The Influence of Cyclones on the Dry Evergreen Forest of Sri Lanka[1]

Wolfgang P. J. Dittus[2]

Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008, U.S.A.

and

Institute of Fundamental Studies, Sri Lanka

ABSTRACT

I assessed damage caused by a cyclone in November 1978 to a dry evergreen forest in Sri Lanka. Damage included defoliation, breakage of twigs, branches and trunks, tree falls and post-cyclone tree mortality. Within the 3 km^2 study area there was a trend for increasing damage with forest height. Tree species in the upper forest layers had significantly more falls and post-cyclone mortality than trees in the more sheltered subcanopy and shrub layers. Mortality was significantly greater among trees which lost 40 percent or more of their branches and trunks than among trees with lesser crown damage. Defoliation and twig loss were extreme in the discontinuous upper layers and probably contributed to the greater tree mortality evident there. Overbrowsing by folivorous primates after the cyclone may have contributed to the demise of some preferred feeding trees. Total tree loss was 46 percent from the upper forest layers, 29 percent from the subcanopy, or 40 percent from all tree layers. Five upper layer tree species were subject to tree losses of 80 to 100 percent representing a virtual elimination of 22 percent of species from the upper layers or 12 percent from the forest.

Dry evergreen forest formerly covered 80 percent of the island's land area, and often has been described as "old secondary climax" in recognition of past disturbance. Extrapolations from meterological data indicate that 33 to 44 percent of the range of dry evergreen forest may be subject to cyclone damage per century. The species composition of dry evergreen forest on a local and wider geographical scale typically is fairly uniform in the subcanopy layer, but variable in the upper layers. I suggest that recurrent cyclone damage may be an important factor contributing to succession in dry evergreen forest and to the variation in species composition of the upper layers.

Tropical cyclones or hurricanes are known to cause extensive damage to human life and property in the coastal regions of the Bay of Bengal in the Indian Ocean. Although natural plant and animal populations are also subject to cyclone damage, published reports addressing this phenomenon are rare and concern areas outside the Indian region (*e.g.,* Webb 1958, Whitmore 1974). A recent cyclone which swept through the dry evergreen forest of Sri Lanka provided an opportunity to study the effects on phenology, forest structure and floristic composition. Quantitative data concerning these features were collected before the cyclone, allowing their comparison before and after the cyclone. The objectives of this paper are threefold: first, to assess the nature and extent of cyclone damage to the forest; second, to examine the causes of tree mortality in the 42 months following the cyclone; and third, to consider the effect of recurrent cyclones on the geographic variation in species composition of the dry evergreen forest of Sri Lanka. The long-term recovery of the forest from cyclone damage will not be examined in this report. Data concerning phenology are considered briefly, however, in order to show the immediate effects of the cyclone.

[1] Received 2 August 1983, revised 11 May 1984, accepted 14 June 1984.

[2] Field address: Smithsonian Institution Primate Project, 4/4 Galkanda Road, Anniewatte, Kandy, Sri Lanka.

NOMENCLATURE AND NATURAL HISTORY

The forest types of Sri Lanka have been classified according to several schemes (*e.g.,* Chapman 1947; Holmes 1956; Koelmeyer 1957, 1958; Gaussen *et al.* 1964; Fernando 1968). Mueller-Dombois (1968) offers an evaluation of these schemes and additional refinements have been made recently by Greller and Balasubramaniam (1980) and Greller *et al.* (1980).

The forest type considered here is commonly known in Sri Lanka as the "dry-zone forest." It has also been referred to as "Tropical Dry Evergreen Forest" (Champion 1935, Chapman 1947, Holmes 1956), "Tropical Dry Mixed Evergreen Forest" (de Rosayro 1950; Koelmeyer 1957, 1958; Andrews 1961), "Semideciduous Forest" (Gaussen *et al.* 1964, 1965), "South Tropical Moist Deciduous Forest" (Chapman 1947, Koelmeyer 1957), "Tropical Lowland Seasonal Rain Forest" (Perera 1975) and "Semi-evergreen Forest" (Dittus 1977). The last label had been selected to conform to Walter's (1971) worldwide classification of tropical vegetation types, although Walter does not specifically refer to the dry-zone forest of Sri Lanka. In the literature the dry-zone forest is most frequently referred to as "Dry Evergreen Forest" and therefore I will follow this tradition here. Taxonomic nomenclature follows Abeywickrama (1959) and Dassanayake and Fosberg (1981, 1983).

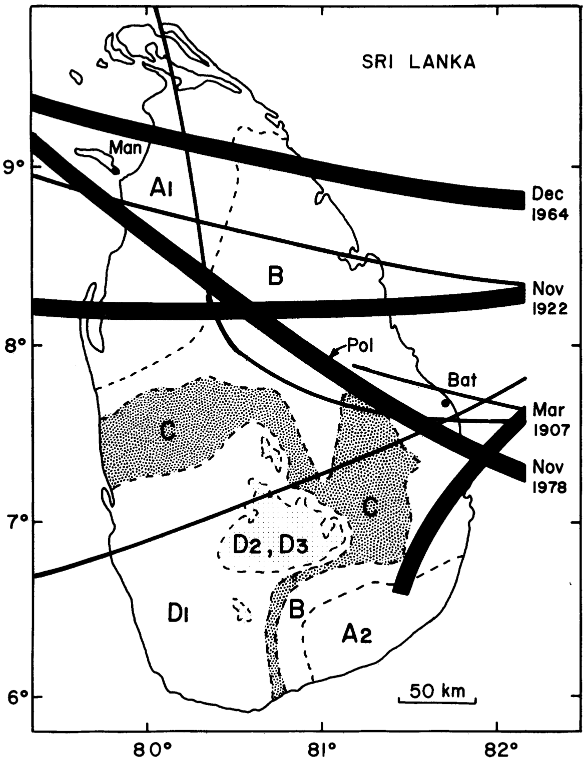

FIGURE 1. Map of Sri Lanka showing the zones of potential natural vegetation and the paths of cyclones (heavy lines) and strong storms (light lines). Forest types are: A1 and A2 = dry evergreen forest of the arid "dry zone"; B = dry evergreen forest of the moist "dry zone"; C = transitional zone forest; D1 = lowland rain forest; D2 and D3 = mid-altitude and high-altitude rain forests (after Gaussen *et al.* 1964, and Mueller-Dombois 1968). The locations of the Polonnaruwa study site (Pol), and of the towns of Batticaloa (Bat) and Mannar (Man) are indicated. The dates of cyclones are shown. Dates of strong storms are, from north to south on the east coast: November 1966; December 1913; December 1919; and December 1967 (Meteorological Department of Sri Lanka and India Meteorological Department 1979).

Dry evergreen forest is typical of the northern and eastern plains that cover 80 percent of the island's area (Fig. 1). In the past the dry-zone forest constituted 87 percent of the island's natural forest cover (Andrews 1961), but recent felling for agriculture has severely reduced its present extent (Geiser *et al.* 1980). Dry evergreen forests in the northwestern and southeastern extremes of their range (or of Sri Lanka), fall in the climatic "arid zones" and are usually differentiated from those in the moister regions (Fig. 1). Dry evergreen forest in the arid and moister regions correspond to climatic zones "A" and "B" of Mueller-Dombois (1968), or to Koelmeyer's (1957) "*Manilkara* Community" and "Mixed Community," respectively. Dry evergreen forest in the arid zone is similar to that in the moister regions but differs in having a lesser height and species diversity. The transition from the arid zone to the moister dry-zone is gradual with no marked separation. Thus depending upon the criteria used for classification, authors differ in the extent of area that they ascribe to the arid zone. The size of zones A1 and A2 (Fig. 1) follow Gaussen *et al.* (1964) and Mueller-Dombois (1968) and indicate their maximum extent. Fernando (1968) confines these zones to narrow coastal belts. Similarly, much of the transition zone C is included in zone B by Fernando (1968).

Dry evergreen forest, as at Polonnaruwa (zone B), has the following features: 2 to 3 tree layers, 15 to 30 m height for the upper layer, few epiphytes and vines compared to wet evergreen forest, 40 to 67 tree species, moderate diversity (Shannon index of tree species diversity H = 4.39 bits per individual and evenness J = 79.4%), 1200 to 1800 mm annual rainfall, and 2 to 5 months of drought duration (Dittus 1977). The drought is accentuated by the strong, dry and constantly blowing Southwest Monsoon wind between May and September. During this dry season some of the trees in the upper layer are at least partially deciduous, while most of those in the lower layers retain their foliage. Although the Dipterocarpaceae is one of the dominant families in the flora of Sri Lankan wet lowland evergreen forest (Gunatilleke and Gunatilleke 1980, 1983) and of the highland wet evergreen forests (Greller and Balasubramaniam 1980), no species of this family are found in the dry evergreen forest. The major dominant families in the dry evergreen forest are the Euphorbiaceae (by virtue of one species, *Drypetes sepiaria* in the subcanopy), Verbenaceae and Sapindaceae. Among shrubs, species of the Rutaceae and Euphorbiaceae have the highest relative densities. In the arid regions, *Drypetes sepiaria* (Euphorbiaceae) is again the most common tree in the subcanopy and *Manilkara hexandra* (Sapotaceae) and *Chloroxylon swietenia* (Guttiferae) are the most frequent trees in the canopy layer.

Archaeological evidence suggests that many parts of the dry zone had been cultivated at different times between 800 to 2000 years ago (Holmes 1956). The ancient civilization of the dry zone dwindled, however, and had largely abandoned the region by about 700 years ago. Although some authors consider the dry evergreen forest to be a climatic climax growth (*e.g.,* Chapman 1947, de Rosayro 1950), in light of the historical evidence much of this forest may be regarded as "Old Secondary Dry Evergreen Forest," or as a "secondary climax" (Koelmeyer 1957). Despite its largely secondary origin its condition is not necessarily sub-seral so that the secondary climax is indistinguishable from the original forest (de Rosayro 1961).

On a regional scale the dry evergreen forest of Sri Lanka is a type intermediate between the Wet Evergreen Forest (or rain forest) and the Tropical Dry Deciduous

Forest described by Champion (1935). In classifying the forests of India and Burma, Champion (1935) does not describe the dry-zone forest of Sri Lanka but in passing considers it to be the best developed example of "Dry Evergreen Forest" which, outside of Sri Lanka, is found only locally in the southeast coastal region of India. Koelmeyer (1957) points out, however, that the Indian type most closely resembles the dry evergreen forest of the arid zone of Sri Lanka, or the "*Manilkara* Community." Most of the dry evergreen forest is of the "Mixed Community" type of climatic zone B and is therefore unique to Sri Lanka.

STUDY AREA

The community of dry evergreen forest considered here is located within the Polonnaruwa Sanctuary and Archaeological Reserve in the northeast dry zone at 07°56′N and 81°00′E. The site encompasses about 3 km^2. The number of tree species found here is 61. The forest at Polonnaruwa has been quantitatively described and compared to other dry evergreen forest sites in Sri Lanka (Dittus 1977). Polonnaruwa had been a center of civilization abandoned more than 700 years ago. The forest at the site probably represents an old secondary climatic climax and is typical of dry evergreen forest elsewhere in Sri Lanka (Dittus 1977).

The study area is situated about 8–10 km north and west of the flood plains of two large rivers, the Amban Ganga and Mahaweli Ganga, and lies a few meters above the immediately surrounding countryside. The topography of the site is generally flat, relief within the area being less than 10 m. According to a soil distribution map (Panabokke 1975) the soil at the study site is typical Reddish Brown Earth that occurs extensively throughout the lowland dry-zone. This soil type is moderately deep and well drained (Panabokke 1967). A direct analysis of the soils at Polonnaruwa was not undertaken.

THE CLIMATE AND CYCLONES OF SRI LANKA

Sri Lanka falls under an equatorial climatic regime modified by monsoons. The average rainfall at Polonnaruwa over a 42 year period is 1671 mm. Most rains at Polonnaruwa are brought by convectional rains in October and November. These foreshadow and grade into the Northeast Monsoon which brings rainfall to a peak in December. A minor dry season often develops from January to March with minimal rainfall in February. A second brief peak of rainfall occurs in April from convectional rains. The northern and eastern regions of Sri Lanka are shielded from Southwest Monsoon rains by a montane region in the central part of the island. In the dry zone, the Southwest Monsoon instead is a strong desiccating wind which brings a two to five month drought to the area between May and September. In the northern arid zone the April rain-peak is minimal so that the dry season in these areas is prolonged (January to September). The climatic pattern at Polonnaruwa is typical for most of the dry-zone region B of Figure 1 (see Discussion).

Cyclones have wind speeds exceeding 90 $km \cdot h^{-1}$ and often reaching 160 $km \cdot h^{-1}$ whereas strong storms have maximum wind speeds of 60 to 90 $km \cdot h^{-1}$ (India Meteorological Department 1979). Cyclones and strong storms occur most frequently in the Bay of Bengal region during October and November when the intertropical convergence zone shifts southwards towards the equator. Though most cyclones originate below 12°N, they travel in a north-westerly direction (Kendrew 1961). As Sri Lanka lies between 6°N and 10°N, it is less affected by cyclones than land masses to the north. The paths of strong storms and of cyclones that have been recorded in Sri Lanka since 1877 are shown in Figure 1. Thambyahpillay (1959) describes eleven cyclones and two storms whose paths traversed mostly the northern half of the island between 1845 and 1958. Meteorological records prior to 1877 are probably incomplete, however, and an unequivocal distinction between storms and cyclones was not made by Thambyahpillay (1959). Therefore the data from the India Meteorological Department (1979) are used in this report.

The cyclone which damaged the east coast of Sri Lanka and the Polonnaruwa area occurred on November 23 and 24, 1978. Meteorological data concerning the cyclone come primarily from the stations at Batticaloa on the east coast and from Mannar on the northwest coast. Only temperature and rainfall were recorded at Polonnaruwa. The cyclone passed over the northern half of the island following a northwesterly path starting south of Batticaloa around 1900 h on November 23rd with winds estimated in excess of 185 $km \cdot h^{-1}$. Barometric pressure at Batticaloa dropped to a 957 mb minimum at the time, compared to a normal pressure of 1012 $\pm$ 2 mb. The eye of the storm was approximately 20 km in diameter and passed over Polonnaruwa close to midnight on November 23rd. The storm brought approximately 200 mm of rain over the 48 hour period of November 23 and 24. For two days, this was more than ten times the average daily rainfall for November.

In the path of the cyclone, winds of hurricane intensity covered an area 35 km wide. The storm leveled most of the town of Batticaloa on the east coast. Most tree falls at Polonnaruwa were towards the SSW direction, suggesting that the most intense wind occurred before the eye of the storm had passed over and the wind had changed direction.

METHODS

The trees and shrubs that were used to measure cyclone damage had been selected and individually marked six months before the cyclone for the purpose of phenological studies. This sample included 400 trees from the 44 most common tree species (as measured by relative density) at Polonnaruwa, and 199 shrubs from 32 shrub species. A sample of ten trees or shrubs had been chosen for most species, but a lesser number had been used for rare species. A sample of 20 or 25 trees had been selected for tree species that were important to concomitant studies dealing with the feeding ecology of primates inhabiting the forest. Trees had been selected at random without special regard for their sizes. The sample of trees was spread over an area approximately three km long in a north-south direction, and less than one km wide in the east-west direction.

In the field, each tree and shrub in the phenology sample was examined once per month before and after the cyclone and estimates were made of the relative amounts of material available in each of the three phytophases: leaves, flowers and fruits. Relative amounts were estimated on a scale of 0 (none available) to 10 (fully available). The mean of these individual scores was calculated for each species for each month. The data thus provide for each species for each month both the number and proportion of trees (or shrubs) exhibiting each phytophase, and also the mean of the estimated amounts of material in each phytophase. Phenological sampling was begun six months before the cyclone and was continued for four years thereafter.

To estimate crown damage each tree in the pre-cyclone sample was visually examined within one month after the cyclone to assess the proportion of large branches (greater than 10 cm in diameter) that had been broken from the crown of the tree. For very large branches and trunks this often involved estimating the proportion of empty space in the crown that was left by a missing limb. Estimates of "proportion of crown missing" were made on a scale of 0 to 10 for each tree. The means of these scores were calculated for each species.

Three estimates of tree loss were made. All are based on the number of trees alive before the cyclone in the pre-cyclone sample, but that died either during or after the cyclone. Not included here are new trees that were selected to replace ones that fell or died as a result of the cyclone (*e.g.,* as was required to maintain a standard sample size for phenological analyses). Thus, "tree falls" refers to all trees that were toppled over and uprooted by the cyclone. They were counted in December, 1978, within one month after the cyclone had passed. "Post-cyclone tree mortality" refers to the number of trees that died within 42 months after the cyclone among those trees that were left standing and alive shortly after the cyclone. Tree condition was examined at least once monthly during regular phenological sampling. A tree was considered as dead in the month when it first ceased to bear any more live phytophase. "Total tree loss" is the sum of trees fallen during the cyclone and of those that died within 42 months after the cyclone.

In an earlier survey of the forest at Polonnaruwa (Dittus 1977), diameter at breast height and tree height were measured for 3015 trees from 55 tree species. The trees were selected based on the 10 percent strip method (Cain and Castro 1959). Trees were defined as woody plants exceeding five meters in height, and shrubs as those less than five meters in height. Most shrubs were in the 1 to 3 m range. At any point in the undisturbed forest, generally there were three layers of trees recognizable above the shrub layer: first, a continuous subcanopy of trees between 6 to 15 m in height; second, a discontinuous canopy ranging up to about 23 m; and third, emergent trees sometimes towering above 30 m. Of all trees, approximately 75 percent were in the subcanopy, 20 percent were in the canopy and five percent were emergents.

Most data in this report were analyzed by tree layer but measurements were taken according to tree species. Notwithstanding, analyses according to tree layer were possible because tree layers differ markedly in their constituent tree species (Dittus 1977). Therefore, I assigned a tree species to a tree layer according to the mean height of trees for that particular species as was measured in the earlier survey. This classification is not wholly exclusive, because some typically short species contribute a few very tall trees to an upper layer, and typically tall species have trees in a lower layer. Typical emergent species, however, have very few short representatives.

In the data analysis two non-parametric statistical tests were used, the *Chi-square* test for two independent samples, and the *Spearman rank correlation coefficient,* r_s (Siegel 1956). In applying the *Chi-square* test, comparisons were made between the actual frequencies (*e.g.,* the numbers of dead trees) in two independent data sets (*e.g.,* canopy versus subcanopy trees). For the sake of clarity in the text these differences in frequencies were expressed in terms of percentages or proportions of the total number of items (*e.g.,* trees) in the data set. The two-tailed level of rejection for the null-hypothesis was used for all probabilities associated with the *Chi-square* values. The probabilities associated with r_s were for one-tailed tests, since the direction of the correlation (positive or negative) was predictable.

RESULTS

Visual inspection of the forest shortly after the cyclone suggested that most damage had occurred in the upper layers of the forest among canopy and emergent trees. Therefore, measures of damage generally were compared among different forest layers.

Loss of twigs, leaves, flowers and fruits.—Virtually all trees that protruded above the closed subcanopy (can-

FIGURE 2. Broken branches (A) and fallen trees (B) caused by a cyclone in the dry evergreen forest at Polonnaruwa. Note that shrubs and subcanopy trees in the background of photograph (A) especially, have retained more leaves and twigs than the taller trees.

TABLE 1. *Comparisons of the mean numbers and proportions of trees flowering and fruiting (a) between November (1978) before the cyclone and the Novembers of four non-cyclone years (1979–1982), and (b) between December (1978) shortly after the cyclone and the Decembers of four noncyclone years (1979–1982).*

	Flowering		Fruiting		Flowering		Fruiting	
	November 1978	November 1979–1982	November 1978	November 1979–1982	December 1978	December 1979–1982	December 1978	December 1979–1982
Mean number of trees	40	33	62	69	2	20	26	76
Mean proportion of trees	10.4%	8.5%	16.1%	17.7%	0.7%	5.1%	9.4%	19.5%
Sample size	384	390	384	390	277	390	277	390
Chi-square	0.652		0.228		8.526		11.989	
P	.30		.50		.005		.001	
Conclusion	similar		similar		different		different	

opy and emergent layers) were totally or almost totally defoliated and stripped of a major portion of their twigs and small branches (Fig. 2). Isolated trees regardless of height were also defoliated. The impact of the extremely heavy rain being driven by the high velocity winds during the cyclone probably contributed to this damage in great measure. In contrast, in the relatively closed and sheltered subcanopy, leaves and twigs were abundant (Fig. 2). Similarly, from visual inspection alone, leaf loss in the shrub layer appeared to be minimal.

To assess the degree of damage to which the cyclone also stripped trees of their flowers and fruits, phenology samples of trees from November (1978), before the cyclone, and from December (1978), after the cyclone, were compared to those from the same months of four non-cyclone years (1979–1982). The statistical values and data of these comparisons are given in Table 1. They indicated that the numbers and proportions of trees that bore flowers or fruits before the cyclone (November 1978) were not significantly different from those of the Novembers of four non-cyclone years. The proportions of trees bearing flowers or fruits shortly after the cyclone (December 1978), however, were significantly less than those in the Decembers of the four non-cyclone years.

In the shrub layer phenological observations were made in October (1978) before the cyclone and in November after it. The same comparisons as were made for trees were made for shrubs (Table 2). The proportions of shrubs flowering or fruiting in October (1978), before the cyclone, were not significantly different from those in the Octobers of four non-cyclone years (1979–1982). After the cyclone, the proportions of shrubs bearing flowers or fruits were less than those from the four non-cyclone years. But, this difference was significant for flowering shrubs only (Table 2). Overall, these data suggest that cyclone damage to flowers and fruits was greater among trees than shrubs.

TREE FALLS.—Comparisons were made of the numbers and proportions of trees uprooted and toppled over during the cyclone among tree species of different tree layers (Table 3). Although the proportion of tree falls among emergent species (39%) was slightly greater than that among species in the canopy layer (35%), this difference

TABLE 2. *Comparisons of the mean numbers and proportion of shrubs flowering and fruiting (a) between October (1978) before the cyclone and the Octobers of four non-cyclone years (1979–1982), and between November (1978) immediately after the cyclone and the Novembers of four non-cyclone years (1978–1982).*

	Flowering		Fruiting		Flowering		Fruiting	
	October 1978	October 1979–1982	October 1978	October 1979–1982	November 1978	November 1979–1982	November 1978	November 1979–1982
Mean number of shrubs	51	50	39	49	4	27	23	42
Mean proportion of shrubs	25.6%	25.5%	19.6%	25.0%	2.6%	13.7%	14.9%	21.3%
Sample size	199	196	199	196	154	197	154	197
Chi-square	0.008		1.367		11.902		1.931	
P	.90		.20		.001		.10	
Conclusion	similar		similar		different		similar	

TABLE 3. *Measures of cyclone damage to tree species of different canopy layers.*

Tree species by canopy layer	No. of tree heights sampled[a]	Mean tree height (m)[b]	No. of trees in pre-cyclone sample[c]	Mean crown loss %	Trees fallen		Post-cyclone tree deaths[d]		Total tree loss	
					No.	%	No.	Rate/100	No.	%
Emergent layer										
Adina cordifolia	89	25	10	45	4	40	1	17	5	50
Elaeodendron glaucum	9	22	10	30	7	70	0	0	7	70
Holoptelea integrifolia	9	24	10	20	6	60	0	0	6	60
Manilkara hexandra	63	21	10	29	2	20	0	0	2	20
Mitragyne parvifolia	20	22	10	25	3	30	1	14	4	40
Schleichera oleosa	122	20	20	32	8	40	1	8	9	45
Sterculia foetida	5	24	10	27	1	10	1	11	2	20
Totals or means			80	30	31	39	4	8	35	44
Canopy layer										
Alangium salviifolium		16	10	90	9	90	1	100	10	100
Alseodaphne semicarpifolia	13	16	10	26	5	50	1	20	6	60
Bridelia retusa	13	17	10	22	4	40	1	17	5	50
Chloroxylon swietenia	11	15	8	0	4	50	4	100	8	100
Diospyros ovalifolia	11	17	7	70	6	86	1	100	7	100
Ficus amplissima	41	17	25	34	4	16	0	0	4	16
Ficus benghalensis	9	19	20	35	3	15	0	0	3	15
Ficus racemosa	3	19	5	38	1	20	0	0	1	20
Ficus religiosa	1	18	2	?	0	0	0	0	0	0
Ficus microcarpa	5	15	10	16	5	50	0	0	5	50
Garcinia spicata	25	19	10	32	5	50	0	0	5	50
Stereospermum personatum	25	19	10	43	4	40	4	67	8	80
Syzigium cumini	38	15	10	46	0	0	0	0	0	0
Tamarindus indica	4	15	2	?	1	50	0	0	1	50
Vitex pinnata	183	16	10	36	3	30	1	14	4	40
Walsura piscidia	84	17	10	55	2	20	7	88	9	90
Totals or means			159	35	56	35	20	19	76	48
Subcanopy layer										
Aglaia roxburghiana	1	13	8	30	6	75	0	0	6	75
Bauhinia racemosa	14	8	10	27	1	10	0	0	1	10
Cassia fistula	175	7	10	20	2	20	2	25	4	40
Cassia roxburghii	127	7	10	36	2	20	0	0	2	20
Cordia sp.	95	8	10	35	4	40	1	17	5	50
Diospyros montana	10	12	10	47	4	40	0	0	4	40
Drypetes sepiaria	552	11	20	21	3	15	0	0	3	21
Ficus mollis	3	13	3	43	0	0	0	0	0	0
Gleniea unijuga	73	12	10	29	2	20	1	13	3	30
Grewia polygama	232	13	10	50	5	50	0	0	5	50
Ixora arborea	112	9	10	35	4	40	0	0	4	40
Lepisanthes tetraphylla	94	10	10	44	1	10	1	11	2	20
Lannea coromandelica	3	12	3	27	0	0	0	0	0	0
Maba buxifolia	9	8	4	0	2	50	0	0	2	50
Polyalthia sp.	47	10	1	?	0	0	0	0	0	0
Premna tomentosa	248	9	10	49	3	30	0	0	3	30
Sapindus emarginatus	24	13	10	42	0	0	0	0	0	0
Strychnos potatorum	142	10	10	21	0	0	0	0	0	0
Totals or means			161	33	40	25	7	6	47	29

[a] The tree heights of 3015 trees from 55 species were assessed in an earlier survey of the forest at Polonnaruwa (Dittus 1977).
[b] The means of the tree heights assessed earlier for each species (*ibid.*)
[c] The pre-cyclone sample is independent of the one used to assess tree heights and is the basis for all measures of cyclone damage (see Methods).
[d] The number and rate dying within 42 months after the cyclone.

TABLE 4. *Measures of cyclone damage to 33 species in the shrub layer.*

No. of shrubs in pre-cyclone sample	Shrubs fallen		Post-cyclone shrub deaths[a]		Total shrub loss	
	No.	%	No.	Rate/100	No.	%
199	41	21	1	1	42	21

[a] Within 42 months after the cyclone.

TABLE 6. *The number and proportion of surviving and dead trees according to the degree of crown damage.*

Degree of crown damage	Surviving trees		Dead trees	
	Number	Proportion	Number	Proportion
<40%	132	57%	9	31%
≥40%	99	43%	20	69%
Totals	231	100%	29	100%

was not significant ($\chi^2 = 1.83$, $P > .10$). The data from these two layers were therefore pooled for further comparisons. The proportion of tree falls among species of the emergent and canopy layers combined (36%) was significantly greater ($\chi^2 = 5.28$, $P < .02$) than the proportion of tree falls (25%) in the subcanopy layer. It was also significantly greater ($\chi^2 = 12.35$, $P < .001$) than the proportion of shrubs fallen (21%; see Table 4). The proportion of tree falls in the subcanopy (25%) did not differ significantly from that (21%) of shrubs fallen ($\chi^2 = 0.68$, $P > .10$).

POST-CYCLONE TREE MORTALITY.—I examined the number of trees from the pre-cyclone sample that survived the cyclone but that subsequently died within 42 months after the cyclone. These data were also expressed as the rate of tree mortality per 100 live trees (Table 3). There was no significant difference in the proportion of trees dying (8%) among species in the emergent layer and that dying (19%) among canopy species ($\chi^2 = 2.37$, $P > .10$). The data from these two layers therefore were pooled. The proportion of trees dying among species in the emergent and canopy layers combined (16%) was significantly greater than that dying (6%) among trees of the subcanopy ($\chi^2 = 5.74$, $P < .02$). The proportion of shrubs that died (1%; see Table 4) among those that had not fallen during the cyclone, was significantly less ($\chi^2 = 4.81$, $P < .05$) than the proportion of trees that died in the subcanopy (6%), and was significantly less ($\chi^2 = 22.00$, $P < .001$) than the proportion of trees that died in the canopy and emergent layers (16%).

Trees died at different times in the 42 months following the cyclone. Of all tree deaths, 45 percent occurred within the first six months, and 82 percent occurred during the first 18 months after the cyclone (Table 5).

TOTAL TREE LOSS.—The numbers of trees that fell during the cyclone and of those that died thereafter were summed and expressed as the percentage total tree loss or mortality from the pre-cyclone sample (Table 3). The proportion of total tree loss (46%) from the emergent and canopy layers combined was significantly greater than that (29%) from the subcanopy layer ($\chi^2 = 11.27$, $P < .001$). It was also significantly greater than the total loss (21%; see Table 4) from the shrub layer ($\chi^2 = 29.57$, $P < .001$). Although the proportion of total tree loss from the subcanopy (29%) was slightly greater than that of shrubs lost (21%), this difference was not significant ($\chi^2 = 2.71$, $P = .10$). Overall, 40 percent of trees were lost from the forest.

CROWN DAMAGE AND ITS RELATION TO POST-CYCLONE TREE MORTALITY.—Estimates of "proportion of crown missing" were presented as percentages of mean crown loss for different tree species and layers (Table 3). Although there was great variation in the degree of crown damage by species, there appeared to be no consistent difference in the degree of crown damage by species of different layers. Trees in the subcanopy suffered as much crown damage as trees in the canopy and emergent layers.

Crown damage was examined in relation to post-cyclone tree mortality. The numbers and proportions of surviving and dead trees were compared according to different degrees of crown damage (Table 6). A significantly greater proportion (69%) of dead trees than of surviving trees (43%) had crown damage of 40 percent or more

TABLE 5. *The temporal distribution of tree mortality.*

Period	Dec 78 to May 79	June 79 to Nov 79	Dec 79 to May 80	June 80 to Nov 80	Dec 80 to May 81	June 81 to Nov 81	Dec 81 to May 82
Number of tree deaths	14	6	6	2	0	1	2
Proportion of tree deaths (%)	45	19	19	6	0	3	6

TABLE 7. *The 15 most common tree species at Polonnaruwa before the cyclone and their relative densities before and after the cyclone.*

Tree species	Before cyclone: Number of trees	Before cyclone: Relative density %	After cyclone: Estimated relative density %
Drypetes sepiaria	635	21.4	25.1
Grewia polygama	278	9.4	7.0
Premna tomentosa	253	8.5	8.9
Cassia fistula	190	6.4	5.7
Vitex pinnata	184	6.2	5.5
Cassia roxburghii	158	5.3	6.3
Strychnos potatorum	142	4.8	7.1
Schleichera oleosa	128	4.3	3.5
Lepisanthes tetraphylla	110	3.7	4.4
Ixora arborea	103	3.5	3.1
Adina cordifolia	84	2.8	2.1
Walsura piscidia	81	2.7	0.4
Cordia sp.	74	2.5	1.9
Manilkara hexandra	69	2.3	2.8
Gleniea unijuga	64	2.2	2.2
Subtotal	2553	86.0	86.0
25 others	409	14.0	14.0
Total	2962	100.0	100.0

($\chi^2 = 7.08$, $P < .01$). These data suggest that extensive crown damage was an important cause of tree mortality.

POST-CYCLONE CHANGE IN TREE SPECIES COMPOSITION OF FOREST.—The 15 most common tree species at Polonnaruwa before the cyclone were arranged in order of decreasing relative density as ascertained seven years before the cyclone (Dittus 1977). These data were compared to the estimated relative densities for the same species after the cyclone (Table 7). The latter were derived as follows. If N_i is the number of trees for the ith species in the pre-cyclone forest survey, and q_i is the total proportion of trees lost from the ith species owing to the cyclone (from Table 3), then the estimated relative density after the cyclone of the ith species among S number of tree species is

$$N_i - N_i q_i / \sum_{i=1}^{S} (N_i - N_i q_i)$$

There was no significant difference between the ranks of relative densities of tree species before and after the cyclone ($r_s = 0.89$, $P < .01$) among the 15 species compared in Table 7, or among 40 species ($r_s = 0.93$, $P < .001$) for which data from before and after the cyclone were compared. However, five tree species (*Alangium salviifolium, Chloroxylon swietenia, Diospyros ovalifolia, Stereospermum personatum* and *Walsura piscidia*) have disappeared or have been greatly reduced in numbers of trees (total tree losses of 80 to 100%) following the cyclone (Table 3). All of these species were from the canopy layer representing a 22 percent loss or great reduction of tree species in the upper forest layers or 12 percent from the forest. The losses were most noticeable for *Walsura piscidia* (Table 7), which was a common tree in the canopy before the cyclone (relative density of 2.7%), and for the moderately common trees, *Chloroxylon swietenia* and *Stereospermum personatum,* which had relative densities of 0.6 and 0.8 percent before the cyclone and 0.0 and 0.2 percent, respectively, thereafter. These estimates of tree losses by species are based on limited sample sizes for most tree species. But ancillary observations of the forest confirm a notable absence of trees of *Chloroxylon swietenia,* and a scarcity of *Alangium salviifolium* and *Walsura piscidia* following the cyclone.

Overall, following the cyclone, a significantly greater number and proportion of tree species decreased in their estimated relative densities in the emergent and canopy layers (78%), than in the subcanopy (38%) ($\chi^2 = 4.16$, $P < .05$).

DISCUSSION

DIRECT CYCLONE EFFECTS ON TREE FALLS AND MORTALITY BY FOREST LAYER.—There were significantly greater proportions of tree falls, post-cyclone mortality, and total tree loss in the emergent and canopy layers combined than in either the subcanopy or the shrub layer. The same types of damage were greater in the subcanopy than in the shrub layer, but only the post-cyclone mortality was significantly greater. Thus, overall, there was a trend for an increase in total tree loss with height of forest layer.

The data suggest that the high wind velocity in the upper canopy was the cause for the greater proportion of tree falls there. The frequency of uprooted trees in general might have been heightened by the wet soil. Woody damage in the shrub layer is attributable almost exclusively to trees and large branches falling onto and knocking over shrubs.

The degree of crown damage was approximately equal between the three tree layers (Table 3). Damage in the emergent layer, however, is probably attributable primarily to high wind velocity, whereas trees in the canopy and especially in the subcanopy were damaged by trees and branches falling onto them from the upper layers, as well as by wind.

Considering the influence of crown damage on tree mortality, a significantly greater proportion of trees died among species with crown damage of 40 percent or more, than among species with lesser amounts of crown damage. This indicates that a high degree of crown damage is detrimental to tree survivorship.

The fact that crown damage caused tree mortality, but was approximately equal between the three tree layers, suggests that there were factors in addition to crown damage that contributed to the greater mortality in the canopy and emergent layers. The loss of twigs and leaves was extreme in the emergent and canopy layers but much less in the relatively closed and sheltered subcanopy (Fig. 2). It would seem that the greater leaf and twig loss in the upper layers, in combination with the loss of woody crown, was responsible for the greater mortality evident there.

POST-CYCLONE TREE MORTALITY IN RELATION TO FOLIVORY BY PRIMATES.—Several species suffered extreme post-cyclone mortality, notably *Chloroxylon swietenia* (100%), *Diospyros ovalifolia* (100%), *Alangium salviifolium* (100%), *Walsura piscidia* (88%) and *Stereospermum personatum* (67%). All of these species were from the canopy layer. Although extensive crown damage may explain much of this mortality in *Alangium salviifolium* and *Diospyros ovalifolium,* other factors may also be involved. The influence of overbrowsing by leaf-monkeys on the survivorship of favoured feeding trees is considered in detail elsewhere (Dittus 1985). A brief consideration follows here.

The folivorous grey langurs, *Presbytis entellus,* and purple-faced langurs, *Presbytis senex,* inhabited the Polonnaruwa study site at high densities before the cyclone (Eisenberg *et al.* 1972). Earlier studies by Hladik and Hladik (1972) had shown that the rates of consumption of foliage by these langurs in relation to the productivity of the trees was near the threshold of endangering the feeding trees. Or, the sizes of the langur populations were at a maximum in relation to their food supply. Within one month following the cyclone the langur populations decreased by about five to 15 percent (Dittus 1979, R. Rudran, personal communication). But, the cyclone destroyed more than 50 percent of the woody vegetation that had produced most of the food for these langurs (taking into account the joint effect of a 40% tree loss and 33% crown loss from the forest). Hence, the cyclone very likely upset the equilibrium between the langurs and their food supply, at least temporarily. The leaves and leaf-shoots of *Walsura piscidia, Alangium salviifolium* and *Chloroxylon swietenia* were highly preferred food items for both langurs at Polonnaruwa before and after the cyclone (Hladik and Hladik 1972 and personal observation). These trees probably were being overbrowsed in the phase of disequilibrium following the cyclone. It is therefore possible that overbrowsing by langurs, particularly at the critical time when trees were recovering from other cyclone damage, had an additional negative effect on the survivorship of some of these trees.

VARIATION IN THE SPECIES COMPOSITION OF DRY EVERGREEN FOREST.—The most extensive survey of the forests of Sri Lanka was made for economic purposes by the Hunting Survey Corporation Limited, Toronto, Canada. Ecological studies concerning the floristic variation among forests have not been made. An appreciation of floristic variation within and among different forest reserves can nevertheless be had from the foresters' stand and stock tables and their descriptive accounts of "ecological variations." Reserves, enclosing 350 to 550 km^2 of natural dry evergreen forest, occur at several locations throughout the dry zone of Sri Lanka and these have been surveyed by Andrews (1961), McCormack and Pillai (1961a, b, c) and Oudshoorn (1961). Most of the dry evergreen forests are considered as "low yield" or "non-productive" by foresters and these correspond to Koelmeyer's (1957) "Mixed Community." The more diverse and higher stature "medium yield" dry evergreen forests are found mostly along streams. Considering the most common or "low-yield" type, and excluding areas that have been disturbed through recent human activity, the above mentioned foresters consistently report that most intrinsic variation in species composition occurs in the upper forest layer among sampling plots within a study site, among different sites or communities within a forest reserve, and among different reserves of dry evergreen forest. For example, within a reserve one canopy species may form a gregarious stand extending for several miles, but a different canopy species will be the most common one at another location. The same pattern is reported for the more localized "medium yield" or riparian forests. For the subcanopy, however, the foresters report a greater uniformity in species composition. Based on a limited quantitative sample, de Rosayro (1961) describes a similar pattern in the dry evergreen forest of zones A and B.

In an earlier report (Dittus 1977), I had attempted to quantify some of the floristic variation by comparing the relative densities of tree species among five geographically isolated reserves[3] within the main area (zone B) of dry evergreen forest. These comparisons indicated that the six most common species (that together made up 61.2 to 69.3% of relative density among the five sites) were identical and typical subcanopy trees at all sites. One subcanopy species, *Drypetes sepiaria,* was the dominant growth at all sites contributing 15.5 to 38.5 percent of relative density. *Drypetes sepiaria* is invariably the most common (by relative density) and dominant (by basal area) tree in all of the dry evergreen forests. In the arid regions it may constitute more than 50 percent of all trees.

INFLUENCE OF CLIMATE AND SOIL ON THE FLORISTIC VARIATION IN DRY EVERGREEN FOREST.—In Sri Lanka ". . . climate is clearly the controlling or master factor in the expression of the vegetation and edaphic factors are clearly

[3] Forest Reserves are: Kantalai, Nuwaragala, Omunagala, Panama, Ratkarawwa.

secondary . . . In fact climate is also the chief determining factor of the soils." (de Rosayro 1950, page 166).

Temperatures are similar in the dry and arid zones, but low rainfall presumably is a major cause for the low stature and species diversity evident in the forests of the arid zones (Oudshoorn 1961). The main area of dry evergreen forest might be considered the large area (zone B) interior to the arid zones and excluding the fingers of dry evergreen forest extending to the far west and to the far south (Fig. 1). The forest reserves compared in the preceding section fall within this area. Climatic data (after Mueller-Dombois 1968), from ten weather stations[4] distributed throughout this main area of zone B, are as follows. The range of ten 50-year averages in annual rainfall is 1403 to 1667 mm, the mean of these averages is 1560 mm, and the standard deviation is 123 mm. The range of ten long-term averages in annual temperature is 26.3° to 27.9°C, the mean of these averages is 27.3°C, and the standard deviation is 0.4°C. The seasonal distribution of rain (*e.g.,* as at Polonnaruwa) also follows a similar pattern in most of zone B. Thus, the climatic pattern in the main area of dry evergreen forest is fairly invariable.

The Reddish Brown Earths are a major soil group of Sri Lanka and occur extensively in the lowland dry zone where annual rainfall is less than 1900 mm. Most of the parent material for these soils is relatively uniform consisting of biotite and hornblende bearing gneisses of the metamorphic Vijayan Series of middle Paleozoic Age (Cooray 1967). The Reddish Brown Earths have been described as highly regular in structure and composition (Joachim 1945). Variations occur in correlation with local features such as streams and slopes: typical drainage associations consist of Low Humic Gley Soils along streams with Yellowish Brown Earths occurring on the slopes between the streams and the more extensive Reddish Brown Earths of the surrounding topography. Additional soils related to the Reddish Brown Earths, but having more limited distributions, are found in the eastern lowlands south and west of Batticaloa. These are the Noncalcic Brown Soils, Immature Brown Loams and Regosolic Alluvial Soils (Panabokke 1967, 1975). De Alwis and Eriyagama (1969) have given very general descriptions of the vegetation that has been found in association with these and more specialized edaphic types in zones A and B. Quantitative data are lacking, however, and the clearest relation between soils and vegetation occurs among soils of limited distribution that are markedly different from the usual Reddish Brown Earths of the dry zone. Widespread soil differences that can be related to floristic variations, as in the rain forests of Brunei (Ashton 1964, Austin *et al.* 1972) for example, have not been described in the dry evergreen forest of Sri Lanka. The available information suggests a considerable uniformity in both climate and soils over a large area of dry evergreen forest. The influence of climate, soils, or any other factor on the floristic variation in the dry evergreen forests of Sri Lanka will remain a matter of speculation, however, until the problem is studied directly.

[4] Weather Stations are: Anuradhapura, Batticaloa, Horowupotana, Lahugala, Maha Iluppallama, Mapakadawewa, Sigiriya, Timitar Estate, Topawewa, Trincomalee.

Cyclones in relation to succession and floristic variation of dry evergreen forest.—Since the cyclone destroyed much of the upper layer at Polonnaruwa, it seems reasonable to consider the extent to which cyclonic storms might contribute to the variation in species composition in the upper layers of dry evergreen forest.

Meteorological records concerning major storms and cyclones in the Bay of Bengal and Sri Lanka are available since 1877 (India Meteorological Department 1979, Meteorological Department of Sri Lanka). In the last 100 years, four cyclones have been recorded in Sri Lanka on the average of one about every 24 years, and four strong storms with wind velocities up to 90 $km \cdot h^{-1}$ have occurred on the average of one every 18 years. The paths of these cyclones and strong storms affected areas of dry evergreen forest more than other forest types on Sri Lanka (Fig. 1).

Cyclones leave a swath of damage 30 to 40 km wide (*ibid.*). With four cyclones having occurred in the last 100 years, destruction will have occurred in a total area of 120 to 160 km in width stretching across the island in a westerly direction. This width of destruction would have affected approximately 33 to 44 percent of the north-south extent of dry evergreen forest in the last 100 years. A proportionately greater area of this destruction is concentrated in the northern half of the island (where the majority of dry evergreen forest is located) because cyclones have occurred more frequently there. Also, more destruction is expected to have occurred in the eastern regions where cyclone intensity is the greatest. However, cyclone damage clearly is not a restricted coastal phenomenon. The cyclone of November 1978 had travelled about 90 km overland, from its starting position on the east coast south of Batticaloa, when it reached Polonnaruwa; and extensive forest damage was evident for another 60 km inland beyond Polonnaruwa in the path of the cyclone. If the pattern of cyclone activity in the last 100 years can be extrapolated in time, then any one location in the range of dry evergreen forest can be expected to have been (or to be) adversely affected by a cyclone on the average of once every 225 to 300 years, with much shorter inter-cyclone intervals in the northern regions. These extrapolations may be conservative as Thambyahpillay's (1959) data might indicate a slightly greater frequency of cyclones (but of uncertain intensities) in Sri Lanka. The areas of dry evergreen forest least subject to cyclones are in the far west of their range below 8°N, where the central mountains act as a protective barrier.

Data in this report indicate that the physical force of the cyclone and its immediate ecological consequences (overbrowsing by primates) caused greatest loss of trees (46%) and of tree species (22%) in the upper forest layers. Though long-term successional changes at Polonnaruwa cannot be assessed yet, the greater damage in the upper layers indicates at least a temporary reduction in the proportion of canopy trees and species. Saplings and other young stages of emergent and canopy tree species are very rare or absent among the regenerating undergrowth and subcanopy layers both at Polonnaruwa before the cyclone (Dittus 1977) and in the dry evergreen forests in general (Holmes 1956). Hence, one might expect an eventual change in the species composition of the upper layers at any one site as new trees and species replace those destroyed by the cyclone. These data, together with the geographical and temporal pattern of cyclone activity just described, suggest that cyclones may indeed be an important factor contributing to the differences in species composition that is observed especially in the upper layers within and among different sites of dry evergreen forest.

Given the poor regeneration of upper layer trees and their variable distribution, de Rosayro (1961) and Dittus (1977) had suggested independently that the composition of the canopy may change cyclically in a manner proposed by Aubreville's (1938) Mosaic Theory of Regeneration. This theory assumes that compositional changes occur cyclically within a climax growth in the absence of outside disturbance. In view of the cyclone data, however, the combination of species at any one location or time may be a seral stage, and the changes part of a normal process of development towards a stable climax. Cycles, such as there may be in this successional process, would be cyclone-induced. Given the temporal and geographic distribution of cyclones in Sri Lanka few areas of dry evergreen forest can be expected to have reached a stable climax in the canopy layer. This is especially so for the far north of Sri Lanka where cyclones are more frequent or for the east where they are more intense. Variation in species composition in the upper layers of dry evergreen forest therefore would reflect, at least in part, differences between sites in the time elapsed since the last cyclone, as well as in the degree of damage that was inflicted. The subcanopy layer is the least altered by cyclone damage and manifests the greatest uniformity in species composition (at least among its principal constituent species) across a wide range of the dry evergreen forest. These facts suggest that a stable climatic climax has been reached in the subcanopy in most dry evergreen forest areas, and that, following a cyclonic disturbance, stability is reestablished in the subcanopy in a shorter time period than in the canopy. The secondary origin of dry evergreen forest has been recognized earlier; Holmes (1956) and de Rosayro (1961) ascribed this to human activity in the dry zone 800 to 2000 years ago. The data here would suggest, however, the dry evergreen forest also has been altered more recently and on a more regular pattern through history by cyclones.

Comparison with cyclone-affected areas elsewhere.—Most studies of cyclone disturbed areas elsewhere (see below) have examined the immediate effect of cyclone damage in the forest in lesser detail than in this report. Nevertheless, these studies reveal a pattern of damage similar to that witnessed at Polonnaruwa. Total defoliation and crown damage of upper canopy trees is generally common (Webb 1958, Whitmore 1975). In a cyclone damaged area of northern Queensland shattered trees and windthrows appeared to be most evident in tree layers above four to seven meters, or among trees of intermediate girth classes averaging 10 to 20 cm (Webb 1958). The destructive effect of cyclones in Queensland is much influenced, however, by local topography (Webb 1958).

Cyclones seem to be less frequent in Sri Lanka than in most other areas where the effect of cyclones on forest structure has been studied. Most of the dry evergreen forest areas of Sri Lanka probably are not comparable to the extreme types of "closed scrub" of southern Nigeria (Jones 1955, 1956; Richards 1955) or to the "cyclone (vine) scrub" of northern Queensland (Webb 1958). Cyclone damage at these locations is so frequent (about once in three to 40 years in Queensland) as to leave a "permanent" and conspicuous effect on the vegetation. At both locations the low stature scrub has been derived from high forest through the periodic destruction of most tall trees. These scrubs are characterized by the presence of a few scattered and vine covered emergents, an abundance of vines in general, and saplings and regenerating trees that are also found in tall lowland rain forest (Webb 1958). Similar "hurricane forests" have been described by Beard (1945) in the West Indies. Areas of dry evergreen forest of Sri Lanka that would be expected to resemble these "cyclone scrubs" most closely lie along the northeast coast where cyclones are most frequent and severe. The dry evergreen forests of the southeastern coast of India (Champion 1935) might be examined in view of the cyclone activity there.

The "storm forests" of Kelantan, Malaysia, appear to be the result of a freak tornado which flattened an extensive area of rain forest in the 1880's and which probably was associated with the eruption of Krakatau in 1883 (Browne 1949, Wyatt-Smith 1954). In addition to the above mentioned sites, cyclone damage has been documented almost exclusively in the rain forests that lie in the cyclone belt of east Asia; for example, Samoa (Wood 1970), the New Hebrides, Fiji (Gane 1970) and the Philippines north of Mindanao, (Nicholson 1970; cited in Whitmore 1975). In the Solomon archipelago between

7° and 11°S, cyclones have become more frequent since 1950 (Whitmore 1975). Many of these studies of Asian rain forest (*e.g.*, Whitmore 1974) emphasize forest regeneration. They have shown that vines and light-demanding species tend to be found in the gaps opened up by cyclones. Such disturbed forests are dominated by long-lived pioneer or near-pioneer species whose life span may exceed a century. The effects of a cyclonic disturbance are thus long lasting (Whitmore 1974). In Mauritius cyclones are so frequent (on the average of one or more per annum) that Vaughan and Wiehe (1937) believe that cyclones have played a significant role in the evolution of a cyclone adapted climax forest. In general, cyclones are recognized to have far reaching effects in upsetting forest equilibrium and perhaps in enhancing their diversity (Jones 1955, 1956; Webb 1958; Whitmore 1975). The data from Sri Lanka suggest that even fairly infrequent cyclones (about four per century) might be an important agent determining the secondary character and the variation that is reported among canopy species of dry evergreen forest. Further ecological comparisons and studies concerning the regeneration of these forests are necessary to examine this supposition.

ACKNOWLEDGMENTS

I thank the Office of the President of the Democratic Socialist Republic of Sri Lanka for permission to do basic research in Sri Lanka, and especially Professor Hilary Crusz for his heroic efforts in securing this permission. The successive Directors of the Institute of Fundamental Studies, Sri Lanka, Professors N. C. Wickramasinghe and Cyril Ponnamperuma, sponsored the research under the aegis of the institute. Neville Selastian assisted with field work and Shirani Nathanael helped with data summarization. I am grateful to the following persons for helpful comments on the manuscript: Peter S. Ashton, S. Balasubramaniam, Anne Baker-Dittus, C. V. S. Gunatilleke, I. A. U. N. Gunatilleke, Martin Kellman, and Peter L. Marks. I had useful discussions with John Seidensticker.

The research was supported by National Science Foundation grants, BNS-7619740, BNS-7924057 and BNS-8300092. Supplementary funding was obtained from the Friends of the National Zoo and from the Smithsonian Institution Bacon Fund. I thank Devra Kleiman for administrative assistance.

LITERATURE CITED

Abeywickrama, B. A. 1959. A provisional check list of the flowering plants of Ceylon. Ceylon J. Sci. (Bio. Sci.) 2: 117–240.

Andrews, J. R. T. 1961. A Forest Inventory of Ceylon. Government Press, Colombo, Sri Lanka.

Ashton, P. S. 1964. Ecological Studies in the Mixed Dipterocarp Forests of Brunei State. Oxf. For. Mem. 25.

Aubreville, A. 1938. La foret coloniale: les forets de l'Afrique occidentale francaise. Annuel Academie Sciences coloniale, Paris 9: 1–245.

Austin, M. P., P. S. Ashton, and P. Greig-Smith. 1972. The application of quantitative methods to vegetation survey III. A re-examination of rain forest data from Brunei. J. Ecol. 60: 305–324.

Beard, J. S. 1945. The progress of plant succession on the Soufriere of St. Vincent. J. Ecol. 33: 1–9.

Browne, F. G. 1949. Storm forest in Kelantan. Malay. Forester 12(1): 28–33.

Cain, S. A., and G. M. de Oliveira Castro. 1959. Manual of Vegetative Analysis. Harper Brothers, New York.

Champion, H. G. 1935. A preliminary survey of the forest types of India and Burma. Indian Forest Records (N. S.) 1(1): 1–286.

Chapman, V. J. 1947. The application of aerial photography as exemplified by the natural vegetation of Ceylon. Indian Forester 73(7): 287–314.

Cooray, P. G. 1967. The Geology of Ceylon. Government Press, Sri Lanka.

Curtis, J. T., and R. P. McIntosh. 1951. An upland continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476–496.

Dassanayake, M. D., and F. R. Fosberg. 1981. A Revised Handbook of the Flora of Ceylon, vols. 2 and 3. Amerind Publ., New Delhi.

———, and ———. 1983. A Revised Handbook of the Flora of Ceylon, volume 4. Amerind Publ., New Delhi.

de Alwis, K. A., and G. J. Eriyagama. 1969. Some observations on soil-vegetation relationships in the lowland dry zone of Ceylon. Ceylon Forester 9(1–2): 53–76.

de Rosayro, R. A. 1950. Ecological conceptions and vegetational types with special reference to Ceylon. Tropical Agriculturist 151(1–4): 209–225.

———. 1961. The nature and origin of secondary vegetational communities in Ceylon. Ceylon Forester 5(1–2): 23–49.

Dittus, W. P. J. 1977. The ecology of a semi-evergreen forest community in Sri Lanka. Biotropica 9: 268–286.

———. 1979. The short-term effects of a cyclone on three sympatric primate populations in Sri Lanka. Paper presented at 7th Int. Cong. Primatol., Bangalore, India, January 8–12, 1979.

———. 1985. The influence of leaf-monkeys on their feeding trees in a cyclone disturbed environment. Biotropica, in press.

Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran. 1972. The relation between ecology and social structure in primates. Science 176: 863–874.

Fernando, S. N. N. 1968. The Natural Vegetation of Ceylon. Swabhasha Printers, Colombo, Sri Lanka.

Gaussen, H., P. Legris, M. Viart, and L. Labroue. 1964. International Map of the Vegetation of Ceylon. Special sheet published by the Ceylon Survey Department.

———, ———, ———, and ———. 1965. International Map of the Vegetation of Ceylon, notice de la feuille, de l'Institut Francais de Pondichery, India, Hors Serie No. 5: 1–78.

GANE, M. 1970. Hurricane risk assessment in Fiji. Commonw. For. Rev. 49: 253–256.
GEISER, U., M. SOMMER, AND A. N. S. BAMINIWATTE. 1980. Forest cover mapping and monitoring using satellite images. Sri Lanka Forester 14(3&4): 131–144.
GRELLER, A. M., C. V. S. GUNATILLEKE, I. A. U. N. GUNATILLEKE, AND S. BALASUBRAMANIAM. 1980. A phytosociological analysis of three stands of forest in the vicinity of Peradeniya, Kandy District. Sri Lanka Forester 14(3&4): 153–161.
GRELLER, A. M., AND S. BALASUBRAMANIAM. 1980. A preliminary floristic-climate classification of the forests of Sri Lanka. Sri Lanka Forester 14(3&4): 163–169.
GUNATILLEKE, C. V. S., AND I. A. U. N. GUNATILLEKE. 1980. The floristic composition of Sinharaja—a rain forest in Sri Lanka with special reference to endemics. Sri Lanka Forester 14(3&4): 171–180.
———, AND ———. 1983. A forestry case study of the Sinharaja rainforest in Sri Lanka. *In* L. S. Hamilton (Ed.). Forest and Watershed Development and Conservation in Asia and the Pacific, pp. 289–358. Westview Press, Boulder.
HLADIK, C. M. 1977. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. *In* T. H. Clutton-Brock (Ed.). Primate Ecology, pp. 323–353. Academic Press, London, England.
HLADIK, C. M., AND A. HLADIK. 1972. Disponsibilities alimentaires et domaines vitaux des primates a Ceylan. La Terre et al Vie 26: 149–215.
HOLMES, C. H. 1956. The broad pattern of climate and vegetational distribution in Ceylon. Ceylon Forester 2(4): 209–225.
INDIA METEOROLOGICAL DEPARTMENT. 1979. Track of Storms and Depressions in the Bay of Bengal and the Arabian Sea 1877–1970.
JOACHIM, A. W. 1945. A review of progress in the study of Ceylon soils. Proc. Cey. Assoc. Sci. 1st Ann. Session.
JONES, E. W. 1955. Ecological studies on the rain forest of southern Nigeria, IV. J. Ecol. 43: 564–594.
———. 1956. Ecological studies on the rain forest of southern Nigeria, IV (cont'd). J. Ecol. 44: 83–117.
KENDREW, W. G. 1961. The Climates of the Continents, Fifth Edition, Clarendon Press, Oxford, England.
KOELMEYER, K. O. 1957. Climatic classification and the distribution of vegetation in Ceylon. Ceylon Forester 3(2): 144–163.
———. 1958. Climatic classification and the distribution of vegetation in Ceylon (cont'd). Ceylon Forester 3(3&4): 265–289.
MCCORMACK, R. J., AND A. K. PILLAI. 1961a. A Forest Inventory of the Nuwaragala and Omunagala Reserves and the Ratkarawwa Proposed Reserve, Ceylon. Government Press, Colombo, Sri Lanka.
———, AND ———. 1961b. A Forest Inventory of the Kantalai Forest Reserve, Ceylon. Government Press, Colombo, Sri Lanka.
———, AND ———. 1961c. A Forest Inventory of the Panama Proposed Forest Reserve, Ceylon. Government Press, Colombo, Sri Lanka.
MUELLER-DOMBOIS, D. 1968. Ecogeographic analysis of a climate map of Ceylon with particular reference to vegetation (with map). Ceylon Forester 8(3&4): 1–20.
NICHOLSON, D. I. 1970. Forest management. Technical Report 3. *In* Demonstration and Training in Forest, Forest Ranges, and Watershed Management, the Philippines. F. A. O., Rome, Italy.
OUDSHOORN, W. 1961. A Forest Inventory of the Madhu Forest Area, Ceylon. Government Press, Colombo, Sri Lanka.
PANABOKKE, C. R. 1967. Soils of Ceylon and Fertilizer Use. Metro Printers, Colombo, Sri Lanka.
———. 1975. Soil Map of Sri Lanka. Special sheet printed by the Survey Department of Sri Lanka.
PERERA, N. P. 1975. A physiognomic vegetation map of Sri Lanka (Ceylon). J. Biogeogr. 2: 185–203.
RICHARDS, P. W. 1955. The secondary succession in the tropical rain forest. Sci. Progr. 43(169): 45–57.
SIEGEL, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Book Company, New York, New York, U.S.A.
THAMBYAHPILLAY, G. 1959. Tropical cyclones and the climate of Ceylon. Univ. Ceylon Rev. 17(3&4): 137–180.
VAUGHAN, R. E., AND P. O. WIEHE. 1937. Studies on the vegetation of Mauritius. I. J. Ecol. 25: 301.
WALTER, H. 1971. Ecology of Tropical and Subtropical Vegetation. Van Nostrand-Reinhold, New York, New York, U.S.A.
WEBB, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, north Queensland. Aust. J. Bot. 6: 220–228.
WHITMORE, T. C. 1974. Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands. Commonw. For. Inst., Paper 46.
———. 1975. Tropical Rain Forests of the Far East. Clarendon Press, Oxford, England.
WOOD, T. W. W. 1970. Wind damage in the forest of western Samoa. Malay. Forester 33: 92–99.
WYATT-SMITH, J. 1954. Storm forest in Kelantan. Malay. Forester 17: 5–11.

ERRATUM

A. J. LACK AND P. G. KEVAN, "On the reproductive biology of a canopy tree, *Syzygium syzygioides* (Myrtaceae) in a rain forest in Sulawesi, Indonesia," Biotropica 16: 31–36. The species studies was incorrectly named. It has been redetermined as *Syzygium lineatum* (DC.) Merr. & Perry (syn. *Eugenia longiflora* (Presl.) Vill.), a widely distributed species through Indo-China, Malaya and islands of the Sunda shelf.