carissa (spinosum ?)	39	4.9	2.5	55	11.0	8.7				760	12.1	7.9
EBENACEAE												2.7
Diospyros ovalifolia				1	0.2	0.2	29	9.7	7.1	193	3.1	2.0
Diospyros (montana?)	39	4.9	2.5	2	0.4	0.3	13	4.3	3.1	60	0.9	0.6
**Diospyros ferrea*				1	0.2	0.2	2	0.7	0.5	9	0.1	0.1
LEGUMINOSAE												2.7
**Cassia roxburghii*	34	4.3	2.2	12	2.4	1.9	9	3.0	2.2	143	2.3	1.5
**Cassia fistula*	22	2.8	1.4	22	4.4	3.5	10	3.3	2.4	96	1.5	1.0
**Bauhinia racemosa*	1	0.1	0.1							5	0.1	0.1
Acacia caesia	1	0.1	0.1	1	0.2	0.2				4	0.1	0.1
Flemingea strobilifera												
POLYGALACEAE												1.3
Salomonia sp.	8	1.0	0.5	2	0.4	0.3	5	1.7	1.2	128	2.0	1.3
SAPINDACEAE												1.3
Allophyllus cobbe	11	1.4	0.7	4	0.8	0.6				65	1.0	0.7
**Schleichera oleosa*	4	0.5	0.3	6	1.2	1.0				32	0.5	0.3
**Lepisanthes tetraphylla*	5	0.6	0.3				3	1.0	0.7	16	0.3	0.2
**Gleniea unijuga*										10	0.2	0.1
MELIACEAE												1.1
**Aglaia roxburghiana*	1	0.1	0.1				1	0.3	0.2	107	1.7	1.1
BORAGINACEAE												1.0
Carmona microphylla	8	1.0	0.5	14	2.8	2.2	2	0.7	0.5	80	1.3	0.9
Cordia sp.	1	0.1	0.1	2	0.4	0.3				7	0.1	0.1
GUTTIFEREAE												0.9
**Garcinia spicata*	18	2.3	1.2							88	1.4	0.9
RHAMNACEAE												0.8
Zizyphus mauritiana	2	0.3	0.2	2	0.4	0.3	1	0.3	0.2	64	1.0	0.7
Scutia myrtina										11	0.2	0.1
SAMYDACEAE												0.7
Casearia zeylanica	31	3.9	2.0	2	0.4	0.3				60	1.0	0.7
TILIACEAE												0.7
**Grewia polygama*	5	0.6	0.3							45	0.7	0.5
Grewia orientalis	5	0.6	0.3	5	1.0	0.8	3	1.0	0.7	19	0.3	0.2
ANNONACEAE												0.6
Polyalthia korinthii										58	0.9	0.6
**Polyalthia longifolia*										2	0.0	0.0
CAPPARIDACEAE												0.4
Capparis divaricata	3	0.4	0.2							35	0.6	0.4
BIXACEAE												0.4
Flacourtia indica	7	0.9	0.5				2	0.7	0.5	38	0.6	0.4

TABLE 8.—Part 2 (Continued)

VERBENACEAE												0.3
**Premna tomentosa*	1	0.1	0.1							16	0.3	0.2
**Vitex pinnata*										5	0.1	0.1
Lantana camara												
MYRTACEAE												0.2
**Syzigium cumini*	10	1.3	0.7							21	0.3	0.2
SAPOTACEAE												0.1
**Manilkara hexandra*										14	0.2	0.1
LOGANIACEAE												0.0
**Strychnos potatorum*										3	0.0	—
CELASTRACEAE												0.0
**Elaeodendron glaucum*												0.0
ANACARDIACEAE												0.0
Lannea coromandelica										1	0.0	—
UNIDENTIFIED												2.8
Type 1	3	0.4	0.2				3	1.0	0.7	51	0.8	0.5
Type 2	108	13.5	6.9							118	1.9	1.2
Others	29	3.6	1.8	7	1.4	1.1	30	10.0	7.3	108	1.7	1.1
Totals	1572	196.5		630	126.0		410	136.7		9629	152.8	

* Species which commonly occurred as trees.

percent of the shrubs in the *Phyllanthus* facies. For example, *Phyllanthus* grew densely at stream edges, and at the base of slopes, wherever the subcanopy was discontinuous. With increasing shade, *Phyllanthus* declined, and *Croton* increased in preponderance. The *Croton* association might be considered an intermediary between the *Phyllanthus* and *Glycosmis* association; it occurred only locally and sparsely. A schematic representation of association changes with degrees of light penetration and moisture is given in figure 10.

Estimates of tree density per each shrub association are not available. However, forested areas with

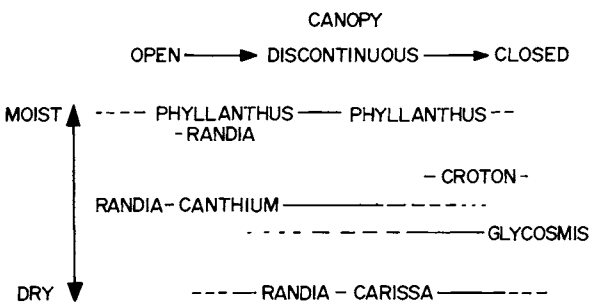

FIGURE 10. Schematic diagram of changes in shrub association with differences in the amount of light and moisture. The types of shrubs growing in association and the dominant growth changes according to differences in the amount of light penetration, as judged by the degree of openness in the subcanopy and canopy, and according to a moisture gradient. See text for an explanation of changes. The species composition of each shrub association is given in table 8.

Glycosmis or *Randia-Carissa* associations as undergrowth had a significantly higher density of trees (190 per hectare) than areas devoid of these associations (146 trees per hectare) ($Chi^2 = 11.5$ $p<.001$).

Tree species occurring as shrubs constituted only 10.6 percent of the total shrub stand. They were most abundant (12.6%) in the climax shrub growth (the *Glycosmis* association). *Cassia* spp. were major constituents in the more exposed associations, forming 20 percent of shrubs in the open. The abundance of most tree species in the undergrowth only roughly reflected their abundance in the tree layers, *Drypetes* forming 34.9 percent of tree species in the shrub layer. With the exception of *Schleichera,* canopy and emergent species were absent or rare. Small tree shoots were not considered as shrubs in table 8.

DISCUSSION

THE SEMI-EVERGREEN FOREST AND MEASURES OF DIVERSITY AND DOMINANCE.—The number of tree species and their relative proportions occurring in the Polonnaruwa study area are normal for dry-zone forests. A comparison of diversity, using the Shannon index of information content, between the Polonnaruwa forest and those surveyed extensively in Thailand by Ogawa *et al.* (1965) shows that the diversity of 4.23 bits per individual for Polonnaruwa falls intermediate to the values of 3.81 bits per individual (Odum 1970, from Ogawa *et al.* 1965) for the deciduous monsoon forests common through

southern Asia, and 5.31 to 5.43 for the tropical rainforest of Thailand *(ibid.)*.

Importance values (IVI) between species in Polonnaruwa were all generally low. The highest was 55.5 for *Drypetes,* the next highest was 12.2, and only an additional eight species had values higher than 10. In an equatorial rainforest on the terra firma of Brazil, Cain, Castro *et al.* (1956) found the highest IVI to be 23.42, only five species ranged above an IVI of 10. Similarly, in an equatorial dipterocarp rainforest of Brunei State, Ashton (1964, figures 43 and 44) indicated the highest IVI equal to approximately 14; other species were below 10. These data indicate that in these rainforests no one or few species had a clear dominance over others. In contrast, a trend towards dominance by one species *(Drypetes)* is evident at Polonnaruwa. All three tropical forests are in marked contrast to a temperate-zone forest in Wisconsin where the maximum IVI was as high as 228, several species were above 100, and all species were above 10 (Curtis and McIntosh 1951).

Compared to semi-evergreen forests, drought conditions are more accentuated in monsoon forests which characteristically have a low annual rainfall of 500 to 1,000 mm, and five- to nine-month-long droughts (Walter 1971). I could find no IVI for monsoon forests; however, in a typically deciduous monsoon forest of the Mudumalai Sanctuary in the Nilgiri Hills of Tamil Nadu, teak, *Tectona grandis,* clearly dominated the forest (pers. observation). Similarly, in the arid zone of Sri Lanka, one species, *Drypetes sepiara,* may form almost pure stands (Oudshoorn 1961). Even within the range of semi-evergreen forests in Sri Lanka, moister regions (Nurawagala Forest Reserve) show a greater number of species and a lesser preponderance of the dominant growths (mainly *Drypetes*) than in drier regions (Andrews 1961). Progression towards the adverse condition of drought, then, correlates with a decrease in species diversity and a trend for one or few species to dominate the community in these tropical forests.

Although edaphic factors may contribute to floristic diversity (e.g., Ashton 1964), the estimate of diversity for the forest at Polonnaruwa does support Walter's (1971) assessment by climatic and structural features in classifying the semi-evergreen forest as a type intermediate between tropical rainforest and deciduous monsoon forest. This classification is further supported by measures of dominance relationships (IVI).

DOMINANCE IN RELATION TO STRATIFICATION.—The general height of the forest decreased as did the number of dominant or emergent species from the rainforest to arid zone or scrub forests in Sri Lanka (Andrews 1961). In the semi-evergreen forest of Polonnaruwa, a plot of the number of all forest trees against height (fig. 7) showed no marked discontinuity in the smoothness of the curve, leading one to believe that there is no stratification. However, the number of trees decreases rapidly with increasing height, and, at any specific location in the forest, a level is reached where the crowns of adjacent trees are no more touching, and a continuous subcanopy overtowered by a discontinuous canopy is recognizable. Here and there emergent species protrude above the canopy. Since most tree species are clumped in their distribution (table 5), the height and distinctiveness of these relative layers varies somewhat with local conditions. The exact definition of layers is therefore somewhat arbitrary; 76 percent of all trees were up to 14 to 16 meters or less, and this figure might be taken as the height of the subcanopy layer. Less than 5 percent emerged above 23 to 25 meters, the height of the canopy layer.

The concept of ecological dominance generally attaches the following attributes to a species: (1) having greatest total biomass (Shimwell 1971), (2) having control over the community (Oosting 1956, Cain and Castro 1959), and (3) prevailing in the superior stratum where most control over the whole is exerted *(ibid.)*. In the Polonnaruwa community, *Drypetes* was clearly the dominant species according to measures of the IVI. Its prevalence in the subcanopy contradicts the view that dominant species prevail in the superior stratum. Other species with high IVIs were *Schleichera oleosa, Vitex pinnata, Grewia polygama,* and *Premna tomentosa.* These species might be considered co-dominant with *Drypetes.*

With the exception of *Premna* all species found representation in the canopy, *Grewia* prevailed at heights slightly above *Drypetes,* but only *Schleichera* and *Vitex* prevailed in the canopy. Dominance therefore appears to be shared between species typical of the subcanopy and canopy in the Polonnaruwa community.

FAMILY DOMINANCE.—The dominant family in Polonnaruwa was the Euphorbiaceae, but only by virtue of the single species, *Drypetes sepiara.* The Verbenaceae and Sapindaceae might be regarded as co-dominant families and adhere more closely to the concept of dominance through the prevalence of more than one species of the same family (Richards 1952). Although the Dipterocarpaceae form the dominant family in the evergreen rain forests of Sri Lanka (Fer-

nando 1968), no species of this family were present in the semi-evergreen forests.

Among the shrub layer, species dominance as approximated by their densities varied according to edaphic and biotic conditions. The climax shrub growth of the *Glycosmis* association consisted mostly (49.8%) of *Glycosmis pentaphylla* of the family Rutaceae.. Shrub species of Euphorbiaceae prevailed in more exposed areas beneath a discontinuous or open subcanopy (table 8 and fig. 10).

DOMINANCE IN RELATION TO SUCCESSION.—The numerical distribution of different-sized trees, as measured by diameter and height, indicated that the large-sized species, or dominants, had a dearth of young trees. Their scarcity or complete absence in the shrub layer further substantiates this conclusion. *Drypetes* had highest representation in the shrub layer; *Premna, Vitex,* and *Grewia* were also represented but in small proportions. Among the tallest or emergent species, only *Schleichera* and *Manilkara* were found in the shrub layer.

To understand fully regenerative patterns, rates of growth and mortality of different-sized (aged) trees need to be known. Nevertheless, it appears that only some of the species of the mature stand are being adequately replaced, the least regeneration being of typically canopy and emergent species. Some species, such as *Aglaia,* were relatively prevalent in the shrub layer, yet were scarce as mature trees.

Mixed tropical forests on the Ivory Coast (Aubréville 1938), in the Cameroons (Mildbraed 1930) of Africa, and in Malaya (Watson 1937) showed a similar pattern. Based on these facts, Aubréville (1938) proposed the Mosaic Theory of Regeneration, which was summarized by Richards (1952) as follows: ". . . the particular combination of species which form the dominants of a given small area of mixed tropical forest is constant neither in space or time. The dominant species vary in composition from place to place . . . and, at the same place over a long period of years . . . an extensive area of mixed forest may be regarded as a kind of mosaic, each unit of the patchwork being a different combination of dominant species. On any one small area different combinations will succeed one another more or less cyclically."

The prevalence of *Drypetes* and several associated species throughout the semi-evergreen forest suggests that a complete cyclic succession is unlikely, and that a partial climax may have been achieved. Compositional shifts appear to affect different species differentially. The lack of young trees, particularly of canopy species, and the variable composition of the canopy throughout the evergreen forests suggest a greater susceptibility to environmental changes among species of this uppermost layer. Andrews (1961) considers these variations to reflect edaphic and local climatic differences. Such local differences have been charted by Mueller-Dombois (1968) for climate and by Fernando (1968) for soils.

Richards (1952) cautions that not all forests support Aubréville's theory, particularly stable edaphic climax communities such as mangrove stands. It is logical, of course, that the most extreme climatic and edaphic conditions would favor the growth of only few specialized species. Oudshoorn (1961), for example, considers the scrub forest of the arid zone to be a climax or near-climax growth for this zone.

A good deal of the semi-evergreen forests have been cultivated prior to the 13th century. That the mosaic compositional pattern of these forests may represent differing successional stages towards some, as yet undefined, climax, cannot therefore be ruled out. If such were the case, we can at least conclude that the complete successional process requires longer than 700 years.

ALTERNATE STRATEGIES TO DOMINANCE IN THE COMMUNITY.—Greatest variability in species composition was in the canopy layer both geographically (Andrews 1961) and locally. With decreasing favorability of growth conditions (mostly moisture), the height of trees decreased as did the number of canopy or emergent species (table 3).

The wider geographical distribution of species in the subcanopy implies a broader tolerance of environmental conditions by these species, whereas the trend towards local dominance and limited distribution by canopy and emergents suggests the contrary, and a specialization for relatively narrow conditions.

One may view dominance of an individual, species, or group of species in an ecosystem (local or global) as the proportion of a limiting resource, especially energy, that it controls per individual or species (Van Valen 1973). Accurate or appropriate measures of energy are rather elusive. As a generalization, however, the amount of biomass per individual or species may be taken as a crude index of the amount of energy stored or controlled by the individual (or species).

Logically, a species may acquire maximum biomass representation through many large trees. Examination of figures 6 and 8 indicates that no species was so represented. Rather, two alternate routes to biomass representation are evident. Species with relatively small trees had many of them, whereas species with the largest trees were uniformly represented across all height and diameter classes and had relatively few

total individuals. Species fell along a grade by these attributes. The ends of the spectrum appear to show alternate strategies towards dominance in the community.

The above observations offer an interesting parallel to correlations in plant size with numerical representation of species and genera in higher taxonomic categories among angiosperms.

Based on examination of global patterns for recent angiosperms, birds, and mammals, Van Valen (1973) has shown that with larger body size there are fewer species and fewer species per genus, but not necessarily less participation in the energy flow on a global scale. That is, small-sized species show a greater incidence of speciation than large-sized species. Size comparisons among the angiosperms concerned trees, shrubs, and herbs *(ibid.)*.

In making the logical connection between patterns in the community to the global, it would appear that a species adaptation towards dominance on a local scale through large size involves specialization with resultant loss of adaptability to new or changing environments (Stanley 1973). A trend for dominance through small size but large numerical representation involves greater tolerance for environmental variations, which, in turn, potentiates wider geographical distribution, and, hence, greater chances for speciation. It may be, therefore, that species differences in the strategy of adaptation within the community underlie size and numerical relationships in the higher taxonomic categories as found by Van Valen (1973). If this hypothesis can be further substantiated, then Stanley's (1973) explanation of Cope's Rule, that is, species proliferation from small-sized species rather than towards large size, may apply to plants as well as animals.

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