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Forest Ecology and Conservation in the Tana River

National Primate Reserve, Kenya

presented by

Kimberly Ellen Medley

has been accepted towards fulfillment of the requirements for

Ph. D. degree in Botany and Plant Pathology

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Riverine forest in the Tana River National Primate Reserve, Kenya.

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FOR

# FOREST ECOLOGY AND CONSERVATION IN THE TANA RIVER NATIONAL

PRIMATE RESERVE, KENYA

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By

Kimberly Ellen Medley

### A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Botany and Plant Pathology

1990



#### ABSTRACT

# FOREST ECOLOGY AND CONSERVATION IN THE TANA RIVER NATIONAL PRIMATE RESERVE, KENYA

By

Kimberly Ellen Medley

The Tana River National Primate Reserve (TRNPR) was established in 1975 to preserve the endemic and endangered red colobus (*Colobus badius rufomitratus*) and crested mangabey (*Cercocebus galeritus galeritus*) and the riverine forest ecosystem. Between 1975 and 1985 the populations of these primates declined to critically low levels. Through a study of current forest ecology I have addressed three primary research questions: (1) do vegetation-based factors explain the recent decline; (2) what are the current status and future status of the Reserve's forest as primate habitat; and (3) which management alternatives would best ensure future preservation?

The research has been directed at the characterization of suitable habitat for the endangered primates, the trends toward the development or loss of suitable habitat, the disturbance factors influencing the current distribution of contrasting habitat, and habitat restoration. Data were collected on forest composition, structure, regeneration, and disturbance within 12 forest areas. Analyses focus on the relationships among these attributes and primate abundance and/or utilization patterns, a comparison among the study areas, and overall characteristics of the riverine forest patches.

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<sup>species</sup> preser <sup>integrity</sup> with The riverine forest mosaic has served as an isolated refuge for plant and animal species adapted to a moist climatic regime. The plant diversity of the ecosystem is demonstrated by the assortment of species from the major floristic regions in Africa and the migration patterns represented by their disjunct occurrences. Downstream, the pattern of river meanders, erosion, and deposition results in the highest diversity of landforms and forest types in the TRNPR vicinity, but regional diversity of the ecosystem is not adequately protected without the inclusion of forests in the Bura and Wema/Hewani regions.

The colobus and mangabey are interior-forest primates, demonstrating a preference for high-stature, closed-canopy forests with high area-to-perimeter ratios and low intraforest disturbance. Forest loss, fragmentation, and consequent reduction in the area-to-perimeter ratio of the remaining forests measured from 1960 and 1975 photos provide a partial explanation for the decline in primate populations. High-quality habitat corresponds to nearly monodominant Pachystela msolo forests or mixed forests with Sorindeia madagascariensis and Diospyros mespiliformis. Ficus sycomorus, a primary food resource, establishes as a pioneer, but persists in association with these forests. Forest regeneration is characterized by an absence of selfreplacement, intraforest heterogeneity attributable to gaps, changing site conditions, and unstable forest communities. Forest restoration would serve to alleviate local disturbances attributed to floodplain dynamics and forest clearing and encourage the establishment of suitable primate habitat. The conservation goal should be to couple species preservation with the preservation of natural ecosystem integrity within this dynamic landscape along the Tana River.

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# Kimberly Ellen Medley

1990

#### DEDICATION

Sr. Agnes Margaret Reinkemeyer, F.S.M. 1923-1989

I will continue upstream now, Perhaps they are being thrown into the river, Until resolved, I shall hope for the strength to pull them out, With love and care, As you did for so many years.

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#### ACKNOWLEDGEMENTS

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It is necessary in any ecological study to acquire information from a number of disciplines and respective sources and this study has been no exception. I thank the staff at the East African Herbarium, especially Mr. Stephen Rucina, for their work on the plant identifications and for the opportunity to work within the herbarium. A warm welcome and assistance were also provided by the staff at the Royal Botanic Gardens, Kew. The in-field assistance provided by botanists Mrs. Ann Robertson and Mr. Quentin Luke was indispensible and

vi

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afforded some of my most exciting days on the Tana. Much of the research design for this study was dependent on concurrent studies on the primates and I am grateful to Barbara Decker, Margaret Kinnaird, Odhiambo Ochiago and Francis Muli for providing census data, and to M. Kinnaird and B. Decker for providing ranging data on the mangabey and colobus, respectively. I thank Katherine Homewood for the afternoons she spent sorting old records and providing 1973-1974 vegetation data for the Mnazini forests, Francine Hughes for three years of helpful comments and also for her vegetation data on the Bura forests, and Clive Marsh for his encouragement and supplemental information. The excellent studies conducted by Homewood (1976), Hughes (1985), and Marsh (1978a, 1986) provided a foundation on which to base this research. Soil analyses were conducted at the Soil Testing Laboratory, Kenya Ministry of Agriculture, and I thank Dr. Boyd Ellis (Crop and Soil Sciences, MSU) for his guidance on the studies of soil salinity and the fertility status of flood deposits. Rainfall data were collected for the Mchelelo area by B. Decker and the Mnazini area by M. Kinnaird. I thank the staff at the the Irrigation Board in Hola and the Kenya Meterological and Hydrological Departments for access to and assistance with rainfall and river discharge data, and Mr. Alexander Njue for helping with the data collection. Ms. Joyce Jefferies, East African Herbarium, Plant Propagation Section, completed the mycorrhizae studies and A. Robertson provided many helpful hints on the propagation of tree seedlings. Dr. Hugh Lamprey, World Wildlife Fund, broadened my perspective tremendously by providing a flight over the Tana. Finally, this project would have been impossible without the field assistance, training, and hospitality provided by the Pokomo.

vii

Most impor each day o dissertati At M Botany and assistant hard-to-sp department given to t National F project an doctoral c Campbell, design, pi perspectiv served as of Fisher: thanks and <sup>stud</sup>ies, 1 my academ I va grateful : Most importantly, I thank Mr. Bakari Mohammed Garise for his assistance each day on the field data collection incorporated into this dissertation.

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I was never really alone in this project and will be forever grateful for the companionship, advice, assistance, and encouragement.

viii

CHAPTER LIS LIS I. CEN II. SIT III. EX Ir Da Re

#### TABLE OF CONTENTS

Page
LIST OF TABLES
LIST OF FIGURES
I. GENERAL INTRODUCTION
Study Design and Rationale
II. SITE DESCRIPTION AND A COMPARATIVE REVIEW OF FOREST FLORA, RESOURCE DIVERSITY AND ECOLOGY
Site Description11Climate13Hydrology and Fluvial Geomorphology14Human Land Utilization18The Forest Mosaic20Forest Flora and Phytogeographical Relationships22Resource Diversity27Ecological Description32Data and Methods32Tropical Forest Comparisons33Regional Comparisons36Local Forest Heterogeneity40Summary of Ecosystem Characteristics and Significance44
III. EXAMINATION OF PRIMATE-TO-HABITAT RELATIONSHIPS 47
Introduction
Data and Methods50Data Acquisition50Correlation Analyses51Discrimination of Intraforest Primate UtilizationPatterns55Compositional Characteristics of High Utilization Plots
Results and Discussion58Correlation Analyses58Discrimination of Intraforest Primate UtilizationPatterns65Descriptive Summary of High-Utilization Areas72Model of High Quality Habitat73

Chapter
I. A
In
D.a.
Re
Co
V. FC
In
Da
Re
Su
VI. FOR

#### Chapter

V.

VI.

# 79 Tree-Species Replacement and Forest Succession . . . . 84 Forest Regeneration Near Three Canopy Tree Species . . . 87 Tree-Species Selection and Classification . . . . 87 88 Statistical Examination of Group Contrasts . . . . 89 Forest Regeneration Near Three Canopy Tree Species . . . 111 Statistical Examination of Group Contrasts . . . 112 126 130 Temporal Comparisons of Forest Composition and

Page

	Project Objectives	•	•	•			•	•		•	•	•	•	•	•	•		•		•	166
•	Project Design	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	167

Chapter

VI. Continued Site

Plan

Disc

VII. CONCLUDI:

APPENDICE

A. B. C. D. E. F. G. H.

LIST OF

# Chapter

VI.	Continued	
	Site Selection	8
	Habitat Expansion Along a Forest Edge	8
	Corridor Establishment	2
	Plant Species Selection	7
	Nursery Propagation of Plant Species	7
	Tree Growth	8
	Discussion	3
VII.	CONCLUDING DISCUSSION	6
	APPENDICES	3
	A. Checklist of the Woody Forest Flora	3
	B. Local Pokomo Plant Names and Uses	1
	C. Forest Area Summaries	1
	D. Association Analysis Chi Square Results	4
	E. Detailed Summary of Significant MANOVA Results 21	5
	F. Forest Temporal Comparisons	6
	G. Ecological Attributes of Three Forest Corridors 21	9
	H. Nursery Propagation of Tree Seedlings 22	2
	LIST OF REFERENCES	4

Table

- 1. Forest st
- 2. Geographi
- 3. Rare plar
- Comparati character
- The Tana the five layers. on relat density IV = 1) elatior from the
- Communicoverag include Kitere (bsb), (cw), C South ( is calc abundar of lowe occurritic
- Comparivalues of rela cm dbh) The for similar the cal 1984).
- 8. Forest and the

#### LIST OF TABLES

Table		Page	1
1.	Forest study areas	• •	7
2.	Geographic affinities of the woody flora	. 2	5
3.	Rare plant occurrences	. 2	8
4.	Comparative review of tropical forest ecological characteristics	3	4
5.	The Tana River forests. A regional comparison based on the five most important tree species at four structural layers. Importance values, in parentheses, are based on relative coverages (TRNPR canopy trees), or relative density (all others), and may range from $0 - 1$ (maximum IV - 1) Barringtonia racemosa (L.) Blume, Acacia elatior Brenan, and Cadaba farinosa Forsk. are absent from the woody flora of the TRNPR (see Appendix A)	. 3	38
6.	Community similarity comparisons based on the relative coverages of canopy trees (> 20 cm). Sampled forests include: Mnazini South (ms), Mnazini North (mn), Kitere West (kw), Baomo South a (bsa), Baomo South b (bsb), Baomo North (bn), Sifa West (sw), Congolani West (cw), Congolani Central (cc), Mchelelo West (mw), Guru South (gs), and Guru north (gn). Community similarity is calculated as a percent based on the relative abundances of co-occurring species (% similarity - sum of lower relative abundance percentages for all co-		
7.	occurring species) (Brower and Zar, 1984) Comparisons among forests within the TRNPR. Importance values are given in parentheses and represent the sum of relative density and coverage for canopy trees (> 20 cm dbh). Values may range from 0 - 2 (maximum IV - 2). The forests are listed in order of decreasing similarity from Mnazini North (left to right) based on the calculation of percent similarity (Brower and Zar, 1984)	4	43
8.	Forest attributes examined in the correlation analyses and the hypothesized relationships	. 5	52

		Tabl	.e
		9.	The most percent i
		10.	Spearman characte
		11.	Mean spec tree spec Abundanc recorded abundanc palms > individu
		:2.	Importan plant sp 3 m in h Species frequenc seven ex identifi
		13.	Descript examinat sycomore madagase attribu varianc
		14.	Canopy- Palm sp layers: Points Species asteris
		15.	Basal a seven c (m2/ha) samplir derivec (variar each tr areas: overdis underd:

Tab	le
-----	----

9.	The most important primate food items and measures of percent utilization by the colobus and mangabey	54
10.	Spearman correlations between primate population characteristics and selected forest attributes	59
11.	Mean species abundances, by habitat rank, for the 24 tree species used in the canonical variate analysis. Abundances for the canopy trees (> 20 cm dbh) are recorded as basal area coverages $(m^2/ha)$ , and abundances for the subcanopy trees $(10 - 20 \text{ cm dbh}, \text{ and}$ palms > 1 m in height) are recorded as densities (# individuals/ha).	66
12.	Importance values and plot occurrences for the woody plant species (trees and vines > 10 cm dbh, and palms > 3 m in height) within the seven high utilization plots. Species importances are based on the sums of relative frequency, density, and coverage (total = 3.00) for the seven examined plots. Primate food items are identified with an asterisk	74
13.	Description of the variables used in the statistical examination of population differences among Ficus sycomorus, Pachystela msolo, and Sorindeia madagascariensis. Compositional, resource, and site attributes used in the multivariate analyses of variance are identified with an asterisk	90
14.	Canopy-tree point occurrences at four structural layers. Palm species were only recorded at three structural layers: canopy, subcanopy, and seedling. The number of points are determined from records taken at 363 points. Species with low replacement are identified with an asterisk (*)	93
15.	Basal area coverages and dispersion patterns of the seven canopy-tree forest dominants. Basal coverages $(m^2/ha)$ are depicted as a mean derived from all sampling points $(n = 363)$ , or, in parentheses, a mean derived from the 12 forest summaries. Dispersion (variance-to-mean ratio) is presented as a measure of each tree species' distribution among the 12 forest areas: random $(s^2/x = 1)$ , uniform $(s^2/x < 1)$ ; overdispersed), and clustered $(s^2/x > 1)$ ; underdispersed) (Brower and Zar, 1984).	100

- Table
- Spearman the fores of correst correlate (euclidea
- Statistic Ficus syc madagasca tree vig statisti Variable
- 18. Results (MANOVA) discrimi probabil defined
- Summary measure human c listed describ
- 20. Compari 1988 fi Nationa and exa collect complet Agricul Agricul
- 21. Basal and that are Pokomo basal a
- 22. Basal a large m
- 23. Site ch the stu

Ta	b]	Le
----	----	----

16.	Spearman correlations depicting the relationships among the forest layers. Each coefficient reflects the degree of correspondence between species abundances at the correlated forest layers based on dissimiliarities (euclidean distances) among the 12 forest areas 106
17.	Statistical examination of population differences among Ficus sycomorus, Pachystela msolo, and Sorindeia madagascariensis, and intraspecies differences based on tree vigor. Listed are the calculated Kruskal Wallis statistics (H), and associated probabilities (prob.). Variable descriptions are provided in Table 13 115
18.	Results from the multivariate analysis of variance (MANOVA), depicting the calculated Wilk's lambda (the discriminating power of the variable group) and its probability. Variables used in the analyses are defined in Table 13
19.	Summary of forest areas, area-to-perimeter ratios, and measured area losses attributed to river erosion and human clearing within the study areas. Forest codes listed in parentheses reference the 12 study areas described in Table 1
20.	Comparison of soil fertility among surface soils and 1988 flood deposits collected within the Tana River National Primate Reserve. Surface soils were collected and examined by Hughes (1985). The flood deposits were collected in this study and soil analyses were completed at the Soil Testing Laboratory, National Agricultural Laboratories, Kenya Ministry of Agriculture (N.A.L.)
21.	Basal area coverages and growth characteristics of trees that are most highly utilized for poles by the local Pokomo population. Utilization is based on the total basal area coverage of wood that is cut
22.	Basal area coverages of trees that are most damaged by large mammals
23.	Site characteristics and sample sizes for trees used in the study of tree-growth patterns

#### LIST OF FIGURES

Figur	e		F	'age
1.	The Tana River basin	•••		12
2.	Monthly precipitation. a. Mean monthly precipitation received at representative locations for the Tana River basin (Muchena, 1987; FAO, 1984). Embu is located near Mt. Kenya, Hola is approximately 35 km north of the TRNPR, and the other localities are identified on Figure 1. b. Monthly precipitation received during the field research at the Mchelelo Research Camp and near Mnazini within the TRNPR (Tana River Primate Project Data collected by B. Decker and M. Kinnaird, respectively).		•	15
3.	The study area located in the south-central sector, TRNPR. The inset depicts the Reserve boundary and riverine forest (shaded)		•	21
4.	Food coverages and primate group abundances in the 12 forest areas: Congolani West (cw), Sifa West (sw), Baomo North (bn), Guru North (gn), Mnazini South (ms), Baomo South b (bsb), Baomo South a (bsa), Kitere West (kw), Mchelelo West (mw), Guru South (gs), Mnazini North (mn), and Congolani Central (cc). a. Scattergram depicting the relationship between primate group abundance and the coverage of highly utilized primate resources. b. Coverage of highly utilized food items in each forest. The number of primate groups occurring in each forest is indicated above the bars.			61
5.	Forest disturbance in the 12 forest areas: Congolani West (cw), Sifa West (sw), Baomo North (bn), Guru North (gn), Mnazini South (ms), Baomo South b (bsb), Baomo South a (bsa), Kitere West (kw), Mchelelo West (mw), Guru South (gs), Mnazini North (mn), and Congolani Central (cc). Forest disturbance is depicted as a summed measure of the basal area coverage of wood that is dead (forest senescence), cut (human forest utilization), and damaged by large mammals (animal impact). The number of primate groups occurring in each forest area is indicated above the bars.			63

## Figure

p	•	~	~	
<b>_</b>	a	ĸ	e	

6.	Canonical variate analysis using 24 canopy and subcanopy trees (see Table 11). The graph depicts the distribution (or discrimination) of a random selection of points based on the extraction of two canonical variates. Group centroids determined from all points are identified for the low, medium, and high utilization classes
7.	Correlations between the variables (tree species) and the two canonical variates. The canopy and subcanopy tree species are listed in Table 11. The highly utilized primate food resources are identified in the graph depicting the correlations to the first canonical variate
8.	Canonical variate analysis using four forest attributes: mean canopy height (meanht), the distance between tree crowns (crndist), and the abundance (density) of the palm <i>Phoenix reclinata</i> . a. Graph depicting the distribution (or discrimination) of a random selection of points based on the extraction of two canonical variates. Group centroids determined from all points are identified for the low, medium, and high utilization classes. b. Correlations between the variables (forest attributes) and the two canonical
9.	<pre>variates</pre>
	utilization plots. Importance is based on relative measures of frequency, density and coverage (maximum IV - 3). Codes refer to species names listed in Table 12 75
10.	Total canopy-tree abundances at four forest layers. Frequencies equal the number of points at which the trees occur (total = 363). Density values (#
11.	Frequencies of seven important canopy-tree species at the seedling (sdl), sapling (sap), subcanopy (sct), and canopy-tree (ct) forest layers. Frequencies equal the number of points at which the species occur (total - 363 points). Seedlings of Sorindeia madagascariensis and Garcinia livingstonei were present at 134 and 135 points, respectively
12.	Densities of seven important canopy-tree species at four forest layers. Densities (# individuals/ha) are
	log-transformed

#### Figure

15.

Figu	re	F	age
13.	Relative densities of Ficus sycomorus (Fs), Pachystela msolo (Pm), Sorindeia madagascariensis (Sm), Diospyros mespiliformis (Dm), Garcinia livingstonei (Gl), Mimusops fruticosa (Mf), and Acacia robusta (Ar) at the canopy and sapling forest layers		99
14.	Graphs depicting the associations between the size classes of selected canopy-tree species and the canopy size-class of Pachystela msolo, Sorindeia madagascariensis, Mimusops fruticosa, Diospyros mespiliformis, Garcinia livingstonei, Ficus sycomorus, and Acacia robusta, respectively. Positive correlations indicate invasion (in the lower size classes), or co-association, while negative correlations indicate non-association		102
	A model of riverine forest succession in the TRNPR. Species are identified as invaders, decliners, or associates depending on the size-class correlations (or chi-square associations; see Appendix D). Correlations to the canopy-tree forest dominants (in the boxes) are indicated as significant (), or nonsignificant (***). The boxes represent separate stages, the distance between the boxes suggest spatial (or temporal) separation between the stages, and the curved dashed lines represent spatial co-occurrences among the communities within a forest patch		108
16.	Subsurface soil texture of the regeneration study plots. The symbols correspond to the vigor classes: young $\bigcirc$ ; mature and vigorous $\bigstar$ ; senescent $\blacktriangle$ ; and dead $\blacksquare$		113
17.	Box plots depicting the range of variation in selected compositional, resource, and site attributes among <i>Ficus sycomorus, Sorindeia madagascariensis, Pachystela</i> <i>msolo</i> , and their vigor states. The box represents the first quartiles from the median, the vertical line in the box represents the median, the horizontal lines extending from the box depict the range, and outliers are shown with an asterisk. The vigor states include: <i>Ficus</i> young (FY), mature (FOK), and senescent (FO); <i>Sorindeia</i> mature (SOK) and senescent (SO); <i>Pachystela</i> mature (POK), senescent (PO), and dead (PD)	116	õ

Figure 18. Map ov change sector inclus West Sifa Baome (mn) 19. Tana stat Depa Disc (cui 20. Mea sam (ms a ( Wes Mot (g: Co Fo al 21. So an 22. So an co Th m no 23. Si w: Sc Cc Ba (k In st <sup>24</sup>. Sc, ar Con Mar are

## Figure

<ol> <li>Tana River discharge measured daily at the Garissa station gauge. Data obtained from the Hydrology Department, Kenya Ministry of Water Development. Discharge is measured in cubic meters per second (cumecs)</li></ol>	18.	Map overlay depicting forest and river position changes between 1960 and 1975 in the south-central sector of the TRNPR. The forest areas of this study include: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms)
<ol> <li>Mean flood heights and the range determined from the sampling points in the 12 forest areas: Mnazini South (ms), Mnazini North (mn), Kitere West (kw), Baomo South a (bsa), Baomo South b (bsb), Baomo North (bn), Sifa West (sw), Congolani West (cw), Congolani Central (cc), Mchelelo West (mw), Guru South (gs), and Guru North (gn). No floodwater was recorded within the Sifa West, Congolani West, Mchelelo West, and Guru South forests. Forest area locations are presented in Figure 18 (see also Table 1; Figure 3)</li></ol>	19.	Tana River discharge measured daily at the Garissa station gauge. Data obtained from the Hydrology Department, Kenya Ministry of Water Development. Discharge is measured in cubic meters per second (cumecs)
<ul> <li>21. Soil cations measured in surface soils (Hughes, 1985) and 1988 flood deposits collected within the TRNPR 140</li> <li>22. Scattergram depicting the relationship between the basal area coverages of cut wood and total basal area coverages for the most highly utilized tree species. The tree species are listed in Table 21. Polysphaeria multiflora, the most highly utilized tree species, is not shown on the scattergram</li></ul>	20.	Mean flood heights and the range determined from the sampling points in the 12 forest areas: Mnazini South (ms), Mnazini North (mn), Kitere West (kw), Baomo South a (bsa), Baomo South b (bsb), Baomo North (bn), Sifa West (sw), Congolani West (cw), Congolani Central (cc), Mchelelo West (mw), Guru South (gs), and Guru North (gn). No floodwater was recorded within the Sifa West, Congolani West, Mchelelo West, and Guru South forests. Forest area locations are presented in Figure 18 (see
<ul> <li>and 1988 flood deposits collected within the TRNPR 140</li> <li>22. Scattergram depicting the relationship between the basal area coverages of cut wood and total basal area coverages for the most highly utilized tree species. The tree species are listed in Table 21. Polysphaeria multiflora, the most highly utilized tree species, is not shown on the scattergram</li></ul>	21.	Soil cations measured in surface soils (Hughes, 1985)
<ol> <li>Scattergram depicting the relationship between the basal area coverages of cut wood and total basal area coverages for the most highly utilized tree species. The tree species are listed in Table 21. Polysphaeria multiflora, the most highly utilized tree species, is not shown on the scattergram</li></ol>		and 1988 flood deposits collected within the TRNPR 140
<ul> <li>23. Spatial distribution of human forest utilization impact within the 12 forest areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Impact is measured as the basal area coverage of cut stems within the sampling plots</li></ul>	22.	Scattergram depicting the relationship between the basal area coverages of cut wood and total basal area coverages for the most highly utilized tree species. The tree species are listed in Table 21. Polysphaeria multiflora, the most highly utilized tree species, is not shown on the scattergram
<ul> <li>24. Scattergram depicting the relationships between the basal area coverages of damaged wood and total basal area coverages for the trees most heavily impacted by large mammals (e.g., elephant, buffalo). The tree species are listed in Table 22</li></ul>	23.	Spatial distribution of human forest utilization impact within the 12 forest areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Impact is measured as the basal area coverage of cut stems within the compliant plots
24. Scattergram depicting the relationships between the basal area coverages of damaged wood and total basal area coverages for the trees most heavily impacted by large mammals (e.g., elephant, buffalo). The tree species are listed in Table 22	<i></i>	stems within the sampling plots
are listed in Table 22	24.	Scattergram depicting the relationships between the basal area coverages of damaged wood and total basal area coverages for the trees most heavily impacted by large
		are listed in Table 22
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25.	Spatial distribution of forest senescence within the 12 forest areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Forest senescence is measured as the basal area coverage of wood that is dead within the sampling plots
26.	Map depicting the plot occurrences of Mimusops fruticosa, Garcinia livingstonei, Sorindeia madagascariensis or Diospyros mespiliformis, Ficus sycomorus, and Pachystela msolo within the forest study areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Co-occurrences are shown for all species except Pachystela msolo 169
27.	Spatial distribution of primate resources present as saplings within the 12 forest areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Primate resources include species that are highly utilized as food items by the colobus and mangabeys (see Table 9)
28.	Forest resources recorded as canopy trees (> 10 m height) and saplings (3 - 10 m in height) in three corridors. Forest resources include species that are highly utilized as food items by the endangered primates (see Table 9), or associates that are present within the high utilization plots (see Table 12). Palm species are included in the measure of canopy trees and saplings
29.	Tree-growth patterns in six forest tree species: Acacia robusta subsp. usambarensis (Ar), Ficus sycomorus (Fs), Populus ilicifolia (Pi), Alangium salviifolium (As), Diospyros mespiliformis (Dm), and Sorindeia madagascariensis (Sm). Table 23 lists the samples used in the calculation of the mean growth rates

#### CHAPTER I

#### GENERAL INTRODUCTION

The Tana River National Primate Reserve (TRNPR) was established in 1975 to preserve the best remaining riverine forest along the Tana River and the primary populations of the endangered Tana River red colobus (Colobus badius rufomitratus) and crested mangabey (Cercocebus galeritus galeritus) (Marsh, 1976). The Reserve is one of the smallest in East Africa (171  $\text{km}^2$ ), and the forest area, which occurs as patches near the river, is much smaller (9.5  $\text{km}^2$  in ~26 patches). North of the Reserve the decrease in available moisture and distance from the coastal floristic element explain the loss of important canopy tree species and a general decline in forest structure. This natural decline, coupled with the development of the Bura Irrigation Scheme (in 1978) and the earlier Hola Irrigation Scheme, suggests that these more northern areas will never attain the diversity and structure of the riverine forests found within the Reserve (Hughes, 1987; Ledec, 1987). South of the Reserve the best development of riverine forest is in the Wema/Hewani area. It was in this area that the first ecological surveys within the floodplain forest were conducted (Andrews et al., 1975) and where Oxystigma msoo (J.B. Gillet 19933), a very large and potentially valuable timber species, was first discovered in Kenya. The Wema/Hewani area is just upriver from the delta and has a somewhat different floristic composition that is rich in coastal species. Currently these forests

are adjacent to the Tana River Delta Rice Irrigation Scheme. It may be possible to maintain the forests through the implementation of this major development project, but management toward forest expansion seems unlikely (Medley et al., 1989). The pressure on the riverine forests has increased at a remarkable rate since the creation of the Tana River National Primate Reserve. It is likely that in the near future the forests within the Reserve will be the only representative of this diverse ecosystem along the Tana River. Prior surveys have indicated that the riverine forests along the Tana River are the only true representatives of this habitat type in East Africa. Recommendations were made for their inclusion in UNESCO's Man and the Biosphere Program for the conservation of representative and unique ecosystems (Marsh, 1976). Riverine tropical forest, obtaining canopy heights to 35 m in an otherwise arid thorn-scrub environment, is among the rarest ecosystems in the world.

The isolated mosaic of forests along the river is the only habitat for the Tana River red colobus and crested mangabey. Their geographical range extends approximately 60 kilometers along the river between the towns of Wenje and Garsen (Groves et al., 1974; Wolfheim, 1983). Both endemic primates are subspecies of more widely distributed rain forest primates. *Cercocebus galeritus galeritus* is separated from its two Central African relatives by approximately 1500 km and its recently discovered South Tanzanian relative by nearly 800 km (Homewood, 1975; Homewood and Rodgers, 1981; Wolfheim, 1983). Its population prior to the establishment of the TRNPR in 1975, estimated at 900-2900 individuals in less than 2000 ha, was in a precarious position and

clearly "endangered" (Wolfheim, 1983). In contrast to the four existing subspecies of mangabeys, the red colobus monkeys (Colobus badius) are a large group of approximately 20 subspecies that have a distribution in Central Africa, West Africa, and Zanzibar Island. Although not as taxonomically unique as the mangabey, in view of its 1973 population estimated at 1500-2000, its restricted range, and its fragmented habitat the colobus was also considered endangered (Marsh and Homewood, 1975; Marsh, 1978b; Wolfheim, 1983). From a global perspective, both primates were ranked among the most endangered in the world (Mittermeier, 1984). In the "Action Plan for African Primate Conservation: 1986-1990", published by the IUCN/SSC Primate Specialist Group, the red colobus and crested mangabey populations along the Tana were rated as vulnerable and high priority for conservation, respectively (Oates, 1985). The evaluation is based on the relative degree of threat on their populations due to habitat fragmentation, their taxonomic uniqueness, and their co-association within this isolated region. Moreover, reserve development and management projects directed at primate conservation were considered high priority in the region. The importance of establishing a research station and continued investigations on the primates and their habitat were emphasized. Upon the establishment of the Reserve the uniqueness of this riverine forest ecosystem, the rarity of the two endangered primates, the threats imposed by habitat loss, and the consequent conservation concerns were clearly established.

Prior research conducted on the red colobus (Marsh, 1978a) and the crested mangabey (Homewood, 1976) provided baseline information from which to monitor population changes. A resurvey conducted in 1985, ten

years after the establishment of the Reserve, revealed an 80% decline in the red colobus (from 1200-1800 in 1975 to 200-300 individuals in 1985) and a 25% decline in the crested mangabey populations (from 1100-1500 in 1975 to 800-1100 individuals in 1985) (Marsh, 1986; Decker and Kinnaird, submitted). The populations of these two primates had crashed and it was suggested that their population reductions may be attributed to a corresponding decline in forest habitat (Marsh, 1986). In response to the survey results, and according to the IUCN/SSC Action Plan (Oates, 1985), a collaborative project was designed and supported by the National Museums of Kenya, the Kenya Wildlife and Management Department, Wildlife Conservation International (New York Zoological Society), and the World Wildlife Fund. Studies were funded that address the behavior and ecology of the two endangered primates, forest soils and hydrology especially as they relate to forest development and agricultural practices, and my own study on forest ecology. The results from our studies will be incorporated into a new management plan that will encourage the preservation of the two endangered primates and their forest habitat.

## Study Design and Rationale

In view of the primate population decline my primary research questions include: (1) do vegetation-based factors explain the recent decline; (2) what are the current status and future status of the Reserve's forests as primate habitat; and (3) which management alternatives would best ensure future preservation? Each of these questions, especially the first, demands an understanding of temporal forest change and primate behavioral adaptation through the ten-year

period (1975-1985). Behavioral and census data are not available for the primates during the ten years of their decline, and insufficient data exist on the vegetation from earlier studies to adequately examine temporal change. Consequently, the determination of causal factors and direct solutions is not a feasible approach. On the contrary, the questions have been addressed indirectly through three primary areas of research on the current forest ecology. First, I have focused on a study of forest habitat quality. determining which forest ecological attributes are most related to the current distribution of colobus and mangabeys in the Reserve. Secondly, I have examined the patterns of tree-species replacement and overall riverine forest succession, focusing especially on the natural regeneration or loss of suitable primate habitat. Third, I have addressed forest condition, obtaining a measure of certain regional and local impacts on the forests as they contribute toward an understanding of the disturbance regime. The research has been directed at the characterization of suitable habitat for the endangered primates, the trends toward the development or loss of suitable habitat, and the factors influencing the current distribution of different habitats. It is a study aimed primarily at understanding natural forest composition, structure, and dynamics as they are related to the habitat requirements of two endangered primates. The results from this investigation are thereby directly applicable to the designation of management recommendations that encourage preservation of the primates within the TRNPR.

Therefore, the past and current studies on the colobus and mangabeys and related data on their population sizes have been critical to the study design. Twelve forest areas were selected that are representative of the variation in forest types and for which census data were available on the endangered primates (Table 1). The data analyses have focused on the examination of plant-species abundances and the compilation of composite variables representative of certain forest attributes. These composite variables may be characterized as structural (e.g., canopy height, distance between tree crowns, and basal area coverages), resource (e.g., summed densities or basal area coverages of primary food items), and spatial (e.g., forest area, areato-perimeter ratios, and spatial heterogeneity) attributes. Most data analyses have reduced the complexity of the species-abundance data by restricting examinations to woody plant species. The colobus diet is almost entirely restricted to the leaves, flowers, fruits, and buds of trees not less than 10 m in height (Struhsaker, 1975; Marsh, 1981a; Decker, 1989). Mangabeys, however, have a much more diverse diet that includes grasses, forbs, and herbaceous vines. Nevertheless, their primary food resources remained within the species examined (Homewood, 1976). The emphasis throughout this study has been on the flora and on forest composition, structure, and dynamics. As part of the collaborative Tana River Project, it will be combined with an ecological study more directed at physical site characteristics (Njue, 1987) and should compliment the studies on the behavioral ecology of the two endangered primates (Marsh, 1978a; Homewood, 1976; Decker, 1989; Kinnaird, 1988).

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Table 1. Forest study areas.

	Primate Populations <sup>1</sup>					
	Forest	Cold	obus	Mangabey		
Forest Area	Area (ha) <sup>2</sup>	1975	1988	1975	1988	Forest Characteristics
Mnazini South (ms)	50.1	3	1(13)	2	1(9)	<u>Mimusops</u> - <u>Garcinia;</u> forest decline, and forest loss due to flooding and fire; Homewood (1976) study site.
Mnazini North (mn)	36.2	3	2(25)	2	2(16)	<u>Pachystela-Ficus</u> dominant; mangabey study area
Kitere West (kw)	18.3	2	1(5)	0	1(17)	Pachystela-mixed; colobus absence between 1985-1987
Baomo South A (bsa)			2(23)		1(16)	<u>Pachystela-Ficus</u> , disturbed lodge site; <u>Pachystela</u> tree death; colobus study site
	122.8	6-8		5-6		
Baomo South B (bsb)			2(22)		1(13)	<u>Pachystela</u> - <u>Sorindeia</u> ; human encroachment southwest
Baomo North (bn)	16.4	2-3	0	1-2	1(25)	Ficus-Pachystela; absence of colobus; forest clearing south-southeast
Sifa West (sw)	2.8	1	0	1	0	<u>Sorindeia-Hyphaene;</u> absence of both primates
Congolani West (cw)	37.2	1	0	1	0	<u>Mimusops-Acacia</u> rouvumae; absence of both primates
Congolani Central (cc)	) 52.4	3-4	2(21)	2	2	<u>Hyphaene</u> -mixed; high primate utilization
Mchelelo West (mw)	16.8	2	1(12)	2	2(45)	<u>Hyphaene-Sorindeia-Diospyros;</u> high primate utilization; primate study site
Guru South (gs)	46	6-8	1(11)	3-4	2	Mixed; most drastic primate declines
Guru North (gn)	4.9	*	1(5)	*	0	<u>Ficus</u> -mixed; smallest forest with colobus

<sup>1</sup>Primate populations are presented as group counts and the estimated number of individuals (in parentheses) (Marsh 1986; Decker and Kinnaird, submitted; Tana River Project unpublished data).

 $^2$  Forest Areas have been estimated from 1975 aerial photos.

Prospectus

The research methods, results, and discussion have been divided into five chapters (Chapters 2-6). Although each is designed to serve as an independent area of investigation, the definition of the overall research problem and study area description are confined to the general introduction (Chapter 1) and Chapter 2, respectively. In addition the second chapter summarizes the ecological significance of the riverine forests protected within the TRNPR through an examination of their floristic, resource, and community diversity. The third chapter examines the relationships between selected forest attributes and the endangered primate populations. My objectives are to determine the characteristics of high-quality habitat and factors that may negatively influence primate populations. Chapter 4 addresses the study of natural forest dynamics, looking first at tree-species abundances at four structural layers (seedling, sapling, subcanopy, and canopy) and their inter-associations, and then specifically at the regeneration patterns near three canopy-tree species. It is a qualitative approach with the objective of determining a general model of forest succession, and then to further characterize the model through a space-for-time substitution (cf. Pickett, 1989. From this basis trends toward the development or decline of high-quality primate habitat are better understood. Chapter 5 applies the results obtained from the study of primate-to-habitat relationships and forest regeneration to a spatial evaluation of forest condition, especially as it is influenced by the disturbance regime characterizing the floodplain landscape. Chapter 6 incorporates the results of all preceding sections into a proposal for forest restoration as a stewardship consideration within the TRNPR. A

concluding discussion (Chapter 7) summarizes the contributions of this research project as they address the original research questions and are related to the ecology and conservation of the riverine forest ecosystem protected within the Tana River National Primate Reserve, Kenya.

## CHAPTER II

## SITE DESCRIPTION AND A COMPARATIVE REVIEW OF THE FOREST FLORA, RESOURCE DIVERSITY, AND ECOLOGY

The rarity and taxonomic uniqueness of the Tana River red colobus and crested mangabey may be partially explained by the geographic isolation this forest community has from the rain forests of Central Africa and the Coast and its current distribution as forest patches. One would expect that the impacts of isolation and current patchiness would be equally apparent in the existing vegetation characteristics. Aside from general studies conducted on food resources and selected tree phenology in the primate study areas (Homewood, 1976; Marsh, 1978a) and a broad ecological study on the impacts of the Bura Irrigation Scheme (Hughes, 1985), no floristic and/or ecological investigations have been conducted on the forest vegetation protected in the TRNPR. During a year of field research and secondary data collection at herbaria and governmental agencies, I completed an inventory of the forest flora, obtained a measure of its botanical resources, and compiled a site and ecological characterization of the ecosystem. A comparative review of the information is used to differentiate this riverine forest ecosystem from other tropical forests and to emphasize its ecological significance. In sum, the occurrence of two very rare primates and their recent population declines have served as indicators of an equally rare forest community existing in a threatened and unpredictable environment. In situ

preservation of the endangered primates must rely on the preservation of their rare habitat (McNeeley et al., 1989). Final management recommendations should be derived from a clear understanding of the ecosystem. This chapter will begin to define the ecosystem by presenting a description of its physical site characteristics, floristic composition, resource diversity, and overall ecological characteristics.

## Site Description

The TRNPR is located in Eastern Kenya along the floodplain section of the Tana River (Figure 1). The Tana is the largest river in Kenya and flows in a wide arc, receiving nearly all its inputs from the highlands near Mt. Kenya and the Abedare mountain range and downcutting from these highlands to as far as Kora Rapids. The river then flows as a meandering stream with an associated floodplain until it meets the delta at Garsen, and proceeds to the Indian Ocean between the towns of Malindi and Lamu. Similar to the Nile, Niger, and Colorado river systems, the Tana is an allochthonous (nonindigenous, exotic) river. These rivers arise in humid regions, or in areas of snow and ice, and flow into dry areas. As the river flows through the arid regime, tributaries decrease or become nonexistent, water is lost in evaporation and soil infiltration, and in essence, the river loses volume and force (Czaya, 1981). Not only is the river exotic to the region, but the vegetation may also be exotic. The narrow corridor of evergreen-semievergreen forest along the Tana is strictly dependent on the presence of this perennial stream. Consequently, the composition,



Figure 1. The Tana River basin.

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structure, and dynamics of the "riverine" or "floodplain" forest are dictated by the hydrological characteristics and dynamics of the river system.

<u>Climate</u>. The Tana is an equatorial river beginning in proximity to the equator and entering the Indian Ocean at less than 4° S. Temperatures are consistently warm. The minimum and maximum temperatures average 23° and 34°C at Garissa (Müller, 1982), 21.4° and 33°C at Hola (Muchena, 1987), and 22.7° and 30.1°C at Malindi (FAO, 1984). During the study period, the temperatures at the research station ranged between 19° and 37°C. In overview, the temperature differences are slight, have little effect on the distribution of the flora (Livingstone, 1975), and the slightly warmer temperatures upstream reflect an upstream decline in precipitation and cloud cover.

In contrast to a humid equatorial climate, East Africa along the equator is anomalously dry (Livingstone, 1975). The lower Tana is located along the western margin of the gigantic seasonal flow of monsoon winds off the Asiatic continent (Trewartha, 1981; Edwards et al., 1983). When the sun is north of the equator (April to October) a southerly flow prevails (Southeast monsoon), and when the sun is south of the equator (October to March) a northerly flow prevails (Northeast monsoon). Along the equator the coriolis force is weak and, when combined with other atmospheric influences, results in the westerly winds rising and generating rain and the easterly winds sinking and producing dry weather (Livingstone, 1975). Only right along the coast is abundant precipitation generated from the monsoonal winds. Therefore, the highlands receive high rainfall from the rising westerly winds carrying moisture from Lake Victoria (Kaplan, 1983) while a large

portion of the lower Tana receives low precipitation from the northeast and southeast monsoons. Precipitation is bimodal along the Tana, averaging 1000 mm in the highlands, as low as 300 mm on the upper floodplain, and above 1000 mm at the coast (Figure 2a). At Hola, the nearest station to the Reserve, long-term climatic records depict an annual average precipitation equal to 470 mm, no months with greater than 100 mm precipitation, an average of 326 dry days, and a growing season of 40 days occurring coincident to the short rains (October -December) (FAO, 1984). The life zone is thorn-woodland (Holdridge, 1967). The riverine forest community is dependent on the groundwater supply provided by the river, and its lateral extent is dictated sharply by the declining water-table gradient from the river (Hughes, 1988).

Although local precipitation is not a contributing factor to the persistence of riverine forest along the Tana, it may be partially responsible for tree establishment and early forest development. This would be particularly true during nonflooding years when all surface soil moisture is dependent on precipitation. Monthly total precipitation for the Mchelelo and Mnazini study areas demonstrates the contrasts that occur within a small area (Figure 2b). Although the higher precipitation at Mnazini may be partially explained by its location 10 km downstream, it also reflects a randomness in the rainfall events that occur in a very small area. The floodplain section of the Tana River is characterized by a gradient upstream toward lower precipitation and an unpredictability in the temporal and spatial distribution of rainfall events that is typical of the semiarid regime (Edwards et al., 1983).





Figure 2. Monthly precipitation. a. Mean monthly precipitation received at representative locations for the Tana River basin (Muchena, 1987; FAO, 1984). Embu is located near Mt. Kenya, Hola is approximately 35 km north of the TRNPR, and the other localities are identified on Figure 1. b. Monthly precipitation received during the field research at the Mchelelo Research Camp and near Mnazini within the TRNPR (Tana River Primate Project Data collected by B. Decker and M. Kinnaird, respectively).

Hydrology and Fluvial Geomorphology. "Floodplain forest" is defined as an ecosytem that exhibits a composition, structure, and function dependent on the river processes of inundation, sediment transport, erosion, and alluvial deposition (Brinson, 1989). For the Tana (and all exotic streams), the importance of the groundwater regime established by the water level within the channel and the permeability of the substrate must be added to this definition (Riggs, 1985). The Tana drops only 225 m along its lower or floodplain section (approximately 350 km upstream from the coast). It maintains a constant grade toward the delta through a meandering pattern that is adjusted by upstream precipitation (water volume), sediment load, and channel width and depth (Leopold et al., 1964). The maintenance of an equilibrium by the river results in a dynamic landscape mosaic of landform features and consequent vegetation patterns.

The primary landform features of the Tana River floodplain are point-bars, oxbow lakes, levees, and backswamp areas. Meanders develop by bank erosion on the outward, concave side of a bend where the river is high and has both a fast flow and a high sediment load (an abrasive force). The material from outside banks is transported to the inside of bends where it is deposited (lateral accretion) in shallow slowermoving water (point-bar formation) (Howard and Mitchell, 1985; Thornbury, 1969). Oxbow lakes form when a meander increases in amplitude and, usually during a time of maximum flow, cuts a straight course (Smith and Stopp, 1978). The erosion-to-deposition ratio decreases downstream due to the decline in the slope gradient and the increase in the suspended load of the river (Brown et al., 1978). As river volume decreases downstream, the result of evaporation and

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infiltration, one would expect a decrease in meandering and consequent cutbank and point-bar formation. Furthermore, stream velocity influences stream competence or the particle size of sediment effectively carried, such that faster velocities can carry coarser material (Gosselink et al., 1981). Rises in the river level are generally biannual in response to the precipitation patterns in the upper catchment (Hughes, in press). The lateral flow velocity rapidly decreases as the river floods, competence declines, and sediments are deposited (vertical accretion). Most of the sediment (particularly the coarser material) is deposited near the banks resulting in the formation of levees. These levees, consisting mostly of sands, build up above all but exceptional floods. Further away from the river, the finer sediments are deposited forming low-lying (backswamp) areas (Howard and Mitchell, 1985; Thornbury, 1969). The floodplain develops through the processes of lateral and vertical accretion. Andrews et al. (1975) found an elevation difference of 5.9 m between the crest of the levee near the Tana River and the basin behind it. Slight topographic differences between the different floodplain landforms influence water availability, period of inundation, and suitability for different plant species.

The soils are alluvial and are principally an expression of the sedimentation history on a particular landform. Soil characteristics are a function of the texture of sediments carried by the river and, to a lesser degree, a function of the river-water quality (Hughes, 1985). The predominating sediments are the weathering products of the metamorphic rocks in the highlands. Detailed analyses of the soils and

flooding patterns within riverine forest types were conducted by Hughes (1985) in selected forests between Bura and the TRNPR. Her research, as well as earlier studies within the TRNPR (Homewood, 1976; Marsh, 1978a), support the classification of forest types principally on the basis of the landform type and consequent sediment or soil characteristics. Furthermore, the forest types also correspond to a particular flooding frequency, emphasizing the close relationship between river dynamics, floodplain development, and forest development (Hughes, in press).

<u>Human Land Utilization</u>. The agricultural Pokomo and pastoral Orma are the two primary ethnic groups along the lower floodplain section of the Tana River (Kaplan, 1983). The Pokomo within and near the Reserve are further subdivided, belonging to the Gwano (north) or the Ndera (south) location. The Wardei, a smaller pastoral group of Somalian origin, also occupy smaller settlements.

The pastoral groups are primarily on the plains above the floodplain and use the river only during the dry seasons. At present no pastoral groups reside in the Reserve, but during the dry season they may graze and water livestock within its boundary. This is especially true during times of drought (Marsh, 1986) and along the east bank where enforcement of park policy is logistically more difficult. While this may be viewed as a serious impact, given the recent reductions in elephant populations (Marsh, 1986) and local extinction of the rhinoceros, the sum of animal impacts along the Tana probably have not increased and within the forest have decreased. In general woody plants have increased on the plains and within the forest understory (Allaway, 1979; Marsh, 1986). Competition between the

cattle and large game for forage and for the limited watering points along the river, however, is a serious threat to the remaining wildlife in this region and justifies the exclusion of cattle from the Reserve (cf. Marsh, 1986).

Productive agriculture is dependent on biannual to annual flooding events, thereby restricting the Pokomo settlements to low-lying localities near the river. The population of the Pokomo ethnic group (located along the Tana from near Garissa to Garsen; see Figure 1) was 29,550 in 1969 (in Decker, 1989) and 39,741 in 1979 (Central Bureau of Statistics, 1986). During this 10-year period, therefore, the growth rate averaged approximately 3.4%, or just below the current national average (-3.8%). Upon the establishment of the Reserve, the resident Pokomo population was estimated at 550 individuals in 88 families (Marsh, 1976). No formal census was conducted during my study, so whether the resident Pokomo population has expanded or contracted since 1975 is not known.

Each family will usually maintain one field near the river and another within a backswamp or oxbow area (or within the Mnazini rice scheme). Settlements within the TRNPR include: agricultural plots (home outside of the Reserve), rural settlements (home at the site of cultivation), and Baomo village and surrounding agricultural lands. Human land utilization accounts for approximately 155 hectares and is distributed in seven locations along the river within the Reserve. Included among these settlements is the National Museums research camp established at Mchelelo.

Agricultural practices closely parallel the river flooding pattern and the water conditions near oxbow lakes. The staple crops

of the Pokomo are bananas and corn, with nutritional supplements provided by legumes, rice, and other vegetables. Mangoes are the primary economic crop. Mango trees and bananas are planted on the sandy levees, corn and beans are planted bianually on the lower lying areas near the levee, and rice is planted along the river on recent alluvial deposits or along oxbow lake edges. High crop production is dependent on a flooding event, but corn and beans may be produced with adequate precipitation, and bananas are a staple during dry, nonflooding seasons (cf. Marsh, 1976). The small-scale irrigation scheme provides a source of food security (potentially three crops a year) outside of the Reserve.

The Forest Mosaic. Although the water regime established by the Tana may be viewed as a corridor, given the dynamics of a large meandering stream and human land utilization in the region, the forests occur more as a mosaic of forest patches (Figure 3). This spatial pattern is typical of large streams and consequent heterogeneous landform development. Two important traits of high spatial complexity are: (1) an increase in ecotones or linear edge per unit area; and, (2) an importance of refugia and "island" biogeographic processes (Roelle et al., 1985). The TRNPR, as established, is only 171 km<sup>2</sup>, extends approximately 25 kilometers along the river, and includes less than 10 km<sup>2</sup> forest area in 26 forest patches. The riverine forest is an isolated remnant of a continuous rain forest belt that extended between the Congo basin and the coast during the moister periods of the Pleistocene (ca. 31,000 to 26,000 BP and 8000 BP). Severe climatic drying after the hypsithermal period (ca. 4000 BP) isolated evergreen



Figure 3. The study area located in the south-central sector, TRNPR. The inset depicts the Reserve boundary and riverine forest (shaded).

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forests in East Africa to highland and riverine localities where they were further fragmented by human land use and natural dynamics. These past and ongoing processes are critical factors in the current distribution of biota (Livingstone, 1975; Hamilton, 1974). The riverine forest mosaic is composed of isolated islands of forest patches, which together are an isolated island of evergreen forest in a semiarid habitat. The floristic composition of these patches, phytogeographical relationships, and structural development within the TRNPR serve to demonstrate the uniqueness of this community and its value as a forest resource in a very dynamic landscape.

### Forest Flora and Phytogeographical Relationships

Evergreen forest in Africa is almost always less diverse when compared to other tropical regions (Richards, 1973). In East Africa, evergreen, or predominantly evergreen forests are restricted to isolated mountain tops and riverine localities (Lind and Morrison, 1974). The forest flora of this region is limited in areal extent, low in diversity (compared to the rain forests of West and Central Africa), and rich in disjunct plant species occurrences. The forest flora of the TRNPR, a reflection of continental and regional influences, may be described as a unique combination of species from different floristic regions that have persisted at this isolated locality.

A checklist for the forest flora within the TRNPR was compiled from the plants collected during one year of field research and records from other collections completed in this area (Appendix A). My plant collection (214 numbers) resides at the East African Herbarium (EAH), with duplicates distributed, as available, to herbaria at Michigan

State University (MSC), Royal Botanic Gardens, Kew (K), and the Missouri Botanical Garden (MO). In addition, I have included on the checklist plant species that were recorded in vegetation sampling plots and/or collected as reference vouchers to be maintained at the research station. Because of the short duration of the collecting periods and the emphasis of my own collection on woody plants, the list does not include forbs, grasses, or herbaceous vines. Although site characteristics are not available on the collection lists, I have attempted to restrict the checklist to plant species that occur in riverine forest, independent of their occurrences in areas of disturbance or on the plains.

A total of 49 plant families, 128 genera, and 173 species occurs in the riverine forest woody flora of the TRNPR. This is a conservative estimate, not including undetermined species in genera that are on the list. Families that have more than ten species include: Rubiaceae (17 spp.), Euphorbiaceae (16 spp.), Sapindaceae (11 spp.), and Capparaceae (11 spp.). Genera with several species include: Ficus (7 spp.), Diospyros (5 spp.), and Cordia (4 spp.). Mangifera indica, Thevetia sp., Ceiba pentandra, and Delonix elata are exotics that were established originally for agriculture or ornament. Epiphytes, ferns, and mosses are not present in this semiarid, groundwaterdependent ecosystem. Consequently, the predominant growth forms are large trees (> 10 m in height; 52 spp.), small trees (34 spp.), shrubs (35 spp.), and vines (43 spp.). Two parasites and three species of strangler figs occur in the forests. The widespread occurrences of palms, including Phoenix reclinata within the forest interior and along disturbed forest edges and Hyphaene compressa predominately

â b e along the forest-savanna edge, are an interesting structural component unique to riverine forest (cf. Burtt, 1942; Bogden, 1958). The woody flora is evergreen-semievergreen. Most of the canopy species are briefly deciduous prior to rains and the understory is composed of evergreen species (White, 1983).

The geographic affinities of the plant species may be classified as East African coastal (Zanzibar-Inhambane), West and Central African (Guinea-Congolian), northeastern (Somalia-Masai), southern (Zambezian), and pan-African (Greenway, 1973; White, 1983). Using the appropriate monographs from the Flora of Tropical East Africa (Turrill et al., 1952- ) and selected floras (Vollenson, 1980; Chapman and White, 1970), I determined the geographic affinities for 98 species on the checklist (Table 2; see Appendix A). Although evergreen-semievergreen forest is isolated in Kenya to riverine forest and an archipelago of highland areas (Afro-Montane region), no plants occur in both areas (Lind and Morrison, 1974; White, 1983). The pan-African species include pioneers such as Trema orientalis (Ulmaceae) and Bridelia micrantha (Euphorbiaceae), and most other species in the family Euphorbiaceae. These species typically have wide dispersal ranges, which would explain their disjunct occurrence along the Tana. Other pan-African species, such as Diospyros mespiliformis, Afzelia quanzensis, and Oncoba spinosa, however, have heavy seeds or fruits. Their presence suggests that the evergreen forests in Africa were once more continuous.

The largest percentage of plants (31%) are endemic to the coast (i.e., Zanzibar-Inhambane floristic region). Andrews et al. (1975) suggest that the large percentage of plants endemic to the coast

Table 2. Geographic affinities of the woody flora.

Regional Classification	Percentage (%) <sup>1</sup>
Africa South of the Sahara	30
Zanzibar-Inhambane (Coastal)	31
Guinea-Congolian	12
Somalia-Masai	16
Zambezian	1
Endemic	6
Exotic	4

<sup>1</sup>Percentage values are calculated from a total of 98 plants for which geographic affinities were determined.

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provides evidence of a long period of isolation from similar evergreen forest genera (i.e., the Guinea-Congolian floristic element). Several species of Rubiaceae are endemic to the coast, indicating considerable speciation within this family subsequent to isolation. The presence of coastal endemics within the isolated forests of the Reserve may be explained by persistence, or reintroduction from forests near the delta.

Most of the plant species endemic to the Somalia-Masai and Zambezian regions are adapted to a low precipitation regime that is not moderated by flooding or groundwater. Many species of the Capparaceae are from this region, and their presence in the forests is usually indicative of a transition toward savanna. Many species of *Ficus* have distributions that coincide with the Somalia-Masai and Zambezian regions, but additionally extend across northern Africa south of the Sahara and into the Middle East. In contrast to the plants typical of these floristic regions, these large semievergreen trees (or strangler vines) are more commonly associated with groundwater-dependent plant communities (e.g., oases or floodplains).

The species of the Guinea-Congolian region are nearly always located within the interior forest. One of the most interesting distributions is that of *Pachystela msolo*. Currently, the only known occurrence of *Pachystela msolo* outside of west-central Africa is on the lower slopes of the East Usambara Mountains in Tanzania (White, 1983) and along the lower section of the Tana River. Uncaria africana is a woody vine that exhibits a similar distribution and its collection within the TRNPR (KM 283) was a first record for Kenya. The recent discovery of a new mangabey subspecies (Homewood and Rodgers, 1981) in southern Tanzania suggests that the crested mangabey (*Cercocebus* galeritus) has a distribution pattern similar to that represented by *Pachystela msolo* and *Uncaria africana*. Together, their absence along the coast may be explained by a northern migration route during a warmer, wetter climate (Homewood, 1975; Hamilton, 1974).

Although the floristic diversity of the riverine forests within the TRNPR is low for tropical forest (e.g., 4000 spp. for Mt. Kinabalu in Borneo; Beaman & Beaman, 1989), the combination of plant species from four floristic regions results in an interesting community composition. Riverine forests vary first as a physiognomic transition between evergreen species dependent on a high water table and flooding, and savanna, which is characterized by plants adapted to low precipitation regimes. They vary second in response to plant migration patterns and survival within the floodplain refuge. Much of the woody flora within the TRNPR is similar to other riverine forests in East Africa (Madwick, 1986; Pichi-Sermolli, 1955; Simpson, 1975; Guy, 1977; Burtt, 1942; Chapman and White, 1970; White, 1983; and Vollenson, 1980), but these areas have higher percentages from the Zambezian or Somalia-Masai region (indicating lower moisture regimes), a lower number of plants from the coast (usually related to distance), or a different composition from Central Africa. Furthermore, forests of the TRNPR also contain some rare, endemic, or disjunct plant species (Table 3).

#### Resource Diversity

The importance of a tropical forest may be demonstrated first by its biotic diversity, presence of rare species, and aesthetic value, or second, by its economic potential for utilization. For this reason, it
Table 3. Rare plant occurrences.

<u>Species</u>	Notes
Acalypha echnis	rare in Kenya
Alafia microstylis	first record for Kenya
Anisocycla blepharosepala subsp. tanzaniensis	first record in Kenya, only recorded once in the Tanzania
Coffea sessiliflora subsp. sessiliflora	endemic
Cynometra lukei	endemic
Oxystigma msoo	first record in Kenya along Tana River
Pachystela msolo & Uncaria africana	disjunct from West Africa, only found along the Tana and in Tanzania
Pavetta sphaerobotrys subsp. tanaica	endemic
Populus ilicifolia	endemic

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was an objective to integrate these two perspectives in this examination of the ecosystem. The patchy distribution and low areal extent of the riverine forests along the Tana make it a noneconomic resource for timber extraction. On the contrary, in this subsistence economy, the value of the forests for nontimber uses are the most important (Booth and Wickens, 1988). The Pokomo are the local ethnic group that reside near the forests and are most dependent on its resources. Vernacular names and uses were compiled from local informants, and from information obtained in earlier studies (Homewood, 1976; Marsh, 1976; Geider, 1985) (Appendix B). In some instances the names may differ between the Ndera and Gwano locations. Additional uses for many of the plant species were identified in ecological and/or ethnobotanical studies conducted in Kenya (Kuchar, 1981; Gichathi, 1987; Geider, 1985; Morgan, 1981), Somalia (Maunder, 1986), and Africa (Booth and Wickens, 1988; Cunningham and Wehmeyer, 1988; Williams, 1949). These represent uses not yet realized by the local Pokomo population or determined from the local informants in this study. Together they provide a measure of the current and potential value of the forests to the local people, and are a comparative measure of the resource diversity of this riverine forest community.

Plant resources may be categorized as timber (poles and canoes; 24 spp.), firewood (9 spp.), medicinal (21 spp.), food (9 spp.), domestic (e.g., poisons, beehives, baskets, traps, mats, ropes; 41 spp.), and symbolic (3 spp.). In order to better understand the selection process for timber uses, specific gravities (sg - wet weight/ volume(1+(moisture %)) were calculated from extracted tree cores of

some tree species as a measure of wood density or strength. Most commercial timbers will range between 0.29, a soft conifer, and .76, a temperate hardwood (Brown et al., 1952).

The most conspicuous uses of forest products include timber extraction for canoes and beehive construction, pole cutting, and palmfrond cutting for mats and roofing. Canoes are constructed only from mature canopy trees (> 60 cm dbh) that are chosen both for durability and the ease with which they may be carved. For instance, Ficus sycomorus (sg = .471) and Populus ilicifolia (sg = .503) are quickly prepared but are suitable for only one and two years, respectively. Diospyros mespiliformis (sg = .663) is a very durable timber, but as a canoe it is susceptible to cracking in the sun. One informant ranked trees for canoe construction in the following hierarchy of increasing quality: Sterculia appendiculata, Ficus sycomorus, Populus ilicifolia, Diospyros mespiliformis, Mangifera indica, Mimusops fruticosa (sg = 0.622), and Blighia unijugata. Canopy trees of low specific gravity (e.g., Ficus sycomorus, Hyphaene compressa) are used in the preparation of beehives. The large trees are burned at the base and then left to partially decay before hollowing. Poles are chosen for their shape (straight and long), strength, and resistance to insect damage and decay. Trees such as Pavetta sphaerobotrys, Surregada zanzibariensis, and Drypetes natalensis, while of suitable size, almost never produce a straight pole. Antidesma venosum and Lecaniodiscus fraxinifolius subsp. scassellatii, produce stems with distinctive bends that are selected for tool handles. Growth differences in a floodplain environment may explain why Bridelia mi crantha and Oncoba spinosa (sg = 0.645) were reported in the

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literature as highly suitable trees for poles, but were not used by the Pokomo because of their susceptibility to decay (Kuchar, 1981). The large, palmate-lobed leaves of Hyphaene compressa are so highly selected for roofing material that they are nearly extirpated from locations outside the Reserve. The palm Phoenix reclinata is used extensively for mats, rope, and baskets. The extraction of canopy trees for canoes and beehives, the cutting of potential canopy trees for poles, and the intensive cutting of Hyphaene compressa result in the loss of the tree or palm and are major forest disturbances. Most subcanopy trees will coppice as a response to pole removal, and Phoenix reclinata appears to reach reproductive maturity at lower height levels. In this case, the structure of the forest would be altered, but the activity may not affect the overall floristic composition.

Currently, the other utilization practices are not a noticeable impact on the forests. Charcoal is not produced by the Pokomo in the vicinity of the Reserve and most firewood acquisition occurs in the surrounding scrub woodland. The collection of firewood within the forests is conducted primarily by families that have a permanent rural residence near a forest, and most of their collections consist of fallen branches from trees. Medicinal and domestic uses require only a small amount of the plant and/or the plants are infrequently collected. The variety of vines and their density within the forests reduce the impact on any one selected species. Quantitative measures of forest extraction will be presented in Chapter 6.

I conclude that much forest utilization, while providing a diversity of products for the local population, does not result in

severe disturbances. The families that live closest to the forests most frequently use nontimber products and maintain a knowledge of the forests' resource potential. Moreover, they are often the most interested in forest preservation. When the population is removed from the forest, supplemented by cash incomes, and no longer dependent (or knowledgeable) on its resources, unnecessary clearing and forest loss occurs. Conservation efforts that are directed at maintaining the resource diversity of existing forests, supporting limited utilization, and encouraging the transfer of knowledge on available resources may best instill a respect for the forests that is critical to proper stewardship at the local level.

### Ecological Description

A most important objective in this study is to obtain an understanding of the habitat critical for the endangered primates, thereby developing management recommendations that are directly applicable to continued preservation of their populations within the TRNPR. Preliminary investigations on the floristic composition and resource diversity of the forests have been included to broaden the scope of this objective to include an equal concern for the botanical resources. Primate habitat is defined in this study by several compositional and structural characteristics of the forests. Much research, therefore, has been directed at compiling an ecological description of the riverine forest habitat within the currently protected TRNPR. Comparative data are incorporated into this description as they serve to clarify the structure of this tropical forest community.

<u>Data and Methods</u>. Field data were collected at 363 points in 12 forest areas (see Table 1 and Figure 3) using a combination of nested plots and point-centered quarter sampling. The sampled area accounts for approximately 0.4 % of the total forest area. Structural layers were defined by tree diameter at breast height (dbh) or by tree height. The calculations of basal area coverage  $(m^2/ha)$  and density (# /ha) are based on the size and number of individuals within a plot, or on the size and distance of trees from the point in each quadrat. Measures of basal area coverage or density are used in the comparisons among forests, and the sampling efficiency was determined from performance curves, based on the cumulative mean coverage or density, respectively (Brower and Zar, 1984). Relative measures of these attributes (e.g., density of sp. A/ density of all spp.) were obtained for each species and either separate (relative coverage, relative density), or summed, are used to demonstrate the relative importance of species within a specified sampling area. A further discussion of these procedures in plant ecological sampling and data compilation is provided in Brower and Zar (1984) and Cox (1985). The density, coverage, and relative importance of plant species are attributes fundamental to the ecological description of vegetation and will be used throughout the following sections. Other attributes obtained at the sampling points include: mean canopy height (clinometer measurements), the distance between tree crowns, and forest closure (densiometer measurements).

<u>Tropical Forest Comparisons</u>. A comparison among several tropical forest ecosystems is presented, based on the structural characteristics of the canopy layer, species dominance, and the presence of vines and palms (Table 4). Typically forests in dry environments have higher Table 4. Comparative review of tropical forest ecological characteristics.

### Ecological Characteristics for Canopy trees (> 10 m height, >10 cm dbh)

			Basal Area				
Forest Area	Richness (# species)	Density (#/ha)	Coverage (m <sup>2</sup> /ha)	Canopy Height (m)	Palms	Dominance (0-1) <sup>1</sup>	References
TRNPR	54	402	23.09	14.4	yes	. 59	this study
Holdridge 1a Dry Woodland		583	21.9	12.8	no	.428	Holdridge (1975)
Holdridge 20d Moist, no dry season		590	44.9	30.0	no	.215	Holdridge (1975)
Holdridge 1F Riverine, with dry season		167	35	33	yes	.469	Holdridge (1975)
Ghana Moist	200	445	25.5	32	no		Hall & Swaine (1981)
Ghana Dry Deciduous		504	24.2	36	yes		Hall & Swaine (1981)
Terre Firme	224		34.6		no	.257	Pires (1978)
Varzea	196				no	. 430	Pires (1978)
Kibale, Uganda rain forest to montane	53	301			no	.481	Kasenene (1987) Struhsaker (1975)

<sup>1</sup>Dominance applies to the relative importance certain species have in the forest. In this case, the importance values of the three most important trees have been summed. As the value approaches one, greater dominance is attributed to fewer species.

densities of smaller trees, hence lower coverages at the canopy layer (trees > 10 cm dbh). In contrast, moist forests are characterized by a lower density of very large trees. Within the Reserve, canopy trees are at a low density and do not obtain diameters typical of trees in a tropical moist environment. The mean height of the canopy (14.4 m) is lower than all but the driest forest (Holdridge dry woodland, 1a) and may be explained by: (1) the low frequency of emergents (trees > 30 m in height) such as *Sterculia appendiculata* and *Acacia robusta* subsp. *usambarensis*; (2) the relatively lower heights (rarely above 20 m) of the dominant canopy trees (*Pachystela msolo*, *Ficus sycomorus*, *Diospyros mespiliformis* and *Sorindeia madagascariensis*); and, (3) the wide gaps in the canopy layer that reduce the overall mean.

The absence of dominance in the tropical moist forest is demonstrated by the comparative importance values summed from the three most important trees. The high importance value obtained for the top species in the Reserve is primarily attributed to the occurrence of nearly monodominant stands of *Pachystela msolo* (IV - .345). The importance of *P. msolo* in one forest area (IV - .663) is close to that observed by the monodominant *Gilbertiodendron dewevrei* (IV - .791) in the mbau forests of Ituri, Zaire (Hart, 1985; Hart, 1990). Of the 10 most important trees, nine are mostly dependent on animals (primarily mammals) for their dispersal.

Additional structural features characteristic of the TRNPR forests are the abundance of vines, a high importance of palms within the forest interior (*Phoenix reclinata*) and along the forest edge (*Hyphaene compressa*), a low abundance of herbs, and an absence of epiphytes. Approximately 27% of the woody species are vines, and within the subcanopy size class (10-20 cm dbh) they account for approximately 30% of the total density. Vines are equally typical of moist forests in Africa where they account for 28% of the woody species in the Ituri forest of Zaire (Hart, 1985) and 40% of the total flora in Ghana (Hall and Swaine, 1981). Their relative abundance, however, is dictated by the presence of forest edge and intraforest openings, which are typical of the Tana River forests. Palms are often a forest component where moisture conditions are transitional between closed moist forest and a forest subjected to a dry season, or along rivers subjected to physical disturbance. Phoenix reclinata is the most important subcanopy species and Hyphaene compressa is the sixth most important species at the canopy layer (trees > 20 cm dbh). In summary, the riverine forests within the TRNPR have a physiognomy characterized by an open upper canopy with few emergents and few extremely large trees, highest species importance attributed to a few tree species, a reliance on mammal (or primate) populations for seed dispersal, and an abundance of palms and vines established primarily along the forest edge and in areas of intraforest disturbance.

Regional Comparisons. Riverine forest extends discontinuously along the Tana from approximately Bura to the delta at Garsen. Earlier studies that addressed the forest ecological characteristics of this region have summarized the forests within the Bura area and the Reserve (Hughes, 1985), or have summarized the forests near Garsen and within the Reserve (Andrews et al., 1975). Lists of the flora compiled for these three locations (Bura, TRNPR, and Wema/Hewani; Hughes, 1985; Gichathi et al. 1987; Andrews et al., 1975), and a general survey of

forest structure and relative dominance at the canopy layer suggested that riverine forest development in the three regions is not similar. To examine these differences, I compiled the vegetation data collected by Hughes for the Bura area (Hughes, unpubl. data) and completed vegetation sampling in the Hewani forest near Wema (see Medley et al., 1989; see Figure 1 for forest locations). Relative importance values were computed for woody plant species (excluding vines) at the canopy, subcanopy, shrub-sapling, and seedling layers (Table 5). The results provide a general comparison of current forest structure and regeneration patterns in the three areas. In addition, percent similarities among the three areas were computed on the basis of the relative abundances of their co-occurring species at the upper canopy layer (Brower and Zar, 1984).

The forests within the TRNPR are transitional between the forests at Bura and Hewani. At the canopy layer, the TRNPR is 29% similar to each forest, respectively, while they are only 7% similar to each other. Only *Ficus sycomorus* occurred as a dominant in all three forest areas. *Pachystela msolo*, a dominant within the TRNPR and Hewani, and the palm *Phoenix reclinata* is absent from the Bura forests. *Barringtonia racemosa*, the dominant in the Hewani forest, is absent from the upstream forest areas, and *Acacia elatior*, a dominant in the Bura area, is absent from the downstream forest areas. Existing gradients that provide a partial explanation for these contrasting compositions and species dominances include: the upstream decline in precipitation (see Figure 2a), the increase in distance from the coastal floristic element, and the upstream decrease in floodplain complexity (Hughes, 1988). The species co-occurrences between the

Table 5. The Tana River forests. A regional comparison based on the five most important tree species at four structural layers. Importance values, in parentheses, are based on relative coverage (TRNPR canopy trees) or relative density (all others), and may range from 0 - 1 (maximum IV = 1). <u>Barringtonia racemosa</u> (L.) Blume, <u>Acacia elatior</u> Brenan, and <u>Cadaba farinosa</u> Forsk. are absent from the woody flora of the TRNPR (see Appendix A).

Tana River National Primate Reserve

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Large Trees	Small Trees	Saplings	Seedlings
Pachystela msolo (.345) Ficus sycomorus (.166) Diospyros mespiliformis (.079) Sorindeia madagascariensis (.066) Mimusops fruticosa (.041)	Phoenix reclinata (.441) Hyphaene compressa (.097) Alangium salviifolium (.064) Polysphaeria multiflora (.033) Spirostachys venenifera (.033)	Polyshpaeria multiflora (.224) Harrisonia abyssinica (.064) Drypetes natalensis (.061) Chytranthus obliquinervis (.05) Rinorea elliptica (.042)	Sorindeia madagascariensis (.281) Garcinia livingstonei (.081) Phoenix reclinata (.068) Polysphaeria multiflora (.055) Pavetta sphaerobotrys (.043)
Hevani Forest- Approximately 30 kil	ometers south of the Reserve		
Large Trees	Small Trees	Saplings	Seedlings
Barringtonia racemosa (.571) Sorindeia madagascariensis (.143) Pachystela msolo (.143) Ficus sycomorus (.071) Antidesma venosum (.071)	Barringtonia racemosa (.607) Pachystela msolo (.180) Sorindeia madagascariensis (.115) Ficus sycomorus (.049) Antidesma venosum (.049)	Barringtonia racemosa (.337) Chytranthus obliquinervis (.149) Pachystela msolo (.040) Polysphaeria multifiora (.034) Diospyros mespiliformis (.029) Rinorea elliptica (.029)	Phoenix reclinata (.145) Barringtonia racemosa (.061) Polysphaeria multifiora (.027) Chytranthus obliquinervis (.027) Sorindeia madagascariensis (.017)

Table 5 (continued).

Bura Forests- Approximately 80 - 105 kilometers north of the Reserve

## Large Trees

Mimusops fruticosa (.184) Acacia robusta (.100) Acacia elatior (.100) Diospyros mespiliformis (.092) Garcinia livingstonei (.092) Trichilia emetica (.092) Ficus sycomorus (.092)

## Small Trees

Spirostachys venenifera (.150) Pavetta sphaerobotrys (.117) Terminalia brevipes (.107) Cordia goetzii (.087) Diospyros abyssinica (.060)

# Saplings/Shrubs

Cadaba farinosa (.129) Phyllanthus somalensis (.083) Cordia sinensis (.077) Salvadora persica (.031) Chytranthus obliquinervis (.031)

### Seedlings

Cordia goetzii (.024) Pavetta sphaerobotrys (.017) Hyphaene compressa (.005) Lecaniodiscus fraxinifolius (.005) Acacia elatior (.005) TRNPR and Bura, especially at the understory layers, are those typical of the forest-savanna transition (e.g., Cordia sinensis, Salvadora persica, Phyllanthus somalensis, and Lecaniodiscus fraxinifolius subsp. scassellatii). They are also representative species of the Somalia-Masai center of endemism (White, 1983). In contrast, species that have low importance or are absent from the Bura forests include many typical of interior riverine forest (e.g., Blighia unijugata, Apporhiza paniculata, Cola minor, and Alangium saviifolium), and are species common to the Zanzibar-Inhambane coastal element (White, 1983; Andrews et al., 1975).

As the Tana proceeds dowstream through the floodplain section, meandering increases, the grain-size of the transported sediment decreases, and the area inundated and period of inundations increase. The Bura forests have a low heterogeneity of depositional landform features, and the Wema/Hewani forests have a low occurrence of welldrained sandy levees and an abundance of tall grassland that is adapted to long periods of inundation (cf. Hughes, 1988). The compositional differences among these three areas demonstrate the regional heterogeneity in the riverine forest ecosystem along the Tana. Among the three localities, maximum forest development occurs in the TRNPR, which is characterized by a higher species diversity and frequency of well-drained floodplain features. The absence of Acacia elatior and Barringtonia racemosa from the Reserve, however, suggests that the regional or gamma diversity of the Tana River forests (Cody, 1986) is inadequately protected.

Local Forest Heterogeneity. In addition to the regional variation in riverine forest development, much local variation in forest composition and structure is present within the Reserve. Contrasting forest types are associated with different landforms (point-bar successional, well-drained levee, back-levee clay, and savanna) and also reflect different stages in development as influenced by river dynamics or human land utilization. Earlier research classified the forest types according to soil type, landform position, and flooding frequency (Homewood, 1975; Marsh, 1978a; Hughes, 1985; Hughes, in press). In this study, I have compiled ecological summaries on canopy tree composition (> 20 cm dbh) for each of the 12 forest areas sampled and computed the percent similarities among the forests. Only two sampled areas are located within one forest patch (see Table 1). Patch-patch heterogeneity provides a partial measure of the local or beta diversity of the ecosystem (Cody, 1986).

The calculated forest similarities range from 84% (Baomo South b-Kitere West) to 4.7% (Sifa West-Mnazini North) (Table 6). Local variation in the composition and relative abundances of canopy-tree species exceeds the regional variation. Moreover, forests originally classified as levee or clay-evergreen (Hughes, 1988; Marsh, 1976) also exhibit high variation and low percent similarities. The heterogeneity of the forests is demonstrated through the comparison of four forests of decreasing similarity to the Mnazini North forest: Mnazini North (100%), Baomo South a (38.4%), Mchelelo West (20.1%), and Congolani West (7.7%) (Table 7). The compositional characteristics of these forests range from a nearly monodominant stand of *Pachystela msolo* in Mnazini North (IV = 1.327) to a mixed forest containing *P. msolo* (IV = .538) in Baomo South a, to Mchelelo West, a forest low in *P. msolo*,

Table 6. Community similarity comparisons based on the relative coverages of canopy trees (> 20 cm dbh). Sampled forests include: Mnazini South (ms), Mnazini North (mn), Kitere West (kw), Baomo South a (bsa), Baomo South b (bsb), Baomo North (bn), Sifa West (sw), Congolani West (cw), Congolani Central (cc), Mchelelo West (mw), Guru South (gs), and Guru North (gn). Community similarity is calculated as a percent based on the relative abundances of co-occurring species (% similarity = sum of lower relative abundance percentages for all co-occurring species) (Brower and Zar, 1984).

### Forest Areas

	ms	mn	kw	bsa	bsb	bn	SW	CW	cc	шw	gs	gn
ms	100.0	7.7	15.2	22.2	25.6	23.6	48.6	78.1	41.9	24.6	41.6	47.8
IIIE)		100.0	57.5	38.4	59.3	44.0	4.7	7.7	10.1	20.1	28.0	14.8
kw			100.0	55.8	84.0	46.2	23.0	14.6	14.7	40.0	30.7	21.0
bsa				100. <b>0</b>	55.1	58.5	25.1	17.2	23.8	37.3	29.5	35.0
bsb					100.0	48.6	24.8	16.8	15.1	34.5	26.8	21.5
bn						100.0	20.6	35.4	26.2	31.2	34.5	51.1
SW							100.0	52.2	53.2	46.5	40.8	31.0
CW								100.0	52.0	53.1	51.9	52.7
cc									100. <b>0</b>	50.6	44.5	33.4
ШW										100.0	57.2	33.0
gs											100.0	41.8
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Mnazini North (100%)	Baomeo South a (38.4%)	Mchelelo West (20.1%)	Congolani West (7.7%)
Pachystela msolo (1.327) Ficus sycomorus (.249) Alangium salviifolium (.138) Apporhiza paniculata (.107) Antidesma venosum (.045)	Pachystela msolo (.538) Ficus sycomorus (.446) Sorindeia madagascariensis (.361) Mimusops indica (.172) Antidesma venosum (.128)	Hyphaene compressa (.413) Diospyros mespiliformis (.283) Sorindeia madagascariensis (.271) Ficus sycomorus (.239) Alangium salviifolium (.108)	Mimusops fruticosa (.392) Acacia rovumae (.248) Hyphaene compressa (.173) Cordia goetzei (.123) Garcinia livingstonei (.121) Standing snags (.155)
13 tree species	21 tree species	26 tree species	25 tree species
Density = 59 trees/ha	Density = 44 trees/ha	Density = 43 trees/ha	Density = 34 trees/ha
Coverage = 28.51 m2/ha	Coverage = 17.10 m2/ha	Coverage = 12.26 m2/ha	Coverage = 8.72 m2/ha

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but containing species typical of levee positions (Diospyros mespiliformis and Sorindeia madagascariensis), and to Congolani West, a declining forest of low density and containing species typical of clay soils (Mimusops fruticosa and Garcinia livingstonei). The occurrence of Hyphaene compressa in Mchelelo West and Congolani West and Acacia rovumae in Congolani West indicate the proximity these forests have to the forest-savanna edge. Highest canopy tree densities and coverages are obtained in the species-poor Pachystela forests. The complexity or beta diversity of these forests is clearly reflected in this descriptive examination of overall forest characteristics. Consequently, total forest area must be evaluated on the basis of the resource attributes of each forest patch. The area of well-developed riverine forest habitat is probably much less than the approximately 1000 hectares of land classified as forest within the Reserve.

### Summary of Ecosystem Characteristics and Significance

This chapter has focused on a general description of the Tana River forest ecosystem. Riverine forest, in an otherwise arid thornscrub environment, is a rare plant community dependent on the groundwater and floodwaters provided by the Tana River. It is an evergreen-semievergreen forest that has persisted in isolation from the tropical rainforests of West-Central Africa and the Coast. Whereas the original protection of the forests was directed at maintaining suitable habitat for the endangered Tana River red colobus and crested mangabey, a study of the botanical diversity and existing or potential forest resources for the local Pokomo population clearly broadens the conservation objective. The plant diversity of the ecosystem is not

đ s , Ξ â t С 0 P s ШU pr fo pra and sug and res the dive fore fores locat #ig:a demonstrated by total species numbers, but rather by the assortment of species from all of the major floristic regions in Africa, and the migration patterns represented by their disjunct occurrences.

The riverine environment has served as a refuge for plant and animal species adapted to a moist climatic regime. The close interrelationships among the forests and the primates are reflected in the food resources provided, and by the dependency many tree species have on animals for seed dispersal. Management directed at the preservation of the primates will be associated with the equally important task of preserving the botanical diversity.

The resident Pokomo population demonstrates the suitability of the system for agricultural production and the land-conflict issues that must be addressed in the management plan. Their forest utilization practices emphasize the known resource diversity and importance of the forests to the local human population. Much of their utilization practices are not in conflict with the preservation of riverine forest, and may indeed result in a greater respect for the forests. It is suggested that the management plan allow for some forest utilization, and thereby encourage stewardship by the local population.

Downstream, the pattern of river meanders, erosion, and deposition results in the highest diversity of landforms and forest types along the Tana River in the vicinity of the TRNPR. While much of the beta diversity is preserved, the gamma or regional diversity of the riverine forest ecosystem is not adequately protected without the inclusion of forests in the Bura and Wema/Hewani regions. Forest loss in these locations increases forest isolation, reduces the probability of plant migration into the Reserve, and places great importance on species

persist charact import plants of the high d demons sugges primat habita habita mosaic persistence through time. The compositional and structural characteristics of the forests within the Reserve emphasize the importance of riverine hydrology as a source of water (absence of plants such as ferns, mosses, and epiphytes that lack deep roots) and of the existing disturbance regime (the importance of palms and the high diversity and density of vines). Inter-forest heterogeneity demonstrates the variable resources provided by each forest and suggests contrasts in their value as habitat for the endangered primates. In order to adequately address the preservation of primate habitat, therefore, it is critical to obtain an understanding of what habitat characteristics are preferred, as represented by the forest mosaic protected within the TRNPR.

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### CHAPTER III

### EXAMINATION OF THE PRIMATE-TO-HABITAT RELATIONSHIPS

### Introduction

The 1985 primate survey (Marsh, 1986) conducted within the Tana River forests revealed an 80% decline in the red colobus (1200-1800 to 200-300 individuals) and a 25% decline in the crested mangabey (1100-1500 to 800-1100 individuals) since the establishment of the Reserve in 1975. The populations of these two endangered primates had crashed, and Marsh (1986) suggested that their population reductions may be a consequence of a corresponding decline in forest habitat. The absence of data on the primates and the forests during the 10-year decline complicates the determination of causal factors or corresponding trends.

A study addressing primate-to-habitat relationships, therefore, must focus on the existing primate populations and forest habitat characteristics. Since 1985 no significant changes in the numbers of groups or group sizes for the colobus and mangabey have occurred (Decker and Kinnaird, submitted). These findings suggest that the populations may have temporarily stabilized and that their population sizes reflect the relative carrying capacities of the existing forests. The abundance of primate groups and their group sizes are used to distinguish the quality of the forests as primate habitat, and the ranging patterns of the primates within a patch reflect the relative

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intraforest patch quality. The selection of forest attributes to be examined, the approach used in the data analyses, and the application of results to recommended stewardship considerations rely on an understanding of the forests as habitat for the colobus and mangabey.

Studies of wildlife-to-environment relationships generally have focused on the development of habitat models that predict animal presence, diversity, or abundance (Verner et al., 1986). These models, most often applied in the study of birds and small mammals, are based on assumed relationships between the animal and its environment and usually are a compilation of the results of earlier studies directed at the examination of each respective relationship (Schamberger and O'Neil, 1986; cf. Hamel et al., 1986). In primate studies, abundances or behavioral patterns have been related to habitat degradation (Struhsaker, 1976; Altmann et al., 1985; Berenstein, 1986), human land utilization (Tarara, 1986; Skorupa, 1986; Johns, 1986), food resources (Terborg and Janson, 1986; Struhsaker, 1975; Wrangham, 1977; Marsh, 1981a; Marsh, 1981b), or forest structural attributes (Skorupa, 1986; Whitten, 1982). Management recommendations should complement the contrasting behavioral responses observed in each species. The attributes examined in these studies provide a comprehensive view of possible factors that influence wildlife populations and assist in the designation of forest characteristics to be examined and the interpretation of the results.

Primate habitat is defined in this study by certain structural, resource, spatial, and compositional attributes of the riverine forests within the range of the two endangered primate species. Habitat quality is distinguished by the relationships between these attributes

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and primate abundance or their utilization (ranging) patterns within a forest area. This approach makes the assumption that these habitat characteristics will determine, or be significantly related to, the success of the primates in view of such limiting factors as food availability, predation, or competition (cf. Skorupa, 1988). Food availability is directly addressed through the examination of resource abundance and overall forest diversity. The structural development of the forest (especially canopy development) and certain spatial characteristics (e.g., forest area) are indirectly related to the ability of the primates to avoid predation and competition. Tree species abundances at the canopy and subcanopy layer and selected forest attributes are applied to the discrimination of primate utilization patterns in order to determine the relationships between canopy composition, or forest structural and resource attributes, and intraforest habitat quality. The compositional characteristics of highly utilized areas within a forest provide a summary of relative species importance in high-quality habitat. Together, the primate-tohabitat relationships determined from this study are incorporated into a model that characterizes preferred primate habitat. The model thereby establishes criteria useful in distinguishing the quality of the existing forests as primate habitat and also establishes management objectives directed at preserving suitable primate habitat within the TRNPR.

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### Data and Methods

### Data Acquisition

I selected 12 forest areas in this study for which data were available on the endangered primates and also areas representative of the variation in forest types (see Table 1 and Figure 3). In ten forests the entire patch was examined, making it possible to also compute forest areas and the area-to-perimeter ratios. Data on the primate populations have been compiled from recent censuses and include the number of colobus and mangabey groups in each forest area and their group sizes (Decker and Kinnaird, submitted; Tana River Primate Project Data). In three forests (Mchelelo West, Baomo South a, and Mnazini North), I was provided intraforest primate utilization data from concurrent studies on the red colobus and crested mangabey conducted by B. Decker (see Decker, 1989) and M. Kinnaird, respectively. Vegetation data were collected for all structural layers using a combination of nested plots and point-centered quarter sampling (a total of 363 points). Species abundances at the canopy (> 20 cm dbh) and subcanopy layers (trees and vines 10 - 20 cm dbh, and palms > 1 m ht) are examined in this study, which is focused on current habitat characteristics, while abundances at the seedling (< 1 m ht) and sapling (trees > 1 m ht and < 10 cm dbh, and vines < 10 cm dbh) layers are examined in a later study addressing forest regeneration (see Chapter 4). At each point data were also collected on the height of the canopy, the distance between tree crowns, and the amount of wood that was dead, cut, or damaged by animals. In addition, I collected vegetation data on all trees and vines greater than 10 cm dbh and all

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palms greater than 3 m in height within seven 50 x 50 m plots that were most highly utilized by the colobus, mangabey, or both species in three forest areas.

### Correlation Analyses

Spearman's rank correlations were computed between selected ecological attributes summarized for a forest area and the respective primate population characteristics. A nonparametric approach, which makes the least assumptions about the data, was judged more appropriate given the small sample sizes (n - 9 - 12) used in the statistical analyses (Conover, 1971). The forest characteristics examined have been categorized as forest structural, resource, and spatial attributes, and forest disturbance (Table 8). The mean height of the canopy and the distance between tree crowns were calculated from averages computed at each point within a forest. Basal area coverages of all canopy trees and food resources have been computed from the diameters at breast height (dbh) of trees greater than 20 cm dbh. Designated food resources are derived from behavioral/ecological studies conducted on the red colobus by C. Marsh (1981a) and B. Decker (1989), and on the crested mangabey by K. Homewood (1978) (Table 9). They represent the food items most utilized by the endangered primates, hence most related to the resource quality of the forest areas. Canopy tree diversity was measured using Simpson's index  $(D_s - 1 - \Sigma n_i(n_i - 1))/$ N(N-1), where *n* equals the number of individuals for each species, and N equals the total number of individuals (Brower and Zar, 1984). The palm Phoenix reclinata has been measured as the number of individuals (> 1 m in height) per hectare. Forest disturbance is equal to basal area

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Table 8. Forest attributes examined in the correlation analyses and the hypothesized relationships.

Forest Attributes	Hypothesized Relationships
Forest Structural Attributes	
Mean canopy height	The colobus is strictly arboreal (restricted to above 10 m), and the mangabey relies on the forest canopy for protection. A higher mean canopy height is related to a better developed arboreal habitat (positive).
Distance between tree crowns	Movement through the forest can be more effectively achieved in a closed upper canopy. A greater distance between the crowns of trees would inhibit travel for both primates and decrease the area of forest available to the colobus (negative).
Total tree basal area coverage	A higher basal area coverage of canopy trees (> 20 cm dbh) is related to a better developed canopy forest, providing a better arboreal habitat for both primates (positive).
Forest Resource Attributes	
Primary food resources	A greater coverage of high quality primate food items would be directly related to the carrying capacity of the forest area (positive).
Secondary & primary food resources	Given the diversity in the diets of the two primates, dependent on the species composition of each forest, a somewhat broader view of food resources may be more appropriate (positive).
Canopy tree diversity	Overall food diversity, including infrequently used items, is directly related to the diversity of the upper canopy. A greater variety of food resources would enhance the food resource quality, hence the carrying capacity of the forest area (positive).
<u>Phoenix</u> <u>reclinata</u> density	This palm species is a primary food item for the crested mangabey and is most frequent along disturbed edges or within forest gaps (positive for mangabeys, negative for colobus).
Forest Disturbance	The combined effects of forest senescence, human utilization, and damage by large mammals are a negative impact on forest structure (negative).

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Table 8 (continued).

Forest Attributes	Hypothesized Relationships
Forest Spatial Attributes	
Forest area	More abundant food resources and a better arboreal habitat would be available in a larger forest (positive).
Forest area-to-perimeter	The colobus and mangabey are forest primates, suggesting that their populations would be highest in patches with little edge and much interior forest (positive).
Intraforest heterogeneity	Intraforest heterogeneity would be high in a forest of high quality, but interspersed with large gaps or areas of disturbance, or in a forest that is unsuitable except for the abundance of small areas of concentrated food resources (negative or positive, respectively).

Table 9 end zan Frimate Fatus All of (<u>Ficu</u> E: E <u> 2005-72</u> Serind Pachys Acacia Saba co Secondar Markife Minisop Selected Phoen : x Utiliza parenth 2 Bamewood 3 Decker Table 9. The most important primate food items and measures of percent utilization by the colobus and mangabey.

Primate Food Items	Mchelelo colobus <sup>1</sup>	Mchelelo mangabey <sup>2</sup>	Mnazini mangabey <sup>2</sup>	Baomo South colobus <sup>3</sup>
Ficus sycomorus	29.4 (17.74)	17.22	17.22	15.00
<b>All other figs</b> ( <u>Ficus bussei, F. natalensis</u> , <u>F. bubu, F. scasellattii</u> )	5.3 (14.13)	2.27	. 04	
<u>Diospyros</u> mespiliformis	(2.08)	14.86	2.73	1.16
<u>Sorindeia madagascariensis</u>	19.6 (25.48)		2.58	18.50
Pachystela msolo	(1.68)	2.92	2.92	27.24
<u>Acacia</u> <u>robusta</u> subsp. <u>usambarensis</u>	15.0 (8.66)	5.04	6.38	. 18
<u>Saba comorensis</u>	1.0 (2.82)	8.69	1.33	4.91
Secondary Food Items				
Mangifera indica	species not present			13.06
Mimusops fruticosa		. 80	9.06	
Selected Food Items				
Phoenix reclinata		21.74	12.83	

<sup>1</sup>Utilization percentages have been taken from Marsh (1981a), and Decker (1989; listed in parentheses).

<sup>2</sup>Homewood (1978)

<sup>3</sup> Decker (1989)

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coverages of wood that was dead, cut, or damaged by large animals. This attribute was examined relative to current primate populations and also relative to the change in primate group abundances between 1975 and 1988 (see Table 1). Forest area (ca. 1975) and the area-toperimeter ratios have been computed from digitized maps and aerial photographs using a geographic information system analysis program (ARC-INFO; ESRI, 1987) available on a VAX 8650 Mainframe Computer. Intraforest heterogeneity has been computed as a multivariate measure of the mean euclidean distance among points within a forest area based on their mean height, distance between tree crowns, food resources, and disturbance. The procedure has been modified from a study conducted by Belsky (1988) in the Serengeti on the heterogeneity of grassland communities along a north-south transect. The euclidean distances among points within a forest were computed using the SYSTAT statistical package for microcomputers available within the Department of Geography at Michigan State University (Wilkinson, 1987).

The data analyses are restricted to the computation of simple correlations (to each forest attribute) using the NCSS statistical package for microcomputers (Hinze, 1987). In contrast to the examination of several attributes simultaneously (e.g., multiple regression), the results from this approach were judged more easily interpretable, and more directly applicable to the designation of management recommendations (cf. Layman and Barret, 1986).

# Discrimination of Intraforest Primate Utilization Patterns

Canonical variate analysis was used as a descriptive multivariate technique that reduces the dimensionality of the plant species



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abundance data as applied to the discrimination of intraforest utilization by the primates (Gittens, 1985; James, 1985; Williams, 1981). The number of utilization records for the primates was the criterion variable used to categorize the vegetation sampling points in the three forest areas (a total of 109 points): high = > 3% of total records within a forest (40 points), medium - > 1% and < 3% of total records (38 points), and low - < 1% of total records (31 points). A line, or canonical variate, is located in the space of p attributes (species abundances), for which the separation of the groups defined by the criterion variable is optimized (James, 1985; Cooley and Lohnes, 1971). When canonical variate analysis is used for descriptive purposes no tightly specified distributional assumptions are necessary (Gitten, 1985). However, for sensible interpretation, it is desirable that the data not depart too drastically from certain norms. For this reason, standardized species abundance data were log-transformed, and to eliminate the problems associated with the high number of zero abundances the final transformation was:  $log(x_i + 1)$  (Gauch, 1982, Jongman et al., 1987).

The total number of tree or palm species present at the canopy and subcanopy layers was 60. In multivariate procedures it is advisable to reduce the number of variables that need to be considered. The result is a more interpretable and practical solution (James, 1985). An analysis of the relative species abundances among the three habitat rankings, stepwise discriminant procedures, and the assessment of the variance explained by each species used in preliminary models (measures of communality) were three techniques used to reduce the original number of plant species to a total of 24 (James, 1985; Gitten, 1985).

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My primary objectives in this analysis were to determine the degree to which the selected species discriminate among the habitat rankings, as depicted on a two-dimensional graph (the extraction of two canonical variates), and to characterize the discrimination through the interpretation of the correlations between the species and the variates. A second canonical variate analysis was computed using selected forest attributes examined in the correlation analyses. The results from the canonical variate analyses, a parametric technique, are compared to the nonparametric nearest neighbor procedure (SAS, 1985; Hand, 1981). In this approach the points were classified as determined by their euclidean distances using the selected predictor variables (species abundances or forest attributes), and the number of misclassified points were examined. The multivariate analyses were completed using the SAS statistical package available on an IBM 3090 mainframe computer at Michigan State University (SAS Institute, Inc., 1985).

#### Compositional Characteristics of High-Utilization Plots

A descriptive summary of high quality-habitat was compiled based on relative plant species importances in high-utilization plots. Seven 50 x 50 m plots were examined: two in Mnazini North (high use by mangabeys), two in Baomo South a (high use by colobus), one in Mchelelo West (high use by two groups of mangabeys and one group of colobus), and two in Mchelelo West (high use by mangabeys). The more important species in all the plots were determined from their mean relative frequency, basal area coverage, and density. Together, they served to characterize the compositional characteristics of high-quality habitat.

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### Results and Discussion

#### Correlation Analyses

In examining the calculated correlations between the primate population characteristics and certain forest attributes (Table 10), the reader should realize that the examination is based on whole-forest summaries for only 12, or nine, forest areas. A forest may have distinct variations in an attribute within its patch that would be masked by the ecological summary, occur as an outlier in the data analysis, and tend to weaken the correlation based on a small sample size. Low variability in the number of endangered primate groups, in contrast to group sizes, would also tend to weaken those correlations. For these reasons, interpretation of the results focuses both on the trend and significance of the calculated correlations.

The positive correlations to mean canopy height and total tree coverage and the negative correlations to the distance between tree crowns are as predicted, and reflect the importance of forest structure to the endangered primates. Significant correlations exist between the number of endangered primate groups, or the number of colobus individuals, and the mean height of the canopy. It is understandable that the number of groups and group sizes of colobus, an arboreal primate that rarely descends below 10 meters, would have higher correlations to canopy height. In contrast, the mangabeys spend much of their time foraging along the ground (Homewood, 1978). The mangabeys may prefer a forest of high stature, but their range of available resources is not as closely related to a closed canopy. Typical of other studies that examine primate-to-habitat relationships, the

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Table 10. Spearman correlations between primate population characteristics and selected forest attributes.

Forest Characteristics	Primate Population Characteristics			
Forest Structural Attributes	Colobus and Mangabey Groups <u>(n = 12)</u>	Colobu <b>s</b> Individuals <u>(n = 12)</u>	Mangabey Individuals <u>(n = 9)</u>	
Mean canopy height	. 626*	.656*	. 555	
Distance between canopies	261	502 <sup>*</sup>	502	
Total tree coverage	.216	. 423	. 412	
Forest Resource Attributes				
Primary food resources	.241	.406	. 512	
Secondary and primary food resources	.216	.413	. 412	
Canopy tree diversity	346	693*	303	
Phoenix density	. 360	. 445	. 630*	
Forest Disturbance	587*	127	311	
Forest Spatial Attributes				
Forest area (n = 10)	. 595*	. 603	270	
Forest area-to-perimeter ratio (n = 10)	.712*	.776*	072	
Intraforest heterogeneity	736**	370	412	

\*Significant correlation (alpha = .05) for one-tailed hypothesis tests  $n = 12; R_g = .552$   $n = 9; R_g = .583$  $n = 10; R_g = .552$ 

\*\* Significant correlation (alpha = .05) for two-tailed hypothesis tests

 $n = 12; R_{g} = .580$  $n = 0; R_{g} = .683$ 

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correlations are unique for each species (cf. Skorupa, 1986). The relationships to the structural development of the forest is less clearly depicted in the correlations to total-tree basal-area coverage. This is in contrast to Skorupa's (1986) study in Kibale where he found highest correlations between all primates and the total basal area of canopy trees. The colobus populations show closest relationships to the structural development of the forests, and their preference is a closed forest canopy at least 10 m in height.

Originally I hypothesized that if highly utilized food resources are abundant, then a higher number of primates would be present. The correlations, however, are positive but nonsignificant. A scattergram of the relationship and a graph depicting the relative measures of the selected food resources in the 12 forests suggests that adequate food resources are available at low coverage values (Figure 4). The trend is positive, however, indicating that a threshold level in food resources may exist, below which a forest becomes unsuitable. Indeed, the food resources currently available in Sifa West and Congolani West may be below that level. Although the food resources available to the primates vary in the different forests, a Ficus species is present in all forests, was highly utilized in the studied forests (recall Table 9), and may indeed be a critical food item. Marsh (1981b) measured a significant correlation ( $R_s = .538$ ; prob < .01) between the ranging pattern of colobus in the Mchelelo forest and the location of Ficus sycomorus and Sorindeia madagascariensis.

The relationship to overall canopy diversity is opposite to that predicted. Low diversity forests occur within the Reserve, primarily due to the monodominance of *Pachystela msolo*, that have high



\* Forest Areas



a.



Figure 4. Food coverages and primate group abundances in the 12 forest areas: Congolani West (cw), Sifa West (sw), Baomo North (bn), Guru North (gn), Mnazini South (ms), Baomo South b (bsb), Baomo South a (bsa), Kitere West (kw), Mchelelo West (mw), Guru South (gs), Mnazini North (mn), and Congolani Central (cc). a. Scattergram depicting the relationship between primate group abundance and the basal area coverage of highly utilized primate resources. b. Basal area coverage of highly utilized food items in each forest. The number of primate groups occurring in each forest is indicated above the bars.

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primate numbers. This is particularly demonstrated by the number of colobus individuals. In Baomo South a Pachystela msolo is the dominant tree and makes up 27.2% of the colobus diet (Decker, 1989; see Table 9). The folivorous colobus, when given a suitable food resource, may be characterized as "banqueters", and can adapt to a low diversity diet within a small range (Oates, 1987). In contrast, the frugivorous (and insectivorous) mangabeys occupy a larger range and maintain a more diverse diet (not restricted to plant species), even in a low diversity forest (Homewood, 1978; cf. Struhsaker, 1969). Both endangered primates differ from chimpanzees, whose abundance and ranging patterns are positively related to the diversity of food resources (Kortlandt, 1984). Finally, the significant relationship between the mangabeys and Phoenix reclinata demonstrates the importance of one food item to that primate. Its positive relationship to colobus, opposite to that predicted, is probably spurious; the palm species occurs in forests that possess adequate food resources and a structure suitable for the colobus. In sum, the relationships to food resources are positive, but are relatively low and nonsignificant. These results may be partially explained by an absence of specificity in the primates' food requirements and their adaptability to low resource diversity.

A significant negative correlation is found between the number of endangered primate groups and forest disturbance. A graphic representation of each measure (forest senescence, human forest utilization, and animal damage) depicts their relative importance as an impact on the studied forests (Figure 5). The highest measures of disturbance are related to forest senescence and the highest levels of

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Figure 5. Forest disturbance in the 12 forest areas: Congolani West (cw), Sifa West (sw), Baomo North (bn), Guru North (gn), Mnazini South (ms), Baomo South b (bsb), Baomo South a (bsa), Kitere West (kw), Mchelelo West (mw), Guru South (gs), Mnazini North (mn), and Congolani Central (cc). Forest disturbance is depicted as a summed measure of the basal area coverage of wood that is dead (forest senescence), cut (human forest utilization), and damaged by large mammals (animal impact). The number of primate groups occurring in each forest area is indicated above the bars.

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forest senescence are the result of natural floodplain dynamics. A major flood event in 1961 resulted in a meander cut-off and the positioning of the Congolani West forest at a distance greater than 1 km from the river. Consequently, the water regime has declined and the forest is changing toward savanna vegetation. Another major flood occurred in 1969 that brought high water into a large monodominant stand of Pachystela msolo in Baomo South, resulting in immediate treefalls or the decline and death of many trees. The graph also indicates that high levels of human utilization, such as those measured in Baomo North and Sifa West, may have a negative impact on the suitability of an area as primate habitat. Large animal disturbance does not appear to be related to the numbers of primates in the studied forests. A negative, but nonsignificant, correlation was also calculated between the decline in the endangered primate groups through the 10-year period (1975 - 1985) and forest disturbance ( $R_s = -.553$ , n = 9). Forest disturbance appears to be related to the primate decline, but the low correlation suggests that it is coupled with other negative impacts.

Primate group numbers and the number of colobus individuals are highly correlated to the forest spatial characteristics. The negative correlations to intraforest heterogeneity demonstrate the negative relationship intraforest disturbance (e.g., large gaps, or forest edge) has to the primate populations. The high positive correlations between forest area and the area-to-perimeter ratio suggest that changes in these attributes may have a significant impact on primate populations. Both primates are interior-forest species and their habitat is clearly not enhanced by forest edge.

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Since the establishment of the Reserve forest loss has been less than 5% within the study area (south-central TRNPR). From an analysis of areal photographs, however, I was able to outline the area of canopy forest in 1960 as it contrasts to that present in 1975. During that 15year period forest area decreased by 56% within the study area. Perhaps more significant, five forest areas were fragmented into 15 forest patches with a decline in the overall area-to-perimeter ratio from .292 to .163. It is very likely that the primates surveyed in 1975 were compressed into small forest patches at a density much higher than their respective carrying capacities. Current behavioral and demographic studies on the primates suggest that the sharp population reductions may have been a decline toward more stable carrying capacities (Decker and Kinnaird, submitted). The reader should note that mangabey group sizes (number of individuals per group), which have low correlations to forest area and the area-to-perimeter ratio, did not show a significant decline between 1975 and 1985 (Decker and Kinnaird, submitted).

## Discrimination of Intraforest Primate Utilization Patterns

Combining the tree and palm species present at the canopy and subcanopy layers, 24 species proved most effective in the discrimination of primate utilization patterns. The mean abundance values for these species within each class (i.e., low, medium, and high utilization) reflect the differences among the habitat rankings (Table 11). Two canonical variates were extracted. The first canonical variate accounts for 45% of the variance (correlation = .67) in the habitat discrimination and the second canonical variate accounts for 37% of the variance (correlation = .57). A two-dimensional graph of a random

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Phoenix Hyphaene Terminal Diospyro Apporhiz Ficus sy Antidesmu Spirostac Rauvolfia Table 11. Mean species abundances, by habitat rank, for the 24 tree species used in the canonical variate analysis. Abundances for the canopy trees (> 20 cm dbh) are recorded as basal area coverages  $(m^2/ha)$  and abundances for the subcanopy trees (10 - 20 cm dbh) and palms > 1 m in height) are recorded as densities (# individuals/ha).

#### Habitat Ranks

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Tree Species	Code	High $(n = 40)$	Medium $(n = 38)$	Low $(n = 31)$
Canopy Trees				
Alangium salviifolium	As	0.86	0.34	0.28
Antidesma venosum	Av	0.24	0.14	1.51
Pachystela msolo	Pm	25.62	9.51	9.60
Albizzia gummifera	Ag	0.40	0	0.15
Pavetta sphaerobotrys	Ps	0.01	0	0
Ficus natalensis	Fn	0	0.13	0
Sterculia appendiculata	Sa	0	2.30	0.01
Ficus bussei	Fb	0	0	0.05
Bridelia micrantha	Bm	0	0	0.10
Borrassus aethiopum (palm)	Ba	0	0	1.30
Cordia goetzii	Cg	0	0.20	0.14
Polysphaeria multiflora	Pm	0	0.03	0
Diospyros mespiliformis	Dm	1.41	2.07	0.76
Cola clavata	Cc	0.03	0	0.02
Standing snag	S	0	0.67	0.02
Subcanopy Trees				
Phoenix reclinata (palm)	Pr	316.97	253.76	106.57
Hyphaene compressa (palm)	Hc	2.23	0	34.56
Terminalia brevipes	Tb	0	0	11.52
Diospyros mespiliformis	Dm	2.23	0	2.88
Apporhiza paniculata	Ap	0	9.40	0
Ficus sycomorus	Fs	0	0	34.56
Antidesma venosum	Av	0	7.05	23.04
Spirostachys venenifera	Sv	2.23	18.79	28.80
Rauvolfia mombasiana	Rm	6.70	0	0

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selection of points depicts the point distribution as determined by the canonical variates (Figure 6). The first canonical variate appears to distinguish the low utilization areas (or poor habitat) from the more suitable habitat, while the second canonical variate discriminates the high utilization plots (better habitat) from the medium utilization plots.

The interpretation of the discrimination is based on the correlations between the variables (plant species) and each canonical variate. The first canonical variate distinguishes the interior forest from the forest along an edge or area of disturbance (Figure 7). Antidesma venosum (as a canopy and subcanopy tree) and Ficus sycomorus as a nonreproductive subcanopy individual occupy areas along depositional river banks and old oxbows. Terminalia brevipes and Spirostachys venenifera occur on the levee along an erosional bank, along the savanna (in association with the palm Hyphaene compressa), or in areas of disturbance. Ficus sycomorus and Diospyros mespiliformis, as subcanopy trees, are indicative of poorer habitat. When these trees are reproductively mature they are primary food resources for both primates (see Table 9). Only four currently available food resources proved useful in the habitat discrimination and one, Phoenix reclinata, is a resource only for the crested mangabey.

The areas of medium utilization are discriminated along the second canonical variate from the higher quality habitat on the basis of seasonal food resources or species associated with those resources (Figure 7). Ficus natalensis, Sterculia appendiculata, Apporhiza paniculata, Cordia goetzii, and Diospyros mespiliformis produce fruit synchronously, often resulting in seasonal high utilization by the

Canonical Variate 2

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Figure 6. Canonical variate analysis using 24 canopy and subcanopy trees (see Table 11). The graph depicts the distribution (or discrimination) of a random selection of points based on the extraction of two canonical variates. Group centroids determined from all points are identified for the low, medium, and high utilization classes.

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**Canonical Variate Two** 





Figure 7. Correlations between the variables (tree species) and the two canonical variates. The canopy and subcanopy tree species are listed in Table 11. The highly utilized primate food resources are identified in the graph depicting the correlations to the first Canonical variate.

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primates in areas possessing characteristics that limit continual use. Ficus bussei is also considered an important seasonal resource for the primates, but its very infrequent occurrence obscures its relationship to the primate utilization patterns.

The neighbor procedure, using the same 24 plant species, results in the correct classification of 51.4% of the points. Misclassifications in this procedure indicate areas that have a species composition similar to preferred habitat but are affected by factors not considered in the analyses (e.g., primate interactions or proximity to human settlements), or areas with primate populations that have not yet stabilized and, consequently, may have future utilization pattern changes in adjustment to the existing habitat. Accordingly, 24.8% of the points were classified higher, and 23.8% of the points were classified lower than the current patterns of utilization would indicate. The robustness of the procedure is demonstrated by the similar classification efficiencies that result from the analysis of individual forests (correct classifications equal 58.1% for Mnazini North, and 40.5% for Baomo South a) (Gauch, 1982).

As an alternative approach, four forest attributes proved most effective in the discrimination of habitat utilization by the primates: mean height of the forest canopy, distance between tree crowns, food resources/total tree cover, and the abundance of *Phoenix reclinata*. The discrimination is not as clear as that computed on the basis of species composition (Figure 8). The first canonical variate explains 33% of the variance (correlation = .58) and appears to distinguish the higher quality habitat from areas of low and medium utilization (Figure 8a). The correlations between the forest attributes and the first

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canonical variate demonstrate the importance of forest structure and a primary food item. Similar to the correlation analyses, combining the abundances of highly utilized food resources does not clearly distinguish the quality of the existing habitat. In the nearest neighbor procedure 45.0% of the points are classified correctly, and 26.6% are classified higher and 28.4% are classified lower than the current patterns of primate utilization would indicate.

The canonical variate analysis further emphasizes the importance of forest edge and intraforest disturbance to the overall quality of the forest patch. Although these areas are at present unsuitable for the primates, they demonstrate some potential for the provision of future resources. In contrast, the composition of high-quality habitat is not as easily defined as are the unsuitable areas. This may be due to certain behavioral characteristics of the primates or their adaptation to a wide variety of food resources. The areas used seasonally (medium habitat quality), in contrast to the core areas, are characterized by the second canonical variate using plant species abundances. The discrimination of intraforest primate utilization patterns on the basis of summarized forest attributes further emphasizes the importance of forest structure and the weak relationship that exists between the endangered primates and a composite measure of high-quality food resources. Finally, point misclassifications determined in the neighbor procedure may reflect unstable primate-to-habitat relationships.

### Descriptive Summary of High-Utilization Areas

It is an assumption in this study that relative forest-habitat quality may be defined by the utilization patterns of the two

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endangered primates. High-quality habitat, therefore, may be described by the compositional characteristics of certain high-utilization areas (or plots). Mangabey preferences are more clearly represented in this summary, with a demonstrated high occurrence in five of the seven plots.

The combined composition of all plots may be summarized as: (1) important primate food resources; and, (2) subcanopy trees or vines that typically co-occur with the primate food items (Table 12). The very high importance of Phoenix reclinata over the other species is partially explained by its growth structure and consequent high basal area coverage (Figure 9). The importance of figs to the quality of habitat is further emphasized in this descriptive summary. Ficus sycomorus occurs in most of the plots and the other figs (F. bussei, F. natalensis, and F. bubu), despite their low overall occurrence in the Reserve (four out of 363 points), are present in six of the seven high-utilization plots. Certain food resources (Tamarindus indica, Cordia goetzii, Mangifera indica, Garcinia livingstonei, and Acacia robusta), are specific to a single plot, reflecting the variability of food resources provided by a single high quality area. Pachystela msolo has a very low occurrence in Mchelelo West and is absent from the highly utilized areas in that forest. This descriptive summary supports the conclusions obtained from the correlation and canonical variate analyses and identifies the plant species and variety of food resources that characterize high-quality habitat.

# Model of High-Quality Habitat

A primary objective in these statistical and descriptive analyses is to develop a habitat model that reflects the preferences of the two

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Table 12. Importance values and plot occurrences for the woody plant species (trees and vines > 10 cm dbh, and palms > 3 m in height) within the seven high utilization plots. Species importances are based on the sums of relative frequency, density, and coverage (total = 3.00) for the seven examined plots. Primate food items are identified with an asterisk.

Species	Codes	Relative Importance	Plot Occurrences
*Phoenix reclinata	Pr	.881	7
Alangium salviifolium	As	.276	7
*Pachystela msolo	Fspp	.215	4
*Ficus spp. (F. bussei, F. bubu,			
F. natalensis)		.166	6
*Sorindeia madagascariensis	Sm	.163	4
*Ficus sycomorus	Fs	.141	4
*Hyphaene compressa	Hc	.138	3
*Diospyros mespiliformis	Dm	.107	4
Rauvolfia mombasiana	Rm	.106	1
*Albizia gummifera var. gummifera	Ag	.103	2
*Saba comorensis	Sc	.098	4
*Tamarindus indica	Ti	.067	1
Drypetes natalensis var. leiogyna	Dn	.058	3
*Apporhiza paniculata	Ар	.055	2
*Cordia goetzii	Cg	.052	1
*Mangifera indica	Mi	.048	1
Polysphaeria multiflora	Pm	.046	2
Pavetta sphaerbotrys subsp. tanaica	Ps	.041	2
*Oncoba spinosa	0s	.034	1
*Garcinia livingstonei	G1	.030	1
*Albizia glaberrima var. glabrescens	Ag	.026	1
Diospyros kabuyeana	Dk	.026	1
Hunteria zeylanica var. africana	Hz	.026	1
Trema orientalis	То	.026	1
Salacia stulhmanniana	Ss	.026	1
Rinorea elliptica	Re	.026	1

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Figure 9. Twelve most important plant species in the high utilization plots. Importance is based on relative measures of frequency, density and coverage (maximum IV - 3). Codes refer to species names listed in Table 12.

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endangered primates. The results clarify the differences between the red colobus and the crested mangabey, but their corresponding trends in the calculated correlations and the discrimination or characterization of their high-utilization areas suggest that a single model will complement both species. The arboreal colobus shows greater relationships to the structural development of the forest. Its preferences are for a high-stature forest with a closed canopy above 10 meters in height. Highest mangabey densities are also associated with a similar forest structure, suggesting that a forest satisfactory to the colobus probably will complement or enhance the mangabey populations.

The colobus and mangabey are forest primates and are susceptible to forest disturbances that reduce forest area, or increase forest edge and intraforest disturbance. In contrast to other primates such as the black and white colobus, their populations are not enhanced by natural, or human-induced, gap-forming disturbances (Tarara, 1986). The better quality habitat is primarily restricted to the forest core, a circumstance in agreement with the findings of Temple (1986) for bird populations in the eastern deciduous forests of North America.

The riverine forests have a wide variety of food resources available for the primates and their adaptation to low-diversity forests suggests that food requirements may be easily satisfied within a forest of suitable structure. Critical food items, or certainly superior food items, would include all species of *Ficus*, and for the mangabey, *Phoenix reclinata*. The utilization patterns of the primates appear to be related to the distribution of seasonal food resources, but the importance of these food items can only be revealed through studies directed specifically at their feeding ecology.

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Overall, the results suggest that a combination of primary food items and seasonal food resources in a high-stature, closed-canopy forest, with a high area-to-perimeter ratio and low intraforest disturbance is the preferred habitat for the colobus and mangabey. Stewardship considerations should be directed at the preservation of these areas or the restoration of forests toward this habitat model. Effective resource conservation, however, will be dependent on how closely forest management complements or coincides with the natural patterns of vegetation change characterizing this riverine forest ecosystem.

### CHAPTER IV

#### A STUDY OF NATURAL FOREST REGENERATION PATTERNS

## Introduction

Two central objectives of this forest ecological study are to determine whether vegetation-based causes explain the sharp reduction in primate populations between 1975 and 1985 and to establish management objectives that will help ensure the preservation of the primates and their forest habitat. Both objectives rely on an understanding of riverine forest development within the TRNPR and especially on the continued presence of highly utilized food resources. Marsh (1986) reports that the decline in colobus and mangabeys during the ten year period may be attributed to a corresponding decline in forest habitat, primarily through the loss of important canopy-tree food resources. Moreover, he suggests that there was insufficient tree regeneration to compensate for the losses observed. His conclusions were based on a survey of canopy trees in the Mchelelo forest during his project (1973-1974) and a second enumeration completed in 1985. He made no systematic data collection on the understory layers at Mchelelo or on overall forest structure at other locations within the Reserve. Hughes (1985) completed a study of riverine forest composition between Bura and the TRNPR. She concluded that pioneer forest areas were absent, and that tree regeneration levels were low at all sampling plots (Hughes, 1988). Both studies, while providing an

overview of forest conditions along the Tana River, support the need for a detailed examination of forest regeneration within the protected area.

I have demonstrated that the forests within the Reserve are probably the best remaining habitat for the colobus and mangabeys, in view of the recorded floristic diversity, the spatial heterogeneity of landform types and forest composition, and the current impacts on unprotected riverine forests imposed by development projects along the Tana River (cf. Chapter 2). The results from my study of primate-tohabitat relationships (Chapter 3) support the assertion for need to increase existing forest area, possibly through the implementation of restoration projects that parallel and thereby enhance natural trends in forest regeneration. A study of tree-species replacement, successional trends, and the patterns of primate-habitat regeneration within the TRNPR will provide a general understanding of riverine forest succession in this region. Moreover, it will provide information critical to the evaluation of vegetation decline and the establishment of management objectives directed at future habitat preservation.

# Study Design and Rationale

The earlier studies of forest composition within the TRNPR have been limited in area (Homewood, 1976; Marsh, 1978; Hughes, 1985) and/or are directed at the canopy trees (Marsh, 1978) or primate food resources (Homewood, 1976). They fail to provide a suitable framework to conduct a detailed study of temporal forest change. In addition, no dates are available for the geomorphic landforms, and the absence of

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annual growth rings prevents the determination of tree ages. Consequently, this examination of successional patterns is based on the size-class distributions of woody plant species, their interassociations, correlations among the forest structural layers, and a detailed study of the site characteristics and community composition near selected canopy trees of three highly utilized food resources. In the present study these analytical techniques provide an objective approach toward understanding qualitative trends in forest development. For future research, the study provides a sampling framework for longterm studies and for the examination of specific hypotheses (Pickett, 1989).

The first question concerns the pattern of canopy-tree species replacement and overall successional trends. Barbour et al. (1987) list eight important life stages in an individual plant: (1) viable seed; (2) seedling; (3) juvenile; (4) immature vegetative; (5) mature vegetative; (6) initial reproduction; (7) maximum vigor; and (8) senescent. Relative abundances among the stages for a species, or all species, provide an insight to compositional change or stability. The invading species are present only in the lower stages, declining species are present only in the upper stages, and a stable situation is represented by equal relative abundances (or frequencies) of individuals in all stages. Low canopy-tree species abundances in the lower life stages reflect an absence of regeneration, and contrasts among the relative species abundances at the lower and upper stages indicate compositional change. It is assumed that these stages correlate with the size of the individual, that the respective size-age



relationships are similar for all species examined, and that the survival of species is similar within a size-class (Austin, 1977; Pickett, 1989). The contrasting life histories of the tree species present problems in the analyses such that conclusions are general and qualitative. Potential canopy trees (i.e., capable of obtaining heights > 10 m) in four size classes (seedling, sapling, subcanopy, and canopy) represent the seedling, juvenile, immature, and maximum vigor or senescent life stages of these species, respectively. An examination of their relative abundances provides a basic understanding of regeneration patterns at the canopy-forest layer (> 10 m in height) within the study area.

Forest succession or stability may also be identified by the inter-associations among species size classes (Zedler and Goff, 1973) and by the correlations among the forest layers (McCune and Antos, 1981). To reduce the complexity of the analyses, indicator species, which occur as forest dominants, are identified a priori from the compositional differences and relative species abundances in the studied forest patches. By looking at the correlations between the point occurrences of a selected canopy-tree forest dominant and the size classes of canopy and subcanopy trees, one can establish a graphical representation of canopy associates and the species that enter (high associations for the small size classes) or leave (low or no association at all or lower size classes) a forest.

The combinations of positive and negative correlations among the indicator tree species may be used to develop a model that depicts the relationships among forest communities. High associations among the size classes of the same species indicate self-replacement and



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potentially a stable forest composition. Forest layers would be highly correlated, attributable to similar relative abundances at each structural layer. Low correlations among the size classes within a species, but high correlations with the small size classes of other potential canopy trees, suggest a change in forest composition. If the patterns of change are consistent throughout the sampled area then the correlation among the forest layers would also be high. Low correlations among the forest layers suggest that spatial similarities or dissimilarities at the canopy layer are not consistent with those measured at the understory layers. The discrepancies may be explained by stochastic tree establishment or contrasting environmental conditions influencing the understory layer (McCune and Antos, 1981). Both factors result in a different understory composition in forests with a similar canopy composition, and consequently complicate the projection of forest succession. Finally, low correlations among the small size classes of all canopy-tree species and a forest dominant indicate low forest regeneration and a possible physiognomic change in the vegetation.

A second question addresses the regeneration patterns near three "indicator" canopy trees that are also highly utilized primate food resources. In the floodplain environment one would expect that the succession of plant communities would coincide with a change in site characteristics (i.e., primary succession). To determine how closely the two coincide, it is necessary to establish a priori a forest successional pathway, and then determine whether significant differences are present in selected site or compositional characteristics. In essence, it is a space-for-time substitution where

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the "space" is defined by the selected canopy tree and its vigor state (e.g., nonreproductive, mature and healthy, senescent, or dead) (cf. Pickett, 1989). By focusing on highly utilized primate food resources one may determine the breadth of site and compositional characteristics associated with suitable habitat for the endangered primates. The results would be applicable to areas disrupted by human land utilization or disturbed forest edges. If the site conditions coincide with those typical of immature, or mature and vigorous primate resources, then habitat restoration that parallels the current patterns of natural succession is a possible option. Nonsignificant population differences among the species and/or their vigor states may be explained by stochastic tree establishment and forest dominance, adaptations to a wide range of conditions, and/or persistence with changing site characteristics. The results will further clarify the forest regeneration patterns within the Reserve and especially those associated with the regeneration or decline of primate food items.

In this chapter I will focus on the data and analyses that address forest regeneration in the TRNPR. The study provides a descriptive summary of tree-species replacement, a model of forest succession, and a descriptive and statistical examination of the site and compositional variability associated with three canopy-tree species. Although the absence of temporal data lessens the rigor of the analyses, the results will elucidate the successional patterns within the riverine forests of this region, and will provide data comparable to other studies and in keeping with established theories on forest succession. Furthermore, this portion of the study will contribute to the designation of

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management objectives, and more specifically will provide a framework for restoration projects and long-term studies.

## Data and Methods

## Tree-Species Replacement and Forest Succession

Data Acquisition. Vegetation data were collected from four structural layers using a combination of point-centered quarter sampling for trees > 20 cm dbh, and nested rectangular plots for trees 10-20 cm dbh (112 m<sup>2</sup> plots), saplings > 1 m in height and < 10 cm dbh  $(24 \text{ m}^2 \text{ plots})$ , and seedlings > 3 cm to < 1 m in height  $(4 \text{ m}^2 \text{ plots})$ . These four size classes will henceforth be referred to as the canopy, subcanopy, sapling, and seedling layers, respectively. Sampling points (n = 363) were located systematically within 12 forest areas, and the quadrats or plots were set at a random orientation from each point. The sampling design is the same as that used in the ecological description of the forest areas (cf. Chapter 2) and the correlation analyses among forest attributes and primate abundances (cf. Chapter 3), with the exception that I have included data on the understory layers. To reduce the complexity of the data set, most analyses are directed at the size-class distributions of species recorded as canopy trees and predominant subcanopy trees.

<u>Descriptive Analyses</u>. The examination of the size-class distributions of trees in the TRNPR is directed at summarized patterns determined for each of the 12 forest areas, and also at overall patterns within the study area through a pooling of the 363 sampling points. In each of the studied forests the sampling area corresponded

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to the census record of primate populations (see Table 1). While it is known that primates may cross between forest patches and utilize the resources of more than one area, this pattern of movement is primarily restricted to mangabeys and its frequency is not clearly understood. Therefore, I have assumed that the forest patch represents suitable habitat (a census record of primate populations) or unsuitable habitat (absence of primates), and a comparison of the regeneration patterns in the 12 forest areas was applied toward an interpretation of future habitat quality.

Furthermore, if one assumes that temporal changes in forest composition may be reflected by different site localities (a space-fortime substitution), then a comparison of the 12 forest areas should reflect temporal differences in forest development. On this basis, species indicative of community differences were identified by the compositional contrasts among the forests. For each forest area, I determined the three most important species based on their relative densities (# individuals of species A/ total number of individuals), and the total number of species (Brower and Zar, 1984). The focus of subsequent analyses were on the more important canopy trees.

I pooled the data from all 363 points, and the size-class abundances of canopy-tree species were derived from their frequencies (# points recorded out of 363) and their densities (# individuals/ha). Basal area coverages and dispersion patterns (mean-to-variance ratio, based on counts) were calculated for selected canopy trees to further describe their occurrence in the forests (Barbour et al., 1987; Brower and Zar, 1984). Point frequencies, densities, and relative densities

at the subcanopy, sapling, and seedling layers were used as measures of tree-species replacement.

Association Analyses. Inter-associations among the size classes of canopy and subcanopy trees were determined by calculating Spearman correlation coefficients and chi-square statistics (SAS, 1985). Both calculations indicate the direction of each association and its statistical significance (Pielou, 1969; Cole, 1949). Chi-squares are commonly computed to determine whether the co-occurrences of species (or size classes of species) are significantly different from random (Barbour et al., 1987; Grieg-Smith, 1983). A plot of the correlation coefficients, when interpretated in view of the calculated chi-square statistics, provides a graphical representation of the inter- and intraspecific associations between a canopy tree and the size classes of selected species (Zedler and Goff, 1973). Four associations were possible:

- Associate: positive correlations with the canopy size-class or all size classes;
- (2) Nonassociate: negative correlations with all size classes;
- (3) Invader: positive correlation with the subcanopy, sapling, and/or seedling size-class;
- (4) Decliner: negative correlations with its small size classes, or with the canopy size-class of a formerly designated associate;

If a successional pathway is evident, one would expect the indicator tree species to enter, dominate, and decline according to a particular sequence.

Vertical integration among the forest layers was measured by first calculating a dissimilarity matrix for each layer (the euclidean

distances among the 12 forest areas based on tree-species abundances) and then calculating Spearman correlation coefficients among the matrices (Wilkinson, 1987; cf. McCune and Antos, 1981). Forest layers would be highly correlated if the total dissimilarity among the forests at one layer (derived from their species abundances) was similar to the correlated forest layer. It is assumed that a high correlation would result if the species composition and relative abundances at the compared layers were similar, thereby indicating a stable forest composition. Low correlations indicate complexity in the successional pathway. On the basis of the descriptive and association analyses a model of forest succession was developed.

#### Forest Regeneration Near Three Canopy-Tree Species

Tree-Species Selection and Classification. Ficus sycomorus, Sorindeia madagascariensis, and Pachystela msolo were selected for this study because they are important primate food resources (Chapter 3, Table 9) and appeared from a pilot study (Medley and Murphy, 1986) to be representative of different forest types and/or stages of development. Analyses were conducted to determine the contrasts among the three species and also among the same or different species in contrasting states of vigor. The selected individuals of Ficus sycomorus were classified as young (FY = 5), mature and vigorous (FOK = 5), and senescent (FO = 6) on the basis of two ratios: (1) crown size (i.e., maximum crown width + depth) / stem basal area at breast height; and (2) crown size / basal area coverage of dead stems in the crown. Together these ratios provide a measure of the photosynthetic capacity or overall productivity of the tree (Kramer and Kozlowski,



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1979). The two ratios were ranked and the final classification was based on the sum of the two ranks. Individuals of Sorindea madagascariensis were classed as mature and vigorous (SOK - 5), or senescent (SO - 5). The selection was restricted to reproductively mature trees, and a tree was classed as senescent if crown dieback was observed. Pachystela msolo was similarly classed as reproductively mature and vigorous (POK - 6), or senescent (PO - 6). Additionally I established plots around three dead Pachystela (PD - 3) to include an examination of natural regeneration in a large area that had experienced stand-level death of this monodominant.

Vegetation and Site Data. Circular plots (radius - 15 m) were established around each of the 41 selected trees and divided into four quadrats along a random orientation. Vegetation data were collected for three structural layers: trees > 10 cm dbh (4 quadrats - 706.86  $m^2$ ), saplings > 1 m in height and < 10 cm dbh and all palms > 1 m height (1 quadrat - 176.72  $m^2$ ), and seedlings (line-intercept method along the radius separating the first and fourth quadrat - 15 m) (Brower and Zar, 1984; Cox, 1985).

Plot positions were carefully mapped in order to acquire distance measurements to the river and nearest forest edge. Within each plot, I dug a 1.5 m soil core. Soil samples were collected just below the organic layer (surface) and also at 30 cm in depth (subsurface). These two depths represent the most recent sediment deposits (surface), and also the soil conditions experienced at the rooting zone of newly established seedlings (subsurface). Percentages of sand, silt, and clay for subsurface soils were determined by the Soil Testing Laboratory at the National Agricultural Laboratories, Kenya Ministry of Agriculture. Soil salinities at the surface and subsurface were determined at the field site using a conductivity meter and standard saline solution: conductivity =  $1 / R \ge K(standard R) \ge dilution$ , where R equals the resistance or meter reading for the soil solution and the standard saline solution, K is a constant determined for the meter, and the dilution factor equaled 7.5 for a 1:3 dilution (U.S. Salinity Laboratory Staff, 1969; Hesse, 1971). The meter was calibrated at Michigan State University by Dr. B. Ellis, Department of Crop and Soil Sciences. Soil moisture percentages were determined by taking dry and wet weight measurements from samples collected at 1.5 m. Samples were collected from all plots within a 26.5 hour period to limit moisture changes attributed to a fluctuating water table. Subsequent to the flood event in May 1988, I measured the maximum water height as evidenced by the markings on each central tree.

Statistical Examination of Group Contrasts. The comparisons among the tree species and tree vigor states were restricted to variables that focus on certain compositional, resource, and site attributes characterizing the plots (Table 13). Vegetation data were compiled to compute the number of species and their abundances at three structural layers, the abundances of primate food resources at each structural layer, and the presence of a certain physiognomic group of plants (e.g., vines or palms). The site analyses were restricted to the position of the tree relative to the river and forest edge, certain soil characteristics, and the water heights attained during the 1988 flood. I calculated the Kruskal-Wallis test statistic to examine the differences between the three species or eight vigor states based on

Table 13. Description of the variables used in the statistical examination of population differences among *Ficus sycomorus*, *Pachystela msolo*, and *Sorindeia madagascariensis*. Compositional, resource, and site attributes used in the multivariate analyses of variance are identified with an asterisk.

## Variable Description

Compositional Attributes - plant species richness or abundance

*	CANSPP	Number of canopy species
*	SAPSPP	Number of sapling species
*	SDSPP	Number of seedling species
*	VINEDEN	Abundance of woody vines (#/ha)
*	PHOENIX	Abundance of Phoenix reclinata palm
		(#/ha)

Resource Attributes- abundance of primate food items

*	CANFOOD	Abundance of primate food resource
		trees > 10 cm dbh $(\#/ha)$
*	SAPFOOD	Abundance of primate food resource
		trees < 10 cm dbh ( $\#$ /ha)
*	SEEDFOOD	Abundance of primate food resource seedlings (#/ha)
	SABACOV	Coverage of <i>Saba comorensis</i> vine (m <sup>2</sup> /ha)

Site Attributes- characteristics of the physical environment

	SURSAL	Surface soil salinity
	SUBSAL	Subsurface soil salinity
*	SAND	Percent sand in subsurface soils
*	MOISTURE	Percent soil moisture measured at 1.5 m
*	FLOOD	Height of 1988 flood
*	RIVDIST	Distance to the river
*	EDGDIST	Distance to the savanna or disturbed forest edge

each characteristic (Conover, 1971; Sokal and Rohlf, 1981). The null hypothesis states that the populations, as defined by the groups (k - k)3, or k = 8), are the same, and the calculation of the statistic is based on the ranks of the observations in all samples (n = 41). Box plots were constructed to determine the source of variation in selected attributes (Sokal and Rohlf, 1981; Wilkinson, 1987). Furthermore, I tested the significance of the variance among groups based on combinations of compositional, resource, and site characteristics (Hand and Taylor, 1987; SAS, 1986) (see Table 13). The technique, multivariate analysis of variance (MANOVA), is designed to study group differences in multi-dimensional space, where the combination of attributes is a dependent vector variable. The test examined the statistical significance among the population centroids, or mean vectors (i.e., the discriminating power of compositional, resource, or site attributes) as evidenced by the calculated Wilk's lambda and its significance (Cooley and Lohnes, 1971).

#### Results and Discussion

## Tree Species Replacement and Successional Trends

<u>Descriptive Analyses</u>. A tabulated summary of the most important species in the 12 forest areas clearly reflects compositional contrasts among the forests (Appendix C). Low similarity measurements among the study areas were previously presented in the ecological description of the riverine forests (Chapter 2, Table 6). The beta diversity of the forests may be partially explained by temporal differences. At the canopy layer *Pachystela msolo* is a most important tree in five forest areas. The rest of the forests have a mixed composition with

Sorindeia madagascariensis (often in association with Diospyros mespiliformis) or with Mimusops fruticosa and/or Garcinia livingstonei. Ficus sycomorus is important in several forests, except those with Garcinia livingstonei as a dominant, and Acacia robusta occurs in most forests except those dominated by Pachystela msolo. The palm Hyphaene compressa commonly occurs at the transition between the forest and savanna (pers. obs.), so that its high relative importance in a sampled forest probably indicates the influence of forest edge on the area. Therefore, I selected seven canopy tree species on which to focus subsequent analyses: Ficus sycomorus, Pachystela msolo, Sorindeia madagascariensis, Diospyros mespiliformis, Garcinia livingstonei, Mimusops fruticosa, and Acacia robusta subsp. usambarensis. These trees are the most important species that occur within the riverine forests as measured by relative density, frequency, and basal area coverage.

An overview of tree species replacement is depicted by the frequency of potential canopy trees (i.e., may obtain heights > 10 m) at four structural layers (Table 14). A primary question in the interpretation of these point occurrences concerns the level at which replacement is ensured. Webb et al. (1972) in a study of regeneration in a subtropical rain forest suggest that the production of abundant seedlings does not ensure adequate regeneration. Furthermore, low abundances at the sapling layer may be compensated by individual persistence, and replacement may occur when adequate conditions prevail (e.g., gap formation). Species abundances and replacement success are not always related. Nevertheless, a very low number of individuals

Table 14. Canopy-tree point occurrences at four structural layers. Palm species were only recorded at three structural layers: canopy, subcanopy, and seedling. The number of points are determined from records taken at 363 points. Species with low replacement are identified with an asterisk (\*).

#### Point Occurrences

Species Name	Canopy	Subc an opy	Saplings	Seedlings	Total
Pachystela msolo	94	4	7	58	163
Sorindeia madascariensis	94	4	76	134	310
Diospyros mespiliformis	72	6	72	54	203
Hyphaene compressa (palm)	70	47	-	6	123
Acacia robusta subsp. usambarensis	62	20	15	6	103
Ficus sycomorus	60	7	12	3	82
Mimusops fruticosa	54	4	16	61	134
Alangium salviifolium	49	50	47	56	203
Garcinia livingstonei	46	5	63	135	248
Cordia goetzei	34	22	33	15	104
Cola clavata	26	9	34	7	76
Acacia rouvumae	24	4	2	5	34
Apporhiza paniculata	19	4	9	18	50
Spirostachys venenifera	19	35	39	1	94
* Lannea schweinfurthii var. stuhlmannii	18	2	0	0	20
Albizia gummifera	15	2	11	1	29
Antidesma venosum	15	9	20	0	44
Ziziphus pubescens	15	5	30	13	63
Blighia unijugata	11	0	4	14	28
Mangifera indica	11	0	2	1	13
* Majidea zanguebarica	10	0	0	0	10
Albizia glaberrima	9	1	5	6	21
Afzelia quanzensis	8	3	0	2	11
Cynometra lukei	7	0	0	2	9
* Populus ilicifolia	6	0	0	0	6
Sterculia appendiculata	6	0	1	4	11
Hunteria zeylanica	6	23	66	35	130
Celtis philippensis	6	1	0	1	8
Terminalia brevipes	6	15	27	0	48
* Kigelia africana	5	3	0	0	8
* Ficus spp. (F. natalensis, F. bussei,					
F. scassellatii, F. bubu)	5	1	1	0	7
Phoenix reclinata (palm)	4	201	-	91	296
Bor <b>assus aethiopum (palm)</b>	4	14	-	0	18
Diospyros kabuyeana	4	12	11	3	30
Markhamia zanzibarica	4	3	3	1	11
Lecaniodiscus fraxinifolius subsp. scassella	tii 4	22	64	64	154
Diospyros ferrea	3	0	3	0	6
Dobera glabra	2	1	6	7	12
Cassia abbreviata subsp. beareana	2	3	3	0	8
Oncoba spinosa	2	1	24	12	38
* Oxystigma msoo	2	0	0	1	3
Haplocoeclum inoploeum	1	0	3	2	5
Tamarindus indica	1	0	2	1	4
Lepisanthes sengalensis	1	0	5	0	6

(presence -< 1 point) at the seedling and sapling layers would suggest inadequate replacement within the region. Populus ilicifolia is a pioneer species that regenerates on recent point-bar deposits outside of the sampled area, and the low record of Ficus spp. regeneration may be related to their initial growth as stranglers and early establishment as epiphytes, especially within the cavities formed by old fronds of Hyphaene compressa (pers. obs.). Regeneration of Lannea schweinfurthii and Majidea zanguebarica was observed at the forest-savanna boundary and within an area of disturbance surrounding the Mchelelo Research Camp, respectively. Similar to Populus ilicifolia, these species appear to have a high light requirement. Kigelia africana, and Oxystigma msoo have inadequate replacement within the Reserve. These two forest species, which have higher abundances downstream, may decline within this area. Overall canopytree replacement, as reflected by total frequency and density at the understory layers, suggests an effective establishment of forest vegetation (Figure 10). The examination must focus on compositional changes and the relative increases or decreases of selected species.

Tree species replacement among the selected trees varies from low frequencies in the small size classes (Acacia robusta and Ficus sycomorus) to a bimodal frequency pattern (Figure 11). Most prominent in the bimodal patterns are the low frequencies observed at the subcanopy layer (cf. Figure 10). This pattern may reflect intermittent establishment, continuous regeneration with a low number of species reaching the canopy size-class (cf. Webb et al., 1972), or a temporal gap in the closure of the canopy subsequent to a treefall. In contrast, Acacia robusta and, to a lesser degree, Ficus sycomorus are


Figure 11. Frequencies of seven important canopy-tree species at the seedling (sdl), sapling (sap), subcanopy (sct), and canopy-tree (ct) forest layers. Frequencies equal the number of points at which the species occur (total = 363 points). Seedlings of Sorindeia madagascariensis and Garcinia livingstonei were present at 134 points and 135 points, respectively.

characteristic pioneer tree species. Low frequencies at the lower size classes may be explained by their intolerance of the low light conditions within the sampled forests. The contrasts among the replacement patterns of these two species and the other canopy trees is also depicted in a summary graph of species densities at the four structural layers (Figure 12).

Equally demonstrated by the summary graph (Figure 12) is the change in the relative densities of the seven trees at each structural layer. At the canopy layer Pachystela msolo is the most dominant tree, representing nearly 35% of all the canopy-tree species (Figure 13). Moreover Pachystela msolo has the highest basal area coverage of the canopy trees and the most highly contagious dispersion pattern (Table 15). These results support my personal observations that the tree occurs in nearly monodominant high-stature forest stands. At the sapling layer (representing well-established seedlings), Pachystela msolo is the least abundant of the canopy trees. Saplings were recorded at only seven points, and the low number of individuals at those points resulted in a very low overall density. Although I have indicated the difficulty in predicting low or nonexistent regeneration when individuals are present at the lower size classes, these results do suggest a potential decline in the dominance of Pachystela msolo within the TRNPR and a consequent change in the composition and structure of much of the riverine forest area.

<u>Association Analyses</u>. The examination of species frequencies, densities, and relative densities provides insight into the overall patterns of tree-species replacement within the study area, but does not address the spatial patterns. The associations among the size



Figure 12. Densities of seven important canopy-tree species at four forest layers. Densities (# individuals/ha) are log-transformed.



Figure 13. Relative densities of Ficus sycomorus (Fs), Pachystela msolo (Pm), Sorindeia madagascariensis (Sm), Diospyros mespiliformis (Dm), Garcinia livingstonei (Gl), Mimusops fruticosa (Mf), and Acacia robusta (Ar) at the canopy and sapling forest layers.

Table 15. Basal area coverages and dispersion patterns of the seven canopy-tree forest dominants. Basal area coverages  $(m^2/ha)$  are depicted as a mean derived from all sampling points (n - 363), or, in parentheses, a mean derived from the 12 forest summaries. Dispersion (variance-to-mean ratio) is presented as a measure of each tree species' distribution among the 12 forest areas: random  $(s^2/\bar{x} - 1,$ uniform  $(s^2/\bar{x} < 1;$  overdispersed), and clustered  $(s^2/\bar{x} > 1;$ underdispersed) (Brower and Zar, 1984).

Tree Species	Basal Area Coverage (m <sup>2</sup> /ha)	Dispersion (s <sup>2</sup> /x)
Ficus sycomorus	3.807 (3.56)	3.32
Pachystela msolo	7.893 (6.44)	14.32
Sorindeia madagascariensis	1.503 (1.11)	1.21
Diospyros mespiliformis	1.817 (1.41)	3.04
Garcinia livingstonei	.785 (0.38)	1.18
Mimusops fruticosa	.943 (0.67)	1.54
Acacia robusta subsp. usambarensis	.306 (0.23)	0.29

classes of the trees depict that spatial pattern and indicate species associates, nonassociates, invaders, and decliners. A computation of the correlations among the size classes of all canopy and subcanopy trees would necessitate the interpretation of 31,684 correlations (178 x 178) and chi-square statistics. In order to reduce the complexity of the analysis, I focused on the inter-associations among the size classes of the potential canopy and subcanopy trees, and the large size-class of the seven canopy trees identified a priori as possibly indicative of forest successional patterns (7 x 178 - 1246). The interpretation of results focuses on these seven canopy trees and other species that demonstrate significant positive or negative associations at one or more size classes (7 x 76 - 532; see Appendix D).

Graphs depicting the positive and negative correlations among the size classes of the selected canopy trees present several patterns of compositional change (Figure 14). Positive associations at the seedling and sapling layers (indicating invasion) are highest for *Pachystela msolo*. Although there appears to be low self-replacement, other potential canopy trees are establishing under the *Pachystela msolo* canopy. Positive associations at the sapling size-class indicates establishment by other canopy trees under *Sorindeia madagascariensis*. In contrast, *Mimusops fruticosa* has an absence of invading species. *Diospyros mespiliformis* and *Garcinia livingstonei* appear to be transitional between these two species, respectively. Self-replacement is highest for the pioneer trees, *Ficus sycomorus* and *Acacia robusta*, but the association between their patterns of regeneration is not significant (i.e., associations among the size classes of the two species are nonsignificant). Significant co-





Sorindeia madagascariensis



Figure 14. Graphs depicting the associations between the size classes of selected canopy-tree species and the canopy size-class of Pachystela msolo, Sorindeia madagascariensis, Mimusops fruticosa, Diospyros mespiliformis, Garcinia livingstonei, Ficus sycomorus, and Acacia robusta, respectively. Positive correlations indicate invasion (in the lower size classes), or co-association, while negative correlations indicate non-association. Diospyros mespiliformis



#### Garcinia livingstonei







Figure 14 (continued).









Figure 14 (continued).

associations at the canopy layer occur only between Pachystela msolo and Sorindeia madagascariensis, although positive nonsignificant associations are also present between Sorindeia madagascariensis and Diospyros mespiliformis and among Diospyros mespiliformis, Garcinia livingstonei and Mimusops fruticosa.

Significant and positive correlations exist between all forest layers except those represented by saplings and canopy trees (Table 16). Seedlings do regenerate beneath a canopy tree, but the low correlation between the sapling and canopy layers suggests that the pattern of survival, hence persistence, is less consistent. This is represented by the very high association mature Pachystela msolo has with its seedlings (recall the high frequencies and densities at both layers reported in the descriptive analyses) and the much lower association with its saplings (and low frequency and density). The low correlation between the sapling and canopy layers suggests that compositional similarities or dissimilarities at the canopy layer are not related to a similar pattern at the sapling layer and weaken the characterization of forest succession. Therefore, the relative associations between the size classes of canopy and subcanopy trees may be used to depict a general pathway of compositional change, but the abundances of species at the respective layers and overall forest structure are less predictable.

<u>A Model of Forest Succession</u>. From the calculated positive and negative associations among these most important canopy trees, including the significant associations to other canopy and subcanopy

Table 16. Spearman correlations depicting the relationships among the forest layers. Each coefficient reflects the degree of correspondence between species abundances at the correlated forest layers based on dissimilarities (euclidean distances) among the 12 forest areas.

	Canopy	Subcanopy	Sapling	Seedling
Canopy	1.000			
Subcanopy	0.337	1.000		
Sapling	0.237	0.524	1.000	
Seedling	0.646	0.536	0.364	1.000

Number of observations = 78 At alpha = .05, the critical value of  $R_s = -.306$ 

trees (see Appendix D), a general model of forest succession has been constructed (Figure 15). Ficus sycomorus is separated as a pioneer species, significantly associated with Antidesma venosum (along the river) and invaded by Sorindeia madagascariensis. Although the association is positive between Ficus sycomorus and Pachystela msolo, it is nonsignificant, supporting a spatial and/or temporal separation between the species. For instance, Ficus sycomorus is a canopy component in all forests that have Pachystela msolo as a dominant and is among the most important trees in three of the five forests (see Appendix C). The regeneration of Ficus sycomorus is spatially distinct, but its occurrence as a canopy tree is in association with other canopy-tree species.

The temporal distinction among Pachystela msolo, Sorindeia madagascariensis and Diospyros mespiliformis is less clear and is depicted as a unit. The higher and significant association between saplings of Sorindeia madagascariensis and canopy trees of Pachystela msolo supports placing the latter species next in the sequence. Both species as saplings are positively associated with Ficus sycomorus, but the low overall frequency of Pachystela msolo weakens the significance of that correlation. The occurrence of Pachystela msolo and Sorindeia madagascariensis overlaps, probably both temporally and spatially. Their co-occurrence within forest patches is demonstrated by the forest summaries (Appendix C). Upon a closure of the forest canopy species common along the river edge decline: Antidesma venosum and Spirostachys venenifera. Diospyros mespiliformis is tolerant of closed forest, as evidenced by its significant invasion under Pachystela msolo and its positive association (nonsignificant) to

The boxes represent separate stages, the distance between the boxes suggest spatial (or temporal) separation, and curved dashed lines represent the co-occurrences among Correlations to the canopy-tree forest Species are identified as invaders, decliners, or associates depending on the size-class correlations (or chi-square associations; see Appendix D). (----), or nonsignificant (\*\*\*). A model of riverine forest succession in the TRNPR. dominants (in the boxes) are indicated as significant the communities with a forest patch. Figure 15.



Sorindeia madagascariensis. Coupling these results with personal observations, I suspect that recruitment by Sorindeia madagascariensis and Diospyros mespiliformis overlaps temporally but not spatially. Sorindeia madagascariensis may replace Pachystela msolo in response to the loss of individual trees, while Diospyros mespiliformis has high regeneration in areas that have experienced a stand-level dieback of Pachystela msolo. The relative dominance of these two trees may be dictated by the pattern of senescence in Pachystela msolo. In view of the low regeneration recorded for Pachystela msolo, one may project a trend toward greater dominance by Sorindeia madagascariensis and Diospyros mespiliformis.

Garcinia livingstonei and Mimusops fruticosa establish under Sorindeia madagascariensis and Diospyros mespiliformis, respectively. Their occurrence as canopy trees is spatially and temporally distinct. Ficus sycomorus, Pachystela msolo, Diospyros mespiliformis, and Sorindeia madagascariensis decline upon this change in canopy-tree dominance. Cola clavata and Cordia goetzii are significant associates, and although regeneration by the seven more important canopy trees is absent, invasion by other tree species is demonstrated. The invaders (Hyphaene compressa, Lecaniodiscus fraxinifolius, and Acacia elatior), however, are species that occur at the forest-plains transition and support the conclusion that the trend may be toward a nonforest community.

The negative or mostly low associations between Acacia robusta and the size classes of the other canopy trees complicate its relationship to the forest communities represented in the model. The tree may invade large areas of disturbance in response to fire (pers. obs. at Mnazini South), in response to severe flooding damage (pers. obs. Baomo South), or in response to large clearings for agriculture (pers. obs. Mchelelo Research Camp). If the moisture conditions are suitable, *Ficus sycomorus* will also become established subsequent to large disturbances (e.g., Baomo South and at the Mchelelo Research Camp). These observations would explain the positive correlation between subcanopy trees of *Ficus sycomorus* and *Acacia robusta* (see Figure 14).

The model presents a pathway of forest compositional change that may occur between an open area near the river and the savanna or plains. At no stage represented by the six canopy trees is there a significant association with (i.e., invasion by) saplings of the same tree species. The model supports the conclusion that forest composition is not stable and emphasizes the dynamics of this ecosystem. The 12 forest areas may be placed along the trend according to their canopy dominants, and it is clear that an increase in species richness is coincident (Appendix C). This trend may be explained by an increase in tree-fall gaps with the decline of earlier established canopy species and replacement by a greater diversity of gap-tolerant species (e.g., Albizia gummifera, Albizia glaberrima, Sterculia appendiculata, and Acacia robusta). Species richness is highest in forests that contain Acacia robusta, indicating that gap formation increases the heterogeneity of these forests. A change in the river course and consequent groundwater regime may disrupt the trend and alter the regeneration patterns to an earlier (retrogressive) or later (progressive) stage. Such disturbances clearly complicate the temporal

(or age) relationships among the communities represented by the model. The consequence of a disturbance could be predicted by determining the species that invade (in reference to the succession model), or by understanding the site conditions characteristic of a particular stage.

# Forest Regeneration Near Three Canopy-Tree Species.

The three primate food resources selected for this comparative study, Ficus sycomorus, Pachystela msolo, and Sorindeia madagascariensis, are represented by the first three stages of the succession model (Figure 15). The amount of overlap or separation among the species is not clearly depicted in the calculated association indices. Comparisons among the site, compositional, and resource attributes of the three species and their vigor states (e.g., young, mature, senescent, and dead) further characterize natural forest regeneration within those communities associated with the highest abundances of primates and their food resources.

The 41 trees are located in 11 of the studied forest areas. In many instances a single forest had several species and several vigor states of a species, further emphasizing the heterogeneity within a forest patch (cf. Chapter 3). For instance, ten trees in Baomo South a were included in the study: PD = 3, POK = 1, PS = 2, SO = 1, SOK =1, FY = 1, and FO = 1. The study of *Pachystela msolo* was restricted to Mnazini North and Baomo South, where it occurs in nearly monodominant stands. The large area of *Pachystela* stand-level death is located in Baomo South a. An examination of the site attributes of these trees, located throughout the study area, serves not only to differentiate the selected tree species, but also partially

characterizes the site variability present within the TRNPR.

Riverine forests are often classified according to landform and soil types, and the Tana River forests have been no exception (Homewood, 1976; Marsh, 1978a; Hughes, 1985). Therefore, as a first examination, the 41 trees are plotted according to the percentage of sand, silt, and clay measured in the subsurface (30 cm) sample (Figure 16). All the trees were located on soils containing less than 50% silt, suggesting that this textural type is not abundant across the floodplain within this region. Ficus sycomorus occurs over the widest range of soil types. This wide distribution may be explained by its early establishment at a pioneer site, and its persistence through a long lifespan characterized by a change in soil conditions. Sorindeia madagascariensis is primarily located on sites high in sand, while Pachystela msolo is located on soils containing less than 50% sand (i.e., loam to clay). The predominance of clay at the Pachystela msolo sites was also identified from a field examination of soils taken at a depth of 1.5 m, supporting a conclusion that the soil texture has not changed in recent times. In contrast to the vegetation classifications presented in earlier reports that associate Pachystela msolo with well-drained levee positions (Marsh, 1978; Hughes, 1985), these results suggest that Pachystela msolo, as a mature tree, is more associated with fine-textured soils, perhaps along the backside of the levee.

<u>Statistical Examination of Group Contrasts</u>. The calculated Kruskal-Wallis statistics demonstrate that, in most cases, the differences among Ficus sycomorus, Pachystela msolo, and Sorindeia



Figure 16. Subsurface soil texture of the regeneration study plots. The symbols correspond to the vigor classes: young  $\oplus$ ; mature and vigorous  $\pm$ ; senescent  $\blacktriangle$ ; and dead  $\blacksquare$ .

madagascariensis are more significant than are the differences among the vigor states (Table 17). This finding supports the results from the association analyses and the placement of the species as separate stages in the model. The significant differences among the groups based on species vigor support the presence of a continuum within a stage. Statistical significance, however, may be attributed to differences between two species or one or more of the tree-species vigor states. The source of the variation is important to the final interpretation of results.

The compositional and resource attributes at the sapling layer (SAPSPP, SAPFOOD), and the number of canopy species (CANSPP), although not all significant, show some interesting differences among the species and/or their vigor states (Figure 17). For instance, the median values and range of variation among the number of canopy species (CANSPP) show a higher species richness associated with Sorindeia madagascariensis, and especially with senescent individuals of this species. This box plot supports the earlier conclusion that there is an increase in species richness along the depicted forest successional trend. Saplings of primate food items (SAPFOOD) appear most abundant near Ficus sycomorus, but the trend toward a higher abundance with the senescence and death of Pachystela msolo is also presented. This trend toward greater resources at the sapling layer is coupled to a very significant increase in sapling species richness (SAPSPP). Together, the two box plots (SAPFOOD and SAPSPP) suggest that treespecies establishment and the regeneration of primate food items increase upon the death of Pachystela msolo.

Table 17. Statistical examination of population differences among Ficus sycomorus, Pachystela msolo, and Sorindeia madagascariensis, and intraspecies differences based on tree vigor. Listed are the calculated Kruskal-Wallis statistics (H), and associated probabilities (prob.). Variable descriptions are provided in Table 13.

Species (df = 2)Vigor (df = 7)Variable Names H prob. H prob. Compositional Attributes CANSPP 5.74 0.057 7.29 0.4 SAPSPP 4.77 0.092 15.73 0.028 0.64 0.726 7.31 0.397 SDSPP VINEDEN 3.84 0.147 6.77 0.453 0.939 PHOENIX 0.12 0.940 2.33 **Resource Attributes** CANFOOD 6.95 0.031 11.14 0.132 SAPFOOD 11.05 0.004 12.12 0.017 SEEDFOOD 2.00 0.367 11.42 0.121 0.25 5.74 0.571 SABACOV 0.881 Site Attributes 2.46 0.292 6.66 0.465 SURSAL 4.18 0.124 10.79 0.148 SUBSAL 9.5 0.009 13.06 0.071 SAND 6.54 0.038 14.52 0.043 MOISTURE 0.076 7.66 0.363 FLOOD 5.16 0.042 13.82 0.055 6.32 RIVDIST EDGEDIST 11.93 0.003 14.82 0.038



Abundance of Primate Resources as Saplings SAPFOOD



Figure 17. Box plots depicting the range of variation in selected compositional, resource, and site attributes among Ficus sycomorus, Sorindeia madagascariensis, Pachystela msolo, and their vigor states. The box represents the first quartiles from the median, the vertical line in the box represents the median, the horizontal lines extending from the box depict the range, and outliers are shown with an asterisk. The vigor states include: Ficus young (FY), mature (FOK), and senescent (FO); Sorindeia mature (SOK), and senescent (SO); and Pachystela mature (POK), senescent (FO), and dead (FD).





% Sand at 30 cm SAND



% Soil Moisture at 1.5 m MOISTURE





Distance to the river and forest edge, soil moisture, and percent sand are significantly different among the three species, and soil moisture and distance to the forest edge are also significantly different among the groups based on vigor (Table 17 and Figure 17). Ficus sycomorus occurs closest to the river, especially as immature trees, while the greater distance of Pachystela msolo from the forest edge is clearly demonstrated. Sorindeia madagascariensis, as a mature and vigorous individual, shows great variability in its distance from the forest edge, but as a senescent tree its proximity to the forest edge is evident. The results support the expectation of an inverse relationship between sand and moisture percentages as represented by the group differences. Contrasts among the species, based on sand percentages, complement the presented diagram (see Figure 16), and demonstrate an adaptation by Ficus sycomorus to a wide variety of sites, the greater sand content of soils associated with Sorindeia madagascariensis, and the low percentage of sand associated with Pachystela msolo. The box plot also shows highest variability in the soil texture associated with senescent Ficus sycomorus, and an increase in sand percentages corresponding to senescence and death in Pachystela msolo. Highest soil moisture contents are associated with young individuals of Ficus sycomorus and mature and vigorous Pachystela msolo. The stand-level death of Pachystela msolo in Baomo South was primarily attributed to a major flood event in 1969. After the 1988 flood I recorded approximately eight fallen Pachystela msolo in Mnazini North. The statistical results suggest that the areas of vigorous Pachystela msolo in these two forests have highest soil

moisture contents, high flood levels, and fine-textured soils. Based on earlier observations and the current results, the long-term survival of *Pachystela msolo* in the studied forest areas is certainly in question.

Expanding the analysis to include a multivariate examination of variables, I found greatest differences among the species based on the site or resource characteristics and among the vigor states based on compositional characteristics (Table 18). MANOVA is similar to canonical variate analysis (cf. Chapter 3): the calculated Wilk's lambda is dependent on the discriminating power of the vector, and that vector is defined by the correlations (or loadings) between the variables and the vector (Appendix E). In the analysis of site differences among the species the computed vector explained ~65% of the variance. All variables except the distance to the river proved useful (i.e., had relatively high loadings) in the analysis. The distance to the river does not distinguish the site conditions at a location, probably a consequence of channel migration, sedimentation history, and floodplain topography. The abundance of canopy food species is the most important resource distinguishing the species groups when combined with the other resource attributes (99.77% variance). The vigor states are significantly different based on the compositional attributes and, although the number of sapling species has the highest loading, no variable is inconsequential. In summary, the differences among the three species and their vigor states is further clarified by examining a combination of site, compositional, or resource attributes.

Table 18. Results from the multivariate analysis of variance (MANOVA), depicting the calculated Wilk's lambda (the discriminating power of the variable group) and its probability. Variables used in the analyses are defined in Table 13.

	<u>Tree Species (n = 3)</u>		<u>Tree Vigor (n -</u>	<u>Tree Vigor (n = 8)</u>	
Variable Group	Wilk's lambda	prob.	Wilk's lambda	prob.	
Compositional	.630	.084	. 204	.026	
Resources	.683	.029	. 388	.052	
Site	.451	.002	.263	.131	

Summary of Results

The examination of canopy-tree size-class distributions, their inter-associations, and a comparative analysis of the compositional, resource and site characteristics of three tree species elucidates several general patterns of natural forest regeneration within the TRNPR. The forest patches vary in composition from those dominated by *Pachystela msolo*, to a more mixed composition with *Sorindeia madagascariensis*, or *Mimusops fruticosa* and *Garcinia livingstonei*. Canopy trees are regenerating within the studied forests, but their low occurrences at the subcanopy layer suggest at least a temporal gap in the closure of the canopy subsequent to the death of earlier established trees. The results reveal significant patterns of compositional change, including a projected decline in the relative importance of *Pachystela msolo*, and a decline in two trees more abundant downstream (*Kigelia africana* and *Oxystigma msoo*).

The model developed from the inter-associations among the size classes of canopy and predominant subcanopy trees clarifies the relative tolerances of species and the relationships among the forest communities that occur between the river and the plains. Pioneer forest communities develop along the river, a dominance by *Pachystela msolo* is obtained, and a mixed forest composition follows that is dominated by *Sorindeia madagascariensis* and *Diospyros mespiliformis*, and later by *Garcina livingstonei* and *Mimusops fruticosa*. Regeneration patterns associated with the latter stages suggest a progressive trend toward a nonforest community. None of the primary canopy-tree species has a high and significant association to its progagules, demonstrating a low level of self-replacement within the

forests. Coupled to the low correlations among the sapling and canopy forest layers, these findings substantiate the absence of a stable (or climax) forest composition. Species richness increases along the trend, possibly attributed to the death of trees and consequent patterns of gap-replacement. Current low regeneration of *Pachystela msolo*, however, may disrupt the trend, lessen its importance as a stage in forest development, and increase the importance of the mixed forests.

The comparative study of Ficus sycomorus, Pachystela msolo, and Sorindeia madagascariensis supports the spatial or temporal separation of these species, the comparatively higher abundance of saplings and food resources in the early stages of succession, and the increase in canopy-tree species richness with forest development. The results also indicate a corresponding change in site characteristics as identified by differences among the three tree species and the presence of a continuum in the conditions associated with tree vigor. The greater site variability demonstrated by vigor states of Ficus sycomorus may be attributed to its early establishment, long lifespan, and its adaptation to changing environmental conditions. A multivariate approach proved effective in the statistical examination of species and intraspecific differences, encouraging the examination of several characteristics in a site classification.

Forest Dynamics in the Tana River National Primate Reserve

The overall mechanism of forest change within the TRNPR floodplain is primary succession. The Tana River, through lateral migration and differential deposition, establishes new land areas that are colonized

by pioneer forest trees. These sites are also invaded early by other canopy tree species. The relative dominance of these species later may be explained by their different tolerances of existing site conditions. It is suggested that the relative dominance of Sorindeia madagascariensis or Diospyros mespiliformis may be partially explained by the pattern of decline in Pachystela msolo (i.e., single treefalls or stand-level death), and accordingly, the amount of light reaching the understory. Tree species established early are replaced by other trees within forest gaps and the size of the gap influences which trees reach the canopy. The overall pattern of compositional change toward the plains is at least partially dependent on the tolerances different tree species have to water stress (a low groundwater table), or anaerobic conditions (flood inundation). Forest succession along the Tana conforms to the tolerance model of succession proposed by Connell and Slayter (1977) and supports the importance of individual canopytree life histories as suggested by Drury and Nisbet (1973). Moreover, the mechanisms of succession are dictated and complicated by regional (e.g., channel migration) and local (e.g., flood events) disturbances, respectively (cf. Pickett et al., 1987). Contrasts in the site conditions (e.g., soil texture and moisture) of the three species examined in this study, and the different flooding regimes of the Tana River forest communities, as measured by Hughes (in press), support the conclusion that the floodplain is developing through lateral and vertical accretion coincident to primary forest succession.

The stand-level death of *Pachystela* msolo is related to its narrow range of tolerance in the floodplain environment. The observed

life-history of this species may be explained by the cohort senescence theory (Mueller-Dombois, 1986):

- (1) initial establishment upon perturbation (point-bar or levee formation);
- (2) cohort growth to maturity;
- (3) stress induced by an environmental factor (floods);
- (4) tree senescence (exhibited by termite infestation and crown die-back);
- (5) tree death (synchrony dictated by the magnitude of the flood).

Flooding, which may be necessary for early tree establishment, becomes a trigger for senescence and death. Coincident to the establishment and growth of a *Pachystela* forest, the position of the site changes relative to the river and consequently the flooding regime within the forest changes. Saplings increase parallel to senescence and death of the cohort, but in contrast to the study of *Meterosideros polymorpha* conducted by Mueller-Dombois in Hawaii, I identified no selfreplacement by *Pachystela msolo*.

After the decline of *Pachystela msolo*, the patterns of forest change are dictated by the death of individual trees and gapreplacement. A similar study of the varzea along the Amazon also shows a transition toward a mosaic forest of greater heterogeneity (Salo and Kalliola, in press). In more humid environments, however, a gapreplacement of species (Salo and Kalliola, in press), or even a cyclical replacement of a monodominant, such as white spruce along the Beatton River in British Columbia (Nanson and Beach, 1977), is similar to the forest dynamics of the upland landscape (Budowski, 1970; Hartshorn, 1980; Nanson and Beach, 1977). On the Tana River, however, the upland vegetation is thorn-scrub. Forest is confined to a narrow band with environmental factors dictating its expansion on either edge. According to the "kinetic" view proposed by Drury and Nisbet (in Veblen, 1987), the process of succession (progressive or retrogressive) is dependent on the dynamics of the river such that the end points are unstable. A stable, or equilibrium, forest community is absent from this riverine environment. Although forest composition and structure may be explained by a certain pattern of vegetation succession, the condition of the existing forests is complicated by the disturbance regime. •

## CHAPTER V

# FOREST CONDITION AND THE DISTURBANCE REGIME

#### Introduction

Forests along the Tana River occur within a mosaic of vegetation communities that represent a landscape defined by the riverine disturbance regime (Godron and Forman, 1983). This landscape is further characterized by certain human and large mammal disturbances associated with the floodplain environment. Forest condition, therefore, may be interpreted in view of the relative impacts imposed through floodplain dynamics, human forest use, and animal impact. The expression of condition, however, is depicted in the composition and structure of the existing forest areas. In compliance with the overall objectives of this study, the evaluation of forest condition is based on an understanding of the attributes of high-quality habitat for the endangered primates and the natural patterns of forest-habitat regeneration. This chapter, therefore, considers forest condition through a descriptive and spatial examination of selected impacts on the forests and also provides evidence of vegetation decline. It serves both as a summary of results from earlier sections that address habitat quality and natural regeneration patterns and as a characterization of the spatial distribution of contrasting habitat within the TRNPR. The discussion should clarify major aspects of the disturbance regime, especially as it influences the riverine forest ecosystem within this landscape.

## Data and Methods

# Descriptive Analyses

Forest condition was first examined in view of certain external impacts on forest habitat quality. I identified and measured four primary external impacts on forest condition: forest loss and fragmentation, floodplain dynamics, human extraction of forest products, and animal impact. Forest loss and the consequent change in the area-to-perimeter ratios of the existing forests were measured from air photos taken in 1960 and 1975, and from ground surveys completed during the field research (1987-1988). The study of floodplain dynamics was restricted to a measure of river length obtained from the 1960 and 1975 photos, ground survey measures of bank erosion, and an examination of certain characteristics of the 1988 flood (e.g., flood heights and the nutrient status of floodplain deposits). River discharge data were obtained for the hydrologic station located at Garissa (see Figure 1) from the Hydrology Department, Kenya Ministry of Water Development. Nutrient analyses for floodplain deposits collected at eight localities within the Reserve were completed by the Soil Testing Laboratory, Kenya Ministry of Agriculture. I compared these data to surface soil analyses completed by Hughes (1985) in the TRNPR. For the purpose of studying human forest utilization and animal impact, basal area coverages of wood cut for poles or impacted by animals were compiled by species during the ecological vegetation sampling in the 12 forest areas (cf. Chapter 3). Whereas a general summary of the forest resources for the Pokomo is presented in Chapter 2 (cf. Appendix B), this section focuses on the relative utilization of each species and certain growth responses.

Secondly, I looked for evidence of vegetation decline through a temporal comparison of canopy-tree composition in four forest areas and a measure of forest senescence in the 12 forest areas. Vegetation data depicting tree species abundances at the canopy forest layer were obtained from K. Homewood (unpubl. data) for the Mnazini South and Mnazini North forests, and from C. Marsh (1978a, 1981a) for the Mchelelo West and Congolani West forests. These data were collected prior to the establishment of the Reserve (~1973-1975). When compared with the ecological data collected in this study (1987-1988), they provided an approximate 12-year measure of vegetation change. The vegetation plots established by Homewood were overlaid to my sampling design, and the comparison focused on changes in species density, frequency, and relative importance within similar sampling areas. Marsh (1978a) completed enumerations of canopy trees in the Mchelelo West and Congolani West forests during his field research, and then completed a re-enumeration in the Mchelelo West forest in 1985 (Marsh, 1986). Temporal vegetation changes in these two forests were determined from density estimates compiled from both of our studies. Wilcoxin Signed Ranks Test for Two Groups was computed for each forest comparison to determine if significant differences (a two-tailed test) in the composition of the forest canopies exist between the two time periods (Sokal and Rohlf, 1986; Hammond and McCullagh, 1980). Although the sampling areas were comparable, the differences in species densities were interpreted in view of possible contrasts between the plot sampling technique used in the studies by Homewood and Marsh and the point-centered quarter method employed in this study (Brower and Zar, 1984).
Forest senescence was measured as the basal area coverage of wood that was dead and on the ground in the vegetation sampling plots. Realizing the discrepancies in recorded versus actual coverages that may be attributed to differential rates of decomposition and/or firewood acquistion, I believe nevertheless that these data represent approximate measures. The coverage estimates were ranked in three classes, depicting low (< 1 m<sup>2</sup>/ha), medium (1-10 m<sup>2</sup>/ha), and high (> 10 m<sup>2</sup>/ha) levels of forest senescence.

### Spatial Analyses

ARC-INFO geographic information system (GIS) software was used as a technical tool to assist in the spatial analyses. Data sources included field data from the vegetation plots, topographic maps, and the 1960 and 1975 air photos. Spatial data, including forest area and river location in 1960 and 1975, current forest distribution, and sampling point locations were digitized. One feature of ARC-INFO, a vector-based GIS system, is the automatic compilation of area and perimeter for each polygon, and the length of each arc (ESRI, 1987a). Forest areas, area-to-perimeter ratios, and river length changes were determined from this output. An overlay of the 1960 and 1975 maps depicted areal changes in forest distribution and river position between the two time periods.

Forest-attribute data were compiled for each of the 363 sampling points in the 12 forest areas (cf. Chapter 3, Chapter 4). Ecological sampling, although conducted at points, was designed to represent areal units. In other words, the variation within a sampled forest area was determined from point interpolation. Theissen polygons were

constructed around all sampling points, based on equivalent interpoint distances (ESRI, 1987b). If all interpoint distances are equivalent, then the respective Thiessen polygons are equivalent. An irregular distribution of points results in unequal polygon areas but an unbiased interpolation (based on equal interpoint distances) of between-point variation. A further discussion of the technique is provided in Burrough (1986) and ARC-INFO TIN (ESRI, 1987b). Ecological attributes for each point (or polygon) were input as text files into the INFO database, following data compilation and appropriate analyses. The geographic database therefore includes information on position (coordinates of all mapped features), topology (e.g., distances between features), and attributes (to be portrayed spatially). Maps were prepared to depict the spatial distribution of selected forest characteristics, using the classed attribute data, the point (or Thiessen polygon) positions, and the forest base map.

# Results and Discussion

#### External Impacts on Forest Condition

Regional Changes in Forest Area. An examination of primate-tohabitat relationships demonstrates the importance of forest area and the respective area-to-perimeter ratios to the abundance of endangered primate groups. The primates are interior forest species, such that a loss in forest area and/or increase in forest edge are negative impacts on their populations. I measured from aerial photographs that between 1960 and 1975 forest area was reduced 56%, five forests were fragmented into 15 forest patches, and the mean area-to-perimeter ratio was reduced from 0.293 to 0.163 (Figure 18). This reduction in forest area



Figure 18. Map overlay depicting forest and river position changes between 1960 and 1975 in the south-central sector of the TRNPR. The forest areas of this study include: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). prior to the establishment of the Reserve is attributed to changes in the river course and also to forest clearing by the local Pokomo population. Marsh (1976) reports that much forest clearing occurred between 1961 and 1969, when many Pokomo moved from the east to west bank to escape raids by the Somali "shifta" (bandits). Much of the forest loss south of Congolani West, however, is probably attributable to forest senescence subsequent to a meander cut-off during the 1961 flood. The most significant decline in primate groups occurred in the Guru South forest (from ~10 to 3 groups). This decline may be partially explained by a narrowing of the forest patch in response to a westward shift in the river course and forest clearing along the north and south edge. Guru South suffered a significant decline in forest area and in its area-to-perimeter ratio.

Since the establishment of the Reserve in 1975, I measured from ground survey within the studied forests an approximate 4% decline in mature or actively regenerating forest (Table 19). These measured losses are related to forest clearing by the Pokomo (54%), and forest loss attributable to erosion (46%) prior to the 1988 flood. Nearly 45% of the land cleared by the Pokomo was not planted through the field research period (1987-1988). Seedlings representative of early succession (e.g., Ficus sycomorus, Sorindeia madagascariensis, and Antidesma venosum) were observed invading these localities, suggesting that natural regeneration in areas of recent disturbance is possible.

<u>Floodplain Dynamics</u>. The evergreen-semievergreen forests along the Tana River are dependent on the groundwater regime provided by this perennial stream. Forest distribution, structure, and composition are

dictated by both the positive and negative influences of floodplain dynamics. Riverine forest occurs within a corridor that is less than 1 km from the river (Hughes, 1985). Both Marsh (1986), and Hughes (1988) suggest that flooding may be a critical factor in seedling establishment. The higher moisture regimes and flood heights associated with young individuals of Ficus sycomorus and mature Pachystela msolo identified in this study support the idea that floods are important to the early stages of riverine forest succession. Moreover, the results suggest a change in floodplain topography, which occurs parallel to forest succession and may be explained by a differential deposition of sediments. Hughes (in press), in a regional study along the Tana (between Bura and the TRNPR), differentiates forest communities on the basis of their height above the river, flooding frequency, and duration of inundation. A. Niue is currently conducting a study that addresses the influences of soils and hydrology on forest ecology within the TRNPR (see Njue, 1987). In view of the importance of floodplain dynamics as a disturbance factor influencing this forest ecosystem, I have compiled data on temporal changes in the river position and also on important characteristics of the 1988 flood that occurred during the field research.

Along the west bank of the river, within the forest areas included in this study, I recorded approximately 7.5 hectares of mature forest lost to riverbank erosion prior to the 1988 flood (Table 19). It is not clear whether or not this loss within the TRNPR was compensated by an equal development of new areas for colonization. Channel migration (i.e., meanders), deposition and erosion, and overall river length should be at equilibrium within the floodplain if the water volume and

	Area	Area-to-perimeter	Forest Loss (hectares)
Forest	(hectares)	ratio	Erosion Clearing
Mnazini South (ms)	50.08	0.781	
Mnazini North (mn)	36.18	0.785	2.2
Kitere West (kw)	18.35	0.517	2.6
Baomo South (bsa, and bsb)	122.80	0.847	0.36
Baomo North	16.44	0.453	3.64
Sifa West (sw)	2.80	0.238	
Congolani West (cw)	37.18	0.591	
Congolani Central (cc)	52.38	1.164	
Mchelelo West (mw)	16.81	0.522	0.17
Guru South (gs)	45.98	0.606	
Guru North (gn)	4.93	0.190	7.30
Totals	403 93		7 47 8 80

Table 19. Summary of forest-patch areas, area-to-perimeter ratios, and measured area losses attributed to river erosion and human clearing within the study areas. Forest codes listed in parentheses reference the 12 study areas described in Table 1.

sediment load of the river remain constant (Hooke, 1984; Petts, 1984). The distance within which the equilibrium is maintained, however, is less clear. Between 1960 and 1975, the two major meander cut-offs and other fluctuations in the river course resulted in an approximate 3.5% decrease in river length (from ~37.6 km to ~36.3 km) within the Reserve. Coupled to erosional losses, the decline in the overall land area suitable for a groundwater-dependent forest (i.e., within the 1 km corridor) provide a partial explanation for the significant forest loss measured in the TRNPR. Turner (1989) states that a dynamic landscape may exhibit a stable mosaic at one spatial scale but not at another. Along the Tana, the spatial scale at which a stable mosaic of forest communities is maintained is not clearly understood.

Much bank erosion and migration of the river channel occurs during floods, but these times are also associated with high soil moisture and an input of nutrients. Within one week during early May, 1988, flood waters entered into all oxbows and low lying areas. The height levels and calculated discharge values recorded by the Kenya Ministry of Water Development at Garissa approximate the flood as a two-to-five year event (Figure 19). Floodwater entered all but three forests, with highest levels near forests bordering old oxbows (Congolani Central), and backwater swamps (Guru North) (Figure 20). All the Pachystela forests (Mnazini North, Kitere West, Baomo South a, and Baomo South b) received high floodwater, and at some locations I measured a 2-5 cm deposit of sediments. Homewood (unpubl. data) recorded flooding at only 9.5% of her sampling plots within the Mnazini North Forest, in contrast to my record of floodwater at 30 out of 31



Figure 19. Tana River discharge measured daily at the Garissa station gauge. Data obtained from the Hydrology Department, Kenya Ministry of Water Development. Discharge is measured in cubic meters per second (cumecs).



Figure 20. Mean flood heights and the range determined from the sampling points in the 12 forest areas: Mnazini South (ms), Mnazini North (mn), Kitere West (kw), Baomo South a (bsa), Baomo South b (bsb), Baomo North (bn), Sifa West (sw), Congolani West (cw), Congolani Central (cc), Mchelelo West (mw), Guru South (gs), and Guru North (gn). No floodwater was recorded within the Sifa West, Congolani West, Mchelelo West, and Guru South forests. Forest-area locations are presented in Figure 18 (see also Table 1; Figure 3). plots (96.7%), and a mean floodwater height equal to 30.5 cm. Coincident to 1988 flood in this forest approximately eight large (> 40 cm dbh) *Pachystela msolo* trees fell, resulting in the formation of many large gaps. These findings suggest a change in the position of this forest relative to the river and a consequent change in the forest composition of these gaps. The regeneration reported near dead *Pachystela msolo* in the Baomo South forest (see Chapter 4) may be predicted to occur within the recent gaps in Mnazini North.

Whereas the loss of Pachystela msolo individuals may be viewed as a negative flood impact on the forests, high soil moisture and new sediments should increase the suitability of these areas for seedling establishment. Floods are most often associated with lateral (pointbar) and vertical (levee) accretion and an increase in the fertility status of existing soils (Gerrard, 1987; Brinson, 1989). Hughes (1985) collected surface-soil samples from several localities within the TRNPR and examined their fertility status. I compared the fertility status of those soils to the flood deposits collected in 1988 (Table 20 and Figure 21). The soil fertility of these soils may be compared by the amounts of potassium, sodium, calcium, and magnesium (the primary cations), the cation-exchange capacity (CEC, a measure of cation availability), or the base-saturation (the sum of the four primary cations/CEC). Each attribute is related to the ease at which cations are absorbed by plants (Tisdale et al., 1985). A comparison of the soils and flood deposits indicate that: (1) the fertility status of each sample is very high, or adequate for crop or tree production; (2) the relative amounts of cations are more closely related to soil texture than to the date the sediments were deposited; (3) the very

Site Description Surface Soils	Potassium (milliequi	Sodium valents	Calcium per 100 g	Magnesium rams soil)	C.E.C	<b>X</b> Carbon	Н	E.C. (mmhos/cm)	Texture	Investigator
Guru South-levee (plot 4A) Congolani West-inactive levee (4B) Mchelelo-inactive levee (4C) Mchelelo-levee (4D) Makere East-point Bar (14A) Baomo South-clay evergreen (14C)	0.59 2.56 1.38 1.38 0.19 1.84	0.26 0.78 0.87 0.17 0.32 0.32	6.10 36.50 24.25 6.90 8.08 37.50	2.99 11.10 12.01 3.04 2.19 15.83	12.0 9.6 55.2	0.593 5.096 3.648 0.779 0.249 3.327	6.35 6.9 7.5 8.0 6.55	1.00 2.65 3.50 2.06 2.06 1.69	sandy loam clay clay/sand loamy sand sandy loam clay	Hughes 1985 Hughes 1985 Hughes 1985 Hughes 1985 Hughes 1985 Hughes 1985
Flood Deposits Guru North-levee (< lm from river) Guru North-levee (4 m river) Guru North-back point bar Mmazini North-(40 m to river) Mmazini North-(levee, <u>Pachystela</u> ) Congolani-(300 m to river) Baomo Village-(15 m to river)	0.65 0.11 0.41 0.49 0.49 0.55	0.77 0.77 0.77 0.77 0.77 0.77 0.77	13.40 3.80 7.60 8.20 8.20 9.20	11.35 2.15 5.35 6.95 6.55 6.55 6.55	38.5 7.0 7.0 46.0 46.0 19.5	0.35 0.04 1.58 1.09 1.09 0.59	8.2 7.6 8.1 8.1 8.1	1.56 0.63 1.56 1.88 1.75 1.88 1.50	clay loam sand clay clay clay clay clay clay	Medley & N.A.L. Medley & N.A.L. Medley & N.A.L. Medley & N.A.L. Medley & N.A.L. Medley & N.A.L. Medley & N.A.L.

Table 20. Comparison of soil fertility among surface soils and 1988 flood deposits collected within the Tana River National Primate Reserve. Surface soils were collected and examined by Hughes (1985). The flood deposits were collected in this study and soil analyses were completed at the Soil Testing Laboratory, National Agricultural Laboratories, Kenya Ministry of Agriculture (N.A.L.).



Figure 21. Soil cations measured in surface soils (Hughes, 1985) and 1988 flood deposits collected within the TRNPR.

high CEC values are probably due to the presence of montmorillonite clays (black-cotton soils), and the difficulty in cation extraction from these soils may explain the low base-saturations; (4) none of the surface soils are saline (E.C. < 4.00 mmhos/cm); and (5) all of the soils are alkaline. The high concentration of calcium in the soils examined by Hughes is probably attributable to capillary water movement and consequent deposition near the surface. The floods are not only important for the influx of nutrients, but also for the removal of high concentrations of carbonates at the surface.

Two major objectives of Hughes' study (1985) along the Tana were to compile ecological data on the riverine forests upon establishment of the Masinga Dam (the fifth dam constructed along the Tana) and to predict possible impacts imposed by river impoundment. The downstream effects are complex. River impoundment can reduce erosion through a reduction in water volume, or increase erosion through a decrease in the sediment load (Petts, 1984). The loss of coarse sediments from the highlands (maintained at the reservoir) and a depletion in the overall sediment load would reduce the rate of over-bank accretion. Reduced flooding, an effect predicted by the Tana River Development Authority (Hughes, 1985), also contributes to reduced sedimentation. Consequently, the development of new floodplain is slowed. Most of the flood deposits observed (and collected) were fine-textured (i.e., clays), with sands occupying only a small area along a few existing levees. Although the effects of the dams and overall floodplain dynamics require further investigation, these results support the

suggestion of a possible decline in forest regeneration that may be attributed to slowed floodplain development and a reduction in colonization sites within the TRNPR.

Human Forest Utilization. The extraction of trees or other woody plants for building materials (i.e., poles), transportation (i.e., canoes), or for domestic and medicinal uses does not directly result in the loss of forest area. In contrast, the plants are selected from the forest with consequent effects on the structure and composition of the existing habitat. Although many ethnobotanical studies have examined the uses of forest products, little quantitative data have been compiled (Hall and Rodgers, 1986). In this study I have compiled ethnobotanical information on the forest resources (see Chapter 2, Appendix B), and have obtained some quantitative measurements on the extraction of forest products within the study area. The basal area coverages of forest resources removed were averaged for each forest area and related to the respective primate populations (see Chapter 3, Figure 5). The results suggest that high levels of extraction may provide a partial explanation for the low number of primate groups observed in two forests (Sifa West and Baomo North). I calculated a significant negative correlation between the number of colobus and mangabey groups and forest disturbance, which included forest senescence, human forest utilization and animal impact. In view of the resident Pokomo population and their use of forest products within this region, this section further addresses human utilization patterns and the possible impacts the extraction of forest products (i.e., woody plants) may have on existing and future habitat quality.

I measured a mean basal area coverage of plant species cut equal to 3.21  $m^2$ /ha. The coverage value is based on measurements of cut stems or palm fronds, so does not include the removal of forbs, grasses or herbaceous vines. Cutting was observed at 42% of the 363 sampling points in the 12 forest areas. Palm fronds account for over 60% of this coverage (total = 1.99  $m^2$ / ha; Phoenix reclinate = 1.38  $m^2/ha$ ). The high coverage value for palms may be partially explained by their basal growth pattern and high basal areas, but also reflects their importance to the local human population. Moreover, the removal of palm fronds was seasonal, so that the measurements are biased by the date at which I sampled a forest area. They are an underestimate of the total quantity removed on an annual basis. The coverage of vines cut equaled .015  $m^2/ha$ , and was primarily attributed to trail clearing, in contrast to their selection as a forest product. In other words, most of the cut vines measured are species not known to be utilized by the Pokomo (e.g., Keetia zanzibaricum). The measurements of cut palms and vines in the forests must be interpreted as general estimates due to seasonal cutting and regrowth patterns, and to their obscurity in the forest (often not rooted within the plot), respectively. More reliable measurements were obtained for the extraction of forest poles  $(1.81 \text{ m}^2/\text{ha})$ , simply by measuring the diameters of cut stems rooted within a plot. Although these coverage estimates provide an overview on the removal of forest products, the relative degree of impact is more related to the species that are selected, the observed impacts on their growth patterns, and the spatial variation in cutting intensity.

A total of 41 tree, seven vine, and three palm species was measured as cut within the study area, or approximately 35% of the total woody species recorded within the plots. Intensive cutting of fronds results in reduced palm heights. For instance, Phoenix reclinata was observed at heights above ten meters, but the mean height of this species within the study area is 5.4 m and the mean height calculated for recently cut individuals is 4.4 m. These results demonstrate a reduction in height growth with cutting, and furthermore suggest that more palms have experienced cutting in the past than were measured in this study. Phoenix reclinata appears to attain reproductive maturity at lower height levels (fruiting was observed on individuals less than 5 meters in height), such that the determination of any positive or negative impact on the reproductive capacity of the species is inconclusive. Intensive cutting on the palm Hyphaene compressa, or the removal of large trees (> 40 cm dbh) for canoes (e.g., Mimusops fruticosa), or beehives (e.g., Ficus sycomorus) results in the death of the individual and a gap in the forest canopy. Impacts on forest composition and structure attributable to the cutting and removal of woody vines is not adequately revealed from the results of this study.

Polysphaeria multiflora is the most highly utilized tree for poles (cut coverage = .292 m<sup>2</sup>/ha), and with an additional 13 species comprise 37.5% of the pole cutting measured within the study area (Table 21). Polysphaeria multiflora is also the most abundant tree at the subcanopy and sapling forest layer. Therefore, a question arises as to whether the utilization of a tree species for poles is related to its relative abundance or to certain preferred characteristics (e.g., specific gravity or the strength of the wood). A scattergram

Table 21. Basal area coverages and growth characteristics of trees that are most highly utilized for poles by the local Pokomo population. Utilization is based on the total basal area coverage of wood that is cut.

	M	iean	Rati	0	Specific
	Coverage (m2/ha)		Stems:Individuals		<b>Gravity</b> <sup>1</sup>
	Total	Cut Stems	Total	Cut	
			(indivi	duals)	
Polysphaeria multiflora (Ps)	2.18	0.292	2.4	2.7	0.629
Sorindeia madagascariensis (Sm)	0.06	0.057	1.2	1.3	0.654
Alangium salviifolium (As)	0.82	0.050	1.7	3.3	0.556
Ficus sycomorus (Fs)	0.22	0.042	1.6	1.0	0.471
Diospyros kabuyeana (Dk)	0.19	0.031	4.2	4.9	
Cordia goetzii (Cg)	0.29	0.031	2.1	3.5	0.609
Lecaniodiscus fraxinifolius (Lf)	0.44	0.031	2.8	6.4	
Diospyros mespiliformis (Dm)	0.11	0.027	1.2	1.4	0.663
Rinora elliptica (Re)	0.26	0.024	2.3	2.2	0.626
Erythroxylum fischeri (Ef)	0.11	0.023	2.5	4.9	
Hunteria zeylanica (Hz)	0.70	0.021	3.8	5.1	
Drypetes natalensis (Dn)	0.28	0.018	1.4	1.6	
Pavetta sphaerbotrys (Ps)	0.37	0.018	1.7	3.2	
Flueggea virosa (Fv)	0.23	0.014	3.0	3.3	

<sup>1</sup>Specific gravity is used as a relative measure of wood density (cf. Chapter 2). It is calculated from a sample of wood cores as: sg = wet weight/ volume(1+(moisture X)) (Brown et al., 1958)

depicting the relationship between the mean coverage of a tree species (at the seedling and subcanopy layers) is not clearly positive and shows disproportionately high coverages of cut wood for Sorindeia madagascariensis, Ficus sycomorus, Diospyros mespiliformis, Diospyros kabuyeana, and Cordia goetzii (Figure 22). Diospyros spp. were also highly selected in a Tanzanian forest studied by Hall and Rodgers (1986), probably related to its relatively dense wood (see Table 21; specific gravity).

An overall response to pole cutting appears to be a reduction in apical dominance and the formation of multiple stems (i.e., coppicing). This observation is demonstrated for most species by the ratio between the number of basal stems (branches at less than ~50 cm from the ground) and the number of individuals rooted (Table 21). Species that do not clearly exhibit this response (Sorindeia madagascariensis, Ficus sycomorus, and Diospyros mespiliformis) are more seriously impacted by pole cutting. These three species are canopy trees, potentially attaining heights above ten meters in the forest. When cut for poles at the sapling or subcanopy layer, the trees are lost and the regeneration of the canopy layer may be reduced. The utilization of most tree species for poles alters the structure of the existing forest, but the positive or negative impact this utilization has on the productive capacity of the selected species is less clear. The selection of canopy trees for poles, with a consequent reduction in the regenerative capacity of the canopy forest layer, is not compatible with forest preservation.

Although the mean cut coverage of woody plant species is 3.21  $m^2$ /ha, the amount cut at some localities is much greater. The



Figure 22. Scattergram depicting the relationship between the basal area coverages of cut wood and total basal area coverages for the most highly utilized tree species. The tree species are listed in Table 21. *Polysphaeria multiflora*, the most highly utilized tree species, is not shown on the scattergram.

intensity of cutting and the corresponding impacts on forest structure vary throughout the sampling area (Figure 23). High intensities are located near settlements, trails, or roads or are associated with the acquisition of a large tree for a canoe or beehive. The localities of more intense cutting at Baomo North, the eastern edge of Baomo South b, and Kitere West are near permanent rural settlements. The high coverages recorded along the river at Mnazini North and at the southern end of Mnazini South are related to the acquisition of Ficus sycomorus for beehives, and Mimusops fruticosa for canoes, respectively. The areas of high cut coverages at the west edge of Guru North, the north and south edge of Congolani Central, the eastern edge of Sifa West, and the northern edge of Mnazini South are near established trails. The intensity of cutting, therefore, is more related to accessibility than to the distribution of resources. Although further studies on the impacts of pole cutting are necessary, management toward a more equitable distribution of the impact would be one conservation strategy.

Animal Impact. Large mammal disturbances (e.g., elephant, buffalo) on the understory forest vegetation include bark removal, browsing, or the breaking of stems. These disturbances varied within the 12 forest patches, such that their contribution to the negative correlation between primate abundances and overall forest disturbance is not clear (see Chapter 3, Figure 9). A mean coverage of  $1.23 \text{ m}^2/\text{ha}$ of damaged wood was calculated within the sampling area. A total of 60 species is recorded as damaged, but approximately 74% of the damage is restricted to 11 species (Table 22). Many of the species (*Rinorea elliptica*, *Terminalia brevipes*, *Grewia trichocarpa*, *Lecaniodiscus* 



Figure 23. Spatial distribution of human forest utilization impact within the 12 forest areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Impact is measured as the basal area coverage of cut stems within the sampling plots.



Figure 23 (continued).

fraxinifolius, and Spirostachys venenifera) are not forest interior species, occurring more commonly along the river, savanna edge, or within old oxbows. A preference for *Rinorea elliptica* is demonstrated, with nearly all of its basal area coverage recorded as damaged (Figure 24).

Animal impact may result in the formation of callus tissue, the production of multiple stems (i.e., coppicing), or tree death. Browsing may also increase stem and leaf production (Roundy and Ruyle, 1989; Belsky, 1986). The migration of large mammals (especially elephant and buffalo) into the riverine forest during the dry season is a natural factor in the disturbance regime (Allaway, 1979; Kortlandt, 1986). For instance, Kortlandt (1986) suggests that figs tend to be highly resistant to debarking by elephants. I observed this resistance in a group of young Ficus sycomorus subsequent to debarking by buffalos within the Guru North forest. The reduction of large mammal populations within the Tana River District has resulted in a reestablishment of woody vegetation on the plains (Marsh, 1986), and probably an increase in forest understory vegetation. There has been a reduction in this natural disturbance factor that may result in an unnatural ecosystem response. The former disturbances to the forest understory caused by large mammals, however, may now be compensated by the utilization practices of the Pokomo. The relationships among animal disturbances, human forest utilization, and the resulting forest ecology require further investigation in this region.

Table 22. Basal area coverages of trees that are most damaged by large mammals.

	Mean Cove	rage (m2/ha)
	Total	Damaged
<i>Rinorea elliptica</i> (Re)	0.26	0.210
Terminalia brevipes (Tb)	0.39	0.129
Grewia trichocarpa (Gt)	0.28	0.098
Lecaniodiscus fraxinifolius (Lf)	0.44	0.098
Ficus sycomorus (Fs)	0.37	0.095
Polysphaeria multiflora (Pm)	0.29	0.091
Pavetta sphaerobotrys (Ps)	0.37	0.043
Spirostachys venenifera (Sv)	0.22	0.042
Cola clavata (Cc)	0.17	0.040
Garcinia livingstonei (Gl)	0.05	0.033
Hunteria zeylanica (Hz)	0.70	0.030



Figure 24. Scattergram depicting the relationships between the basal area coverages of damaged wood and total basal area coverages for the trees most heavily impacted by large mammals (e.g., elephant, buffalo). The tree species are listed in Table 22.

## Vegetation Decline

Temporal Comparisons of Forest Composition and Structure in Four Forest Areas. The ecological data collected on the canopy forest layer by Homewood and Marsh prior to the establishment of the TRNPR in 1975, the resurvey completed by Marsh (1986) and the data collected in this study enable an approximate 12-year comparison of forest change in the Mnazini South, Mnazini North, Mchelelo West and Congolani West forests (see Figure 3 for forest locations). In the resurvey report compiled by Marsh (1986), he states that Mnazini South had experienced a significant decline in forest area and that senescence had occurred within the remaining forest. Approximately 70% of the south sector of Mnazini South (examined by Homewood, 1976) lacks trees and was not included in my sample. A comparison of the remaining portion reveals a significant decline in the canopy-tree densities between the two time periods (Wilcoxon Signed Rank Statistic (T) = 46, n = 25, p < .05) (Appendix F). Overall canopy tree density has declined from ~143 to 95 trees/ha. It is important, however, to qualify some of the measured differences. Cola clavata has a much higher density at the earlier time period, but a lower frequency. This may indicate clumping, which is a difficult measure to obtain in point-centered quarter sampling. The much higher relative importance of Mimusops fruticosa and Garcinia livingstonei is in accordance with the successional pathway presented in Chapter 4 (see Figure 15). In sum, however, Mnazini South has experienced a significant decline in forest area and a decline in canopy tree resources within the remaining forest patch.

In contrast to the decline observed in Mnazini South, Mnazini North has had an increase in forest resources (Appendix F). The calculated differences between the tree-species densities are not significant (T = 22, n = 12, p > .05). The much higher density of *Pachystela msolo* in Homewood's study may be partially explained by the differences between plot and point-centered quarter sampling when sampling closely spaced individuals, or by natural thinning with the growth of *Pachystela* individuals. The much higher density of canopysized (> 10 m in height and > 20 cm dbh) individuals of *Ficus sycomorus* and the higher density of the vine *Saba comorensis* has increased the available primate food resources. The suitability of Mnazini North as primate habitat has improved through the 12-year time period.

From the results of the 1985 tree enumeration in Mchelelo West, Marsh (1986) reports a loss of many canopy-tree species. Based on his two enumerations, I calculated a significant decline in the density of canopy trees (T = 17 [z = 4.1], n = 27, p < .05). The most significant declines were in Albizia gummifera, Diospyros mespiliformis, Sorindeia madagascariensis and Ficus sycomorus. The latter three species are highly utilized food resources for both endangered primates (see Chapter 3, Table 9). Marsh's enumerations and the data collected in this study suggest declines in canopy-tree densities, but the relative importance of each canopy-tree species has not changed significantly. In other words, Mchelelo West has had a decline in resource quantity, but not in composition.

Congolani West is a senescent forest characterized by a loss in forest area and a decline in forest resources subsequent to the meander

cut-off in 1961. This conclusion, however, is not clearly demonstrated through the 12-year time period (Appendix F). On the contrary, a significant increase in the density of tree species (T - 76)[z = 2.7], n = 27, p < 0.05) is measured between the two time periods. One explanation for this discrepancy is that the area originally sampled by Marsh (see Marsh, 1981b) is no longer in forest, and was not really in forest during his enumeration. His sampling area and density measurements were defined by the range of a colobus group that moved northwest from the oxbow to one Ficus bussei tree. I did not observe this tree in my survey and the corridor to the tree's locality is unforested. His tree-density estimates may have been calculated using a large area, most of which was unforested. The forest during the earlier time period had a greater number of trees typical of riverine forest (e.g., Albizia gummifera and Cola clavata) and was apparently lacking canopy trees of Salvadora persica and Cordia sinensis that are typical of savanna vegetation. It is quite probable that the change in overall tree density has not been significant, but the loss of one large Ficus bussei resulted in the area becoming unsuitable for colobus.

The results from these temporal comparisons demonstrate that forest decline from the loss of individual trees within a forest may be equally important to the resulting habitat as is a loss in total forest area. If the species that have declined in density are important (i.e., highly utilized) food items and no replacement resources exist, the impact on the suitability of the area for primates may be significant. In a resource-poor area, such as Congolani West, the loss

of a single tree may make an area unsuitable. An understanding of the behavioral responses of the primates to resource gain and loss is extremely important in predicting the future suitability of forests as primate habitat. For instance, the expansion of the colobus range in Mchelelo West identified by Decker (1989) may be related to its decline in resource density. The similarity in the colobus diet within Mchelelo at the two time periods supports the conclusion that the change in resource composition to date has not been significant (Marsh, 1978; Decker, 1989). Demographic and behavioral differences among the existing primate populations in Mnazini North (an area of resource gain) to those of Mchelelo West (an area of resource decline) and Mnazini South (an area of forest loss and resource decline) may be related to these temporal patterns of forest change.

Forest Senescence. In the study of primate-to-habitat relationships, I determined a significant negative correlation between forest disturbance (a combined measure of forest senescence, human forest utilization, and animal impact) and the number of endangered primate groups within a forest area (cf. Chapter 3) Much of the forest disturbance was related to forest senescence (Chapter 3, Figure 5). Highest levels of forest senescence were measured in Congolani West (explained by a decline toward savanna vegetation) and in Baomo South (the loss of many *Pachystela msolo* trees subsequent to the 1969 flood).

The spatial variation among all sampling points in basal area coverages of dead wood further demonstrates these patterns, and emphasizes the impact forest edge has on tree mortality (Figure 25). Lovejoy et al. (1986) report that elevated rates of tree mortality are



Figure 25. Spatial distribution of forest senescence within the 12 forest areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Forest senescence is measured as the basal area coverage of wood that is dead within the sampling plots.



Figure 25 (continued).

associated with isolated plots of 1 and 10 ha in the ongoing study of Amazonian forest patches. Within the forests of this study, relatively high forest senescence has occurred along erosional river banks (e.g., Guru North, Guru South, Mchelelo West, and Congolani Central), along disturbed forest edges (e.g., Sifa West, Baomo North, and Mnazini South), and along the savanna edge (e.g., Guru South, Mchelelo West, and Congolani West). Forest edge may encourage forest decline. The map further demonstrates the senescence of *Pachystela msolo* in the Baomo South forests and to a lesser degree in Kitere West. Mnazini North has the largest contiguous area of low forest senescence. Coupled to its high density of canopy trees (-59 trees/ha) and abundance of primate food resources, Mnazini North ranks currently as the most vigorous forest within the sample.

## Summary and Management Implications

Forest loss and fragmentation between 1960 and 1975 may provide a partial explanation for the sharp decline in the endangered primate populations between 1975 and 1985. Current behavioral studies on the primates suggest that the 1975 populations of colobus and mangabeys were compressed into small forest patches at a density above the existing carrying capacities (Decker and Kinnaird, submitted; Decker, 1989). The primates are interior forest species, as demonstrated by their negative correlations to forest edge and the overall spatial heterogeneity characterizing a forest patch. The 56% decline in forest area, 44% reduction in the area-to-perimeter ratio of the existing forests, and intraforest senescence are primarily attributable to

shifts in the river position, meander cut-offs, high flood levels, and human forest clearing. Moreover, river length was reduced 3.5%, with a consequent reduction in the land area suitable for a groundwaterdependent forest. The disturbance regime characterizing this riverine ecosystem prior to the establishment of the TRNPR has contributed to the lower populations of colobus and mangabeys within the protected area.

Since the establishment of the Reserve in 1975, I measured within the studied forests an additional 4% decline in forest area attributable to riverbank erosion (46) and forest clearing by the resident Pokomo population (54%). The decline in canopy resources within Mnazini South and Mchelelo West may be explained by the death of certain canopy-sized tree species and a temporal gap in the replacement of those individuals at the canopy layer. The change in forest composition and structure is in accordance with the successional pathway determined from the size-class associations. High floods provide a partial explanation for the forest loss identified in the southern sector of Mnazini South (Marsh, 1986), and the 1988 flood resulted in the loss of approximately eight canopy-sized Pachystela msolo in Mnazini North. It is suspected that river impoundment through the construction of five dams along the Tana River may contribute to a decline in the sediment load, a decline in flood-levels, and an overall decline in vertical and lateral accretion along the Tana River (i.e. floodplain development). My observations and the flood-deposit collections from the 1988 flood support the suggestion that there is a paucity of coarse-textured sediments, but floodplain development within the TRNPR requires further investigation. The extraction of canopy

trees for canoes, beehives, and poles, and the intensive cutting of Hyphaene compressa result in a decline in the existing canopy and also in the regenerative capacity of the canopy layer. The impacts (negative or positive) imposed by most pole extraction, Phoenix reclinata frond removal, and large mammals are inconclusive. The riverine forests along the Tana are currently influenced by many factors that inhibit forest expansion and reduce the suitability of the existing forest areas as primate habitat. The current small size of the TRNPR (171 km<sup>2</sup>) and the existing forests (9.5 km<sup>2</sup> in ~26 forest patches) may not be suitable to ensure preservation, given the dynamics and stochastics of disturbance within this small landscape area.

Therefore, management must carefully address the long-term maintenance of species populations and community integrity. The results from this study demonstrate a trend toward decreasing resources. A maintenance of the status quo, even with a restriction of activities enforced on the resident Pokomo population, may result in a low assurance of long-term preservation. It is on this basis that forest restoration is supported as a stewardship consideration. I estimate that 45% of the land area cleared by the Pokomo since 1975 has not been cultivated. Moreover, tree species typical of high-quality forest habitat are regenerating at the uncultivated localities. Areas where local disturbances have had a retrogressive effect on natural forest succession may be restored through managed tree plantings. The floodplain environment, as demonstrated by the fertility of surface soils and flood-deposits, is naturally productive. Restoration activities would serve to alleviate local disturbances and encourage
the establishment of suitable primate habitat. A management design that includes restoration must rely on the present spatial distribution of contrasting forest habitat within the TRNPR, and an understanding of the propagation and growth of selected plant species.

#### CHAPTER VI

## FOREST RESTORATION AS A STEWARDSHIP CONSIDERATION

Forest condition and the external disturbances that contribute to forest loss or decline support forest restoration as a stewardship consideration for the Tana River National Primate Reserve. Restoration is by definition the replacement of the structural and functional characteristics of a community that have been disrupted or destroyed by external disturbances (Cairns, 1988; Bradshaw, 1987). A primary objective is to return the site to its pre-disturbance ecological state. Along the Tana River, the goals of restoration are more directly related to establishing some control over landscape disturbances that reduce forest area (Bruns, 1988). The unpredictability of disturbances imposed by floodplain dynamics and human forest clearing and the natural instability of all existing forest communities complicate the determination of pre-disturbance conditions. Furthermore, the environmental conditions may have changed, making the pre-disturbance vegetation inappropriate. Restoration as a management strategy within the TRNPR is more specifically a rehabilitation of disturbed localities toward a forest composition and structure suitable for the red colobus monkeys and crested mangabeys (cf. Bradshaw, 1987). Emphasis is necessarily placed on careful manipulation of the existing community to achieve a selected management goal (Zedler, 1988). The primary goal is the long-term preservation of the endangered primate populations.

The success of restoration is dependent on some comprehension of the natural ecology (Ashby, 1987; Bradley, 1989). As a management strategy, the objectives of restoration are based on an understanding of relative habitat quality as derived from the study of primate-tohabitat relationships (Chapter 3). Project design, however, is dependent on the natural patterns of forest regeneration (Chapter 4), and the characteristics of plant-species establishment. The results from these ecological studies are directly applicable to a proposal supporting restoration.

Additional data, however, are necessary to address the questions of site and species selection. First, I examined site selection through an interpretation of maps depicting the spatial distribution of canopy and sapling resources, and also through an ecological investigation of forest corridors. It is assumed that restoration would be most successful when it closely parallels or encourages the existing forest-regeneration patterns. Secondly, I conducted nurserypropagation trials on several tree species important as primate food resources or representative of different forest types and collected tree-growth measurements on six tree species. While species selection is primarily based on their ecological value to the restored area, the characteristics of their propagation, projected time to reproductive maturity, and persistence within the restored community are important factors (cf. Hodgson, 1989). Together these data contribute to a proposed strategy for forest restoration within the TRNPR. This chapter presents a proposal for forest restoration as a stewardship consideration to help ensure the preservation of the endangered primates within the protected TRNPR.

Project Objectives

Two overall objectives of a forest restoration project are to increase forest area and reduce the area-to-perimeter ratios of the existing forests. Both objectives may be achieved through the establishment of tree and palm species along a forest edge, or within corridors between forest patches. Managed plantings, including some protection from competition, will increase the rate of recovery toward suitable primate habitat (cf. Franklin et al., 1988). Red colobus population sizes are more closely related to the structural development of the forest (i.e., forest stature and canopy closure), such that their habitat preferences dictate the requirements of forest restoration. If the habitat is utilized by the colobus, it will probably be suitable for the mangabeys. The nonsignificant correlations between the endangered primate population sizes and the abundance of food resources and the variability in the food resources that characterize high-utilization areas suggest that increasing available food resources through forest enrichment can only be supported as an objective in currently unsuitable forest habitat. Furthermore, these results suggest that once an adequate forest structure is obtained (i.e., a closed canopy > 10 m in height) habitat restoration may be possible without a significant alteration of the existing resource base. Indeed a single food resource, as evidenced by the Ficus bussei tree in Congolani West (cf. Chapter 5), may determine the suitability or unsuitability of a restored area. Corridors would be most appropriate for restoration where they connect a resource-poor forest to a forest comparatively richer in resources. An increase in interior forest and an increase in the resource base through corridor

development should increase primate populations within the protected area and decrease inbreeding depression among existing populations, respectively (cf. Harris, 1984; Gilpin, 1987; Kinnaird, 1988). I am assuming that larger population sizes improve the probability of longterm preservation. Primate population sizes, therefore, serve as an indirect measure of project success.

#### Project Design

While the objectives of a forest restoration project should be based on an understanding of certain habitat relationships demonstrated by the endangered primates, the project design is dependent on the existing vegetation patterns. The natural patterns of forest regeneration are characterized by spatial variability in the composition of the canopy-tree layer (> 20 cm dbh, or > 10 m in height), the associated sapling layer (i.e., established seedlings), and certain floodplain characteristics (e.g., soil moisture and soil texture). The absence of a stable forest composition suggests that community restoration (or rehabilitation) must rely on an understanding of the inter-associations among the forest structural layers and site conditions in the selection of appropriate species. In other words, the success of a restoration project will be at least partially related to how closely it parallels the natural patterns of forest succession and floodplain development.

Furthermore, the establishment of forest vegetation through managed plantings demands an understanding of the physical environment and the adaptations that characterize the selected plant species. The climatic conditions within this region are suitable for thorn-scrub

vegetation (cf. Chapter 2). Forest vegetation is dependent on the groundwater regime provided by the Tana River. One may assume that early plant establishment relies on high soil moisture that may be provided by floods or possibly seasonal rainfall (cf. Chapter 4; Hughes, 1988; Marsh, 1986), but the assumption has not been adequately researched. No data exist that quantitatively describe the seasonal soil moisture regime relative to seed dispersal, seed germination, seedling establishment, and tree survival within the riverine forests. Experimental investigation of early plant establishment for selected species is a necessary component of the restoration project design. Controlled plot experiments would address establishment under natural or managed (e.g., tillage and irrigation) conditions, and the conclusions would be derived from long-term investigation (Zedler, 1988; Anderson et al., 1985).

### Site Selection

Habitat Expansion Along a Forest Edge. The potential for habitat restoration along a disturbed edge may be partially revealed by the vegetation occurring in the nearby forests. The study of natural regeneration identified canopy trees that are indicative of compositional (and site) differences, and then outlined a successional pathway on the basis of the inter-associations among these species and their respective size classes (Chapter 4, Figure 15). The spatial distribution of these species, presented as plot occurrences, provides some insight into the natural patterns of regeneration characterizing disturbed forest edges within the study area (Figure 26). The plant species selected for restoration plantings at a locality should



Figure 26. Map depicting the plot occurrences of Mimusops fruticosa, Garcinia livingstonei, Sorindeia madagascariensis or Diospyros mespiliformis, Ficus sycomorus, and Pachystela msolo within the forest study areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Co-occurrences are shown for all species except Pachystela msolo.



Figure 26 (continued).

parallel the successional stage that is revealed by the distribution of these canopy species.

High-quality primate habitat, as represented by the presence of highly utilized food resources and suitable forest structure, corresponds to forest communities with Ficus sycomorus, Pachystela msolo, Sorindeia madagascariensis, and Diospyros mespiliformis. In contrast, the establishment of primate food resources along forest edges that are now occupied by Mimusops fruticosa and Garcinia livingstonei would require greater manipulation of the existing habitat. Management would have to be directed at encouraging retrogressive succession. On this basis, it is not only possible to identify disturbed sites that may be suitable for habitat restoration, but also the species that may be most successful. For instance, Pachystela msolo is present along disturbed forest edges at Mnazini North, Kitere West, Baomo South b, and Baomo North. It may be possible to establish primate food resources along these edges that parallel the current patterns of forest succession. The occurrence of Sorindeia madagascariensis and/or Diospyros mespiliformis and Ficus sycomorus along the south edge of Mchelelo West suggests that this area may also be suitable. In view of the present distribution of Mimusops fruticosa and Garcinia livingstonei, restoration along the northwest edge of Mnazini South or along the west edge of Congolani West would be more difficult. The map also reflects the relatively wide distribution of Ficus sycomorus, supporting its adaptability as a mature individual to a variety of sites (cf. Chapter 4).

Another approach is to examine the spatial distribution of primate food resources present at the sapling layer within the forests (Figure 27). The objective is to identify forest edges that have a high density of regenerating food resources with the assumption that these localities would be best suited for the expansion of primate habitat. Natural forest expansion may be occurring along those edges, but the rate of recovery may be enhanced by managed plantings. In most cases the localities are similar to those identified through the examination of canopy-tree occurrences (Figure 26). For example, the distribution of canopy-sized Pachystela msolo within the Mnazini North, Kitere West, Baomo South, and Baomo North forests is associated with a high density of suitable primate resources at the sapling layer. Isolated localities of high sapling density within forest patches such as Mchelelo West and Guru South may be related to treefall gaps, and the potential establishment of primate resources in a mosaic forest. Finally the high density of saplings located at the north end of Mnazini South, coupled with the high density along the west edge of Mnazini North, identifies a possible locality for corridor establishment. Both maps (Figures 26 and 27) provide an overview of the status of habitat regeneration within the study areas, and thereby assist in the initial designation of sites for restoration along forest-patch edges.

<u>Corridor Establishment</u>. Corridors of suitable habitat may potentially increase the range and available resources for a colobus or mangabey group. Moreover, the value of a resource-poor forest patch may be enhanced by connecting it to another forest (MacClintock et al., 1977). With distance from the forest edge, however, it is difficult to



Figure 27. Spatial distribution of primate resources present as saplings within the 12 forest areas: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South a (bsa), Baomo South b (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). Primate resources include species that are highly utilized as food items by the colobus and mangabeys (see Table 9).



Figure 27 (continued).

predict the site conditions and potential for restoration. Therefore, I established belt transects between three corridors to compile data on the existing vegetation at the canopy (> 10 m ht) and subcanopy (< 10 m ht) forest layers. In the study by Kinnaird (1988) she observed mangabeys utilizing corridor areas between the Mnazini forests and between Mchelelo West and Congolani Central (Mchelelo South). The transects established at those locations closely approximate the route followed by the mangabeys. An additional transect was examined between the Mchelelo West forest and the Research Camp (Mchelelo North). The composition and ecological attributes of these corridors are summarized in Appendix G.

A comparative evaluation of the three corridors as potential sites for restoration is based on existing primate food resources (Decker, 1989; Homewood, 1978) and associates characteristic of high-utilization areas (see Table 12). The existing forest resources provide some indication of the natural patterns of regeneration and site conditions characterizing a corridor (Figure 28). On this basis Mchelelo South has the highest density of total resources. Mnazini has a higher resource base at the canopy layer than the Mchelelo corridors, but has a paucity of regeneration at the subcanopy layer. Regeneration within this corridor may be improved through restoration plantings. The densities of subcanopy resources along the Mchelelo South and North corridors are primarily attributed to high densities of Hyphaene compressa (16.7% and 20% of total density, respectively). Although Hyphaene compressa may be an important resource for the endangered primates (principally the mangabeys), the palm most commonly occurs along the forest-savanna edge. It may be difficult to establish other



Figure 28. Forest resources recorded as canopy trees (> 10 m height) and saplings (3 - 10 m in height) in three corridors. Forest resources include species that are highly utilized as food items by the endangered primates (see Table 9), or associates that are present within the high-utilization plots (see Table 12). Palm species are included in the measure of canopy trees and saplings.

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tree species at these localities. Ecological studies addressing overall vegetation composition and structure, as well as site conditions, are necessary to clearly predict the future establishment of habitat resources within forest corridors. The results from this preliminary examination of forest corridors and the maps depicting the spatial distribution of resources at the canopy and sapling forest layers provide a general perspective on site suitability for restoration within the study area. The information contributes to the designation of sites and to a certain extent, plant species, in a proposed restoration project.

#### Plant Species Selection

Nursery Propagation of Plant Species. The selection of plant species suitable for forest restoration should be based on their value as a component of primate habitat and their ease in propagation and/or in-field establishment. During the year of field research, I experimented with the nursery propagation of several forest species (Appendix H). For each trial, data were collected on the percentage of seeds that germinated, germination time, seedling survival, and seedling vigor. Shortly after collection, seeds were placed in water. Those seeds floating after 24 hours were considered nonviable (Nwoboshi, 1982; Evans, 1982) and removed from the trial. In all cases the seeds were planted after collection, so no data are available on seed viability after storage.

Trees that were particularly successful in the nursery include: Sorindeia madagascariensis, Pachystela msolo, Oncoba spinosa, Phoenix reclinata (a palm), Mimusops fruticosa, Garcinia livingstonei, Acacia rovumae, and Majidea zanguebarica. In addition, all the fig species were easily propagated from seed, but early growth was slow. I was not successful propagating Ficus sycomorus from stem cuttings (< 10% of the stem cuttings survived), although I did observe adventitous roots develop from fallen stems in the field and the species commonly regenerates as root sprouts. The roots from nursery-grown seedlings and forest seedlings of Sorindeia madagascariensis, Pachystela msolo, and Ficus sycomorus were examined by J. Jeffries, East African Herbarium, Plant Propagation Section. She determined that endomycorrhizae were present in all species and that the symbiotic relationship was not reduced through nursery propagation. The results from this preliminary study support the propagation of forest resources in a nursery for eventual restoration plantings. Insufficient data are available, however, on the success of nursery transplants at designated in-field sites for restoration.

Tree Growth. The restoration of primate habitat along forest edges or within corridors between forest patches is dependent on the establishment of the selected tree species, their growth patterns at the site, and their persistence as mature individuals within the restored locality. The projected recovery time, characterized by the availability of reproductively mature primate food resources or suitable forest structure (> 10 m in height), is partially dependent on tree-growth rates. I measured annual diameter increment in six riverine forest tree species (Table 23). Measured differences in diameter increment among these species provide information on relative growth rates, site and size-class differences in tree-growth rates, and tree-growth periodicity.

Table 23. Site characteristics and sample sizes for trees used in the study of tree-growth patterns.

		Sample Size	(n)
Tree Species	Site Characteristics	1988	1987
<u>Acacia robusta</u> subsp. <u>usambarensis</u>	Pioneer in large disturbed areas, usually above the floods	22	20
Ficus sycomorus	Pioneer along depositional river banks or large disturbances that flood or have a high water table	71 8 (Mnazini North 27 (< 10 cm dbh) 44 (> 10 cm dbh)	20
<u>Populus ilicifolia</u>	Pioneer along depositional riverbanks, or oxbow lakes	37	17
<u>Alangium salviifolium</u>	Subcanopy tree to 12 m in height, within Pachystela msolo and Sorindeia/Diospyros mixed forests	12	10
<u>Diospyros</u> mespiliformis	Canopy tree (> 10 m in height) in mixed forests	15	12
<u>Sorindeia madagascariensis</u>	Canopy tree (> 10 m in height) in mixed forests	22	25

Annual diameter increment varied among the species from a mean equal to 0.16 cm/year for Sorindeia madagascariensis to 2.01 cm/year for Acacia robusta (Figure 29a). Trees that typically become established in high light or pioneer localities exhibit faster growth rates: Acacia robusta, Ficus sycomorus, and Populus ilicifolia. The mean growth rates in Acacia robusta and Ficus sycomorus (> 1 cm/year) is higher than that recorded for inundation forest species in Central Amazonia (Worbes, 1989), or undisturbed tropical forests (Weaver, 1979). The greater variation among the anuual growth rates in Ficus sycomorus individuals may be partially explained by site differences (Figure 29b). For instance, the mean annual diameter increment for all trees is 1.89 cm (n - 71), but the mean annual diameter increment for trees on a low riverbank levee within Mnazini North (n - 8) is 3.23 cm/year. Size-class differences in this species' growth rate are less apparent. Although the mean annual diameter increment for Ficus sycomorus trees > 10 cm dbh is higher (1.98 cm/year) than trees < 10 cm dbh (1.45 cm/year), the differences are not significant relative to site differences. Given optimal site conditions, the growth rate of Ficus sycomorus is impressive.

When compared to the pioneer trees, Alangium salviifolium, Diospyros mespiliformis, and Sorindeia madagascariensis have lower growth rates. Slow growth rates may be an adaptation to low light environments that have enabled saplings of these species to become established beneath the Pachystela msolo canopy (cf. Figure 15). The differences between the growth rates of Sorindeia madagascariensis and Diospyros mespiliformis suggest contrasting adaptations, and support the earlier suggestion that differences in their relative dominance may



I standard deviation 8 Mean



Figure 29. Tree-growth patterns in six forest tree species: Acacia robusta subsp. usambarensis (Ar), Ficus sycomorus (Fs), Populus ilicifolia (Pi), Alangium salviifolium (As), Diospyros mespiliformis (Dm), and Sorindeia madagascariensis (Sm). Table 23 lists the samples used in the calculation of the mean growth rates.

a. Tree growth 1987 - 1988

c. Annual tree growth comparisons

be in response to small-gap or large-gap disturbances (cf. Chapter 4). In large gaps *Diospyros mespiliformis*, with its faster growth rate, has the competitive advantage. Furthermore, the longer persistence of *Sorindeia madagascariensis* as depicted by it positive association to species that occur at the canopy layer (Figure 15) may also be partially explained by its slow growth rate. These results suggest that a disturbed site may be rehabilitated more quickly by the establishment of pioneer species (particularly *Acacia robusta* and *Ficus sycomorus*), but persistence of the restored community may be best achieved by plantings of species exhibiting fast growth (shade intolerant) and slow growth (shade tolerant), respectively.

The six tree species are also characterized by annual and seasonal variation in their diameter increment. *Populus ilicifolia* and *Acacia robusta* had noticeably higher growth increments during the 1986-1987 measurement period (a nonflooding year) than in the 1987-1988 measurement period (a flooding year) (Figure 29c). Similar to Worbes's study (1989) in Central Amazonia, tree growth may be inhibited by periods of inundation. Among the pioneer trees, the slower growth rates of *Populus ilicifolia* may be explained by its proximity to the river and longer periods of root inundation.

Seasonal differences in tree growth rates would be expected in response to changes in the river level, groundwater regime, and precipitation patterns (Amobi, 1973; Alvim and Alvim, 1978). Through the 1987-1988 measurement period, I took an intermediate measurement of growth between approximately October 1987 and March 1988. During this period the river did not attain flood level, and precipitation, especially in the northern sector of the study area, was low (Chapter

5, Figure 19; Chapter 2, Figure 2b). Growth rates for all species were low and negative growth, or shrinkage, was measured in many individuals. For instance the mean growth rate for Sorindeia madagascariensis (n = 21) during this period equaled -0.04 cm/  $\sim$ 5 months. Periods of suppressed growth, or shrinkage, are reported for many tree species in tropical wet-dry environments (Daubenmire, 1972; Worbes, 1989; Amobi, 1973). The periodicity may be reflected in wood formation and possibly in the development of distinctive tree rings (Jacoby, 1989; cf. Bormann and Berlyn, 1981). During this study I collected and examined wood cores from Populus ilicifolia and Ficus sycomorus. I observed narrow bands of axial parenchyma in Ficus sycomorus (cf. Fahn et al., 1981; Carlquist, 1988), but its relationship to tree-growth patterns is inconclusive. Nevertheless, annual and seasonal variations in tree growth demonstrate adaptations by the tree species to floods and seasonal drought and emphasize the importance of timing (the date trees are transplanted) and maintenance (possibly through irrigation) to tree survival at the restoration site. Species selection may be dictated by the availability of tree seedlings and plantings of species with different growth rates will encourage fast establishment and community persistence, but the survival of plantings may require some control over the stochastics of this semiarid climatic regime.

# Discussion

In view of past and ongoing disturbances impacting the riverine forests within the Reserve, forest restoration is supported as a stewardship consideration. Forest restoration is, however,

manipulative management that must be firmly based on an understanding of riverine forest ecology within this region. The results from the study of primate-to-habitat relationships are applied to the designation of project objectives and results from the study of natural regeneration are applied to the development of a research design. Restoration is more specifically a rehabilitation of a disturbed locality to one suitable for the endangered primates. Preservation is thereby encouraged through a consequent increase in primate population sizes. The ease at which primate resources may be established, however, is dictated by the factors influencing natural forest regeneration. Although restoration is proposed as a management project, it must follow a research design. Emphasis is placed on the need for quantitative data that clarify the site requirements for early plant establishment. Restoration is necessarily a long-term study in applied ecology.

Additional data have contributed to the designation of sites and plant species appropriate for a restoration project. For instance, the disturbed forest edges at Mnazini North, Kitere West, Baomo South b and Baomo North appear suitable for the establishment of primate resources, as reflected by the existing canopy composition and density of primate food resources present at the sapling forest layer. Restoration management may increase the rate of recovery in areas experiencing natural forest expansion. Managed plantings may also improve the paucity of regeneration recorded within the Mnazini corridor or a similar locality. A buffer to an existing forest edge, or forest connection, may be quickly established by planting fast growing pioneer species such as Acacia robusta or Ficus sycomorus. Subsequently,

planting slower growing forest species would encourage the development of a mixed forest composition and potentially improve the persistence of the established community.

Although restoration plantings may include all species that can be propagated within a nursery or established through direct seeding, *Ficus* spp. may be especially important to the success of the project. For instance, *Ficus sycomorus* is a primary food resource for both primates, and this study has demonstrated its adaptation to a wide variety of sites, promising success in nursery propagation, and fast growth rates at established sites. The other indigenous figs appear to be of similar value to the primates and exhibited similar success in the nursery trials. Their rare status within the TRNPR may be improved through the propagation of transplants. Primate resources may be established along a forest edge or within a forest corridor first through the establishment of indigenous fig species.

The results from this study, however, do not specifically address in-field trials of selected species. On the contrary, the discussion of the climatic and hydrologic characteristics of this region, as evidenced by tree-growth periodicity, suggest potential difficulties. Success will be dependent on careful timing and plot maintenance subsequent to all plantings. Irrigation may encourage successful establishment. In sum, this ecological study contributes a proposal directed at the long-term investigation of forest restoration as a stewardship consideration for the TRNPR. An applied study of forest restoration would, in return, contribute significantly to our current understanding of the natural ecology that characterizes this region.

#### CHAPTER VII

## CONCLUDING DISCUSSION

The riverine forests along the lower Tana River, Kenya, are the only habitat for the endangered Tana River red colobus monkey (*Colobus badius rufomatratus*) and crested mangabey (*Cercocebus galeritus galeritus*). Between 1975 and 1985 the populations of these two primates declined to critically low levels. In accordance with a management strategy aimed at the preservation of biological diversity (cf. McNeely et al., 1989; Miller, 1989), their protection within the Tana River National Primate Reserve should be a management concern for the Kenya Wildlife Service. In situ preservation of the primates is dependent on the maintenance of suitable habitat. Therefore, a study of riverine forest ecology as habitat for the two endangered primates has been a most important component of this research project directed at their continued survival.

Through an ecological study of current primate habitat I have addressed three primary research questions: (1) do vegetation-based factors explain the recent decline in the endangered primates; (2) what are the current status and future status of the Reserve's forests as primate habitat; and (3) which management alternatives would best ensure future preservation. Both primates, especially the red colobus, are interior forest species. An examination of primate-to-habitat

relationships demonstrates their preference for a closed forest canopy greater than 10 m in height. The relationships to food resources are less clear, but they suggest that suitable primate habitat may be characterized by variable abundances of food resources within a forest patch, a low diversity of highly utilized food resources, and a variety of food resources among forests. The primates show negative relationships to disturbance (i.e., forest senescence, human forest utilization, and animal impact), a decrease in forest patch size, edge effects, and to intraforest spatial heterogeneity that may be attributable to forest edge or gaps. While the primates exist in a heterogeneous floodplain environment, they appear to prefer a homogeneous forest habitat. Further investigation that addresses the behavioral ecology of the primates in relatively poor habitat would elucidate their adaptations to the riverine forest ecosystem.

The significant forest loss and fragmentation that occurred during the 15 years prior to establishment of the Reserve in 1975 provides a partial explanation for the primate population decline. During this period within the south-central sector of the TRNPR 56% of the forest area was lost, five forests were fragmented into 15 forest patches, and the overall area-to-perimeter ratio was reduced by 44%. Forest loss may be explained by human forest clearing and natural river dynamics, and it is unclear which has had the more serious impact. Although measured forest loss is significantly less since the establishment of the Reserve (1975-1988; ~4% within the studied forests), the disturbances that influence the areal extent of forest must be considered when evaluating the status of primate habitat.

The forest habitat best suited for the primates corresponds to the earlier stages of primary forest succession. High-quality habitat varies from a forest dominated by Pachystela msolo to a mixed forest with Sorindeia madagascariensis and Diospyros mespiliformis. Ficus sycomorus establishes as a pioneer, but occurs less frequently as mature individuals in association with these two communities. The absence of self-replacement by these trees and the contrasts in their site characteristics suggest that the floodplain is developing, through vertical and lateral accretion, parallel to forest succession. Consequently, the occurrence of high-quality primate habitat is naturally not stable. The sites of colonization are spatially distinct from the present localities of high-quality habitat. Whereas the regeneration of mixed forests is occurring beneath senescent Pachystela forests, Pachystela msolo currently has low regeneration within the study areas. The change toward a mixed forest is achieved through gap-replacement. This transition is characterized not only by increased spatial heterogeneity (i.e., gap disturbances), but also by potential food shortages with tree death and a delay in the maturation of suitable canopy-tree resources (i.e., gap closure). High-quality primate habitat, therefore, is represented by only a portion of the forest communities identified within the floodplain. The overall status of primate habitat may be negatively impacted by a loss of mature monodominant Pachystela stands, or by the processes of gap replacement that characterize a mixed forest. Forest succession (progressive or retrogressive) toward the establishment of high-quality habitat and its persistence are dictated by the regional and local

dynamics of the disturbance regime: channel migration, floods, forest clearing, human forest utilization, and animal impact.

In view of the critically low colobus and mangabey populations within the TRNPR, and the factors that naturally inhibit the expansion of suitable habitat within this region, forest restoration is proposed as a most important management alternative. The overall objective is to increase primate populations by increasing the area of suitable forest habitat. This may be best achieved through forest expansion along a forest-patch edge or within a corridor between two forests. Restoration plantings directed at the establishment of primate food resources should attempt to parallel the natural patterns of forest succession. Suitable sites may be identified on the basis of canopytree composition, or the occurrence of primate food resources at the sapling layer. Plantings of pioneer tree species that are shade intolerant and have fast growth rates, followed by plantings of forest interior species with slow growth rates, would encourage the establishment of suitable primate habitat and its persistence as a forest community. Project success would be evaluated primarily on the basis of primate populations, assuming that an increase in populations is a greater assurance of long-term preservation.

A question that remains, however, is whether or not the primates serve as an adequate measure of ecosystem integrity. The groundwater regime provided by the Tana River has allowed for the development of a narrow corridor of riverine forest along the lower section of the Tana River (Bura to Garsen; ~150 km). The corridor has served as a refuge within a limited range for the two endangered forest primates (located only between the Wema/Hewani area and the TRNPR) and also for the

evergreen or semievergreen plant species that have migrated from the rain forests of West and Central Africa and also from along the Indian Ocean coast. While the overall floristic diversity of the ecosystem is not great (~173 woody plant species), the combination of plant species with different geographic affinities provides insight on the biogeography of Eastern Kenya. The regional diversity of riverine forest, as depicted by the distribution of certain canopy-tree dominants, is not adequately protected within the TRNPR. The loss of forest areas outside the TRNPR may limit the migration of plant (or animal) species in response to environmental change, and consequently lower the overall species diversity of the riverine forest ecosystem.

The spatial heterogeneity of floodplain landforms and consequent local diversity of forest communities is highest within the TRNPR. All communities have a characteristic adaptation to the floodplain regime (cf. Tilman, 1988), and, despite their current value to the primates, are a critical component of the forest ecosystem. A most prominent feature is the occurrence of large monodominant stands of *Pachystela msolo*. The low regeneration of *Pachystela* within the studied forests, coupled with its death in response to flooding, suggests that the status of this species within the TRNPR is under threat. Indeed the decline of *Pachystela msolo* may be an indicator of overall change in the floodplain environment. One possible explanation is that the tree is dependent on high floods and sediment deposition for the dispersal and establishment of seeds at newly developed colonization sites (i.e., low levees). Its low regeneration may be evidence supporting the idea that flooplain development has slowed, which was a predicted outcome of

dam construction along the upper river basin (Hughes, 1985). While this species may be replaced by a mixed forest suitable for the endangered primates, the loss of monodominant *Pachystela* stands within this region would result in a significant change in the overall composition and structure of riverine forest within the TRNPR. The restricted range of the primates within the floodplain, their preference for a small number of the forest communities present within the region, and their nonspecific relationships to food resources limit their value as an indicator of overall ecosystem integrity. Future studies on the habitat requirements of the two endangered primates should coincide with ecological research on the mechanisms of natural succession that maintain the local and regional diversity of the riverine forest ecosystem (Walker, 1989).

Restoration is supported as a stewardship consideration in view of the disturbances that result in habitat loss and the small size of the protected TRNPR. The data suggest, but do not conclusively support, the supposition that the Reserve is too small to maintain sufficient forest habitat for the long-term survival of the endangered primates (cf. White and Bratton, 1980; Pickett and Thompson, 1978). The forests occur as a mosaic in a heterogeneous landscape defined by the disturbance regime. Disturbances attributable to river floodplain dynamics, humans, and large mammals are a natural component of the landscape (cf. Risser, 1987; Pearl, 1989). Clearly, research on the landscape-level responses to these disturbances, or more specifically a long-term study on shifts in the forest mosaic within the landscape, would contribute greatly toward understanding the scale at which an equilibrium is maintained (cf. Forman, 1987). Therefore, while the

preservation of the endangered primates and their critical forest habitat should be a management priority, it would be unwise to promote a management strategy that negatively alters the natural heterogeneity of the landscape (Western, 1986; Westoff, 1983; Noss, 1987). A policy, such as the one promoted by the Man and the Biosphere Program, that integrates preservation (as core areas) with restoration, resource conservation, and local stewardship (as buffer areas) would provide a framework for management at the landscape level (Lusigi, 1981; MAB, 1987). The conservation goal should be to couple species preservation with the preservation of the riverine forest ecosystem and the natural integrity of the landscape that characterizes the Tana River floodplain. APPENDICES

APPENDIX A

### APPENDIX A

Checklist of the Woody Forest Flora,

Tana River National Primate Reserve

This plant list is based on a personal collection, collection records obtained from the East African Herbarium, and the collection notes of J.B. Gillett. Collections were made in the TRNPR by Katherine Homewood (KH), Clive Marsh (CM), Homewood and Marsh (HM), J.B. Gillett and S.P. Kabuwa (JK), Ann Robertson and Quentin Luke (RL or LR), James Allaway (JA), Barb Decker (BD), and myself (KM). All collections are filed at the East African Herbarium (EAH). The list also includes species that are in a reference collection at the TRNPR, and plants not collected but recorded in the vegetation-sampling plots. The checklist includes family name (Hutchinson, 1973), species name (Turrill et al., 1952- ; Dale and Greenway, 1961), growth habit, collection numbers, and floristic affinities. The growth habits include: tree (> 10 m height), st (small tree < 10 m), shrub, sc shrub (scandent shrub), suff shrub (suffrutescent shrub), wv (woody vine), swv (semi-woody vine), hv (herbaceous vine), str (strangler), and wp (woody parasite). Floristic affinities, when known, are summarized as Zanzibar-Inhambane (ZI), Somalia-Masai (SM), Guinea-Congolian (GC), Zambezian (Z), and Africa south of the Sahara  $(\mathbf{A})$ . I have also identified plants that are exotic (X) or appear to be riverine endemics (RE).

#### Alangiaceae

Alangium salviifolium (L.f.) Wangerin (tree). KM 223, HM 2, KH 89, KH 2, RL 4572, GK 19986. ZI (& Asia).

### Anacardiaceae

Lannea schweinfurthii (Engl.) Engl. var. stuhlmannii (Engl.) Kokwaro (tree). KM 224, HM 36, KH 36, RL 4585. A. Mangiferia indica L. (tree). X. Sorindeia madagascariensis DC. (tree). KM 217, KH 1. ZI.

#### Annonaceae

Monanthotaxis trichocarpa (Engl. & Diels) Verdc. (wv). KM 281, ?HM 43, HM56, LR 1153. ZI. Uvaria scheffleri Diels (wv). KM 324. Apocynaceae

Alafia microstylis K. Schum. (wv). KH s.n., LR 1183.
Carissa edulis (Forssk.) Vahl (wv). KM 259, KM 280, KH s.n. SM.
Hunteria zeylanica Thw. var. africana (K.Schum.) Pichon (st). KM 231.
Rauvolfia caffra Sond. (st). HM 67.
Rauvolfia mombasiana Stapf (st). KM 225, HM 46.
Saba comorensis (Boj.) K. Schum. (wv). KM 210.
Schizozygia coffaeoides Baill. (shrub). KM 277.
Strophanthus courmontii Franch. (wv). KM 312.
Strophanthus sp. (wv). KH s.n.
Strophanthus ?petersianus Klotzsch (wv). LR 1196.
Thevetia cf. peruviana (shrub). X.

Asclepiadaceae
Parquetina nigrescens (Afz.) Bullock (wv). KM 306, KM 364.

Pergularia daemia (Forssk.) Gniov. (swv). KM 333.

Bignoniaceae

Kigelia africana (Lam.) Benth. (tree). KM 243, KM 202. Markhamia zanzibarica (DC.) Engl. (tree). TRNPR s.n.

### Bombacaceae

Ceiba pentandra (L.) Gaertner. (tree). X.

Boraginaceae

Cordia fauknerae Verdc. (st). KM 272. Cordia goetzei Guerke (tree). KM 269, HM 33, KH s.n., KH 33, LR 1154. Cordia sinensis Lam. (tree). KM 258, CM 29, KH 15, LR 1189. Cordia sp. - Verdcourt 1862 A. (wv). HM 75.

Burseraceae

Commiphora campestris Engl. subsp. glabrata Engl. Gillett (st). JA 48, HM 54, HM 82.

Caesalpiniaceae

Afzelia quanzensis Welw. (tree). KM 299. A.
Caesalpinia volkensii Harms (shrub). KM 338. ZI.
Cassia abbreviata Oliv. subsp. beareana (Holmes) Brenan (tree).
KM 305, KH 34, HM 34, HM 88, KM 340. ZI.
Cassia afrofistula Brenan var. afrofistula (shrub). LR 1210.
Cassia singueana Del. (tree). KM 228. A.
Cynometra lukei Beentje (tree). KM 381, KM 222, KM 409, 7HM 5, KH 5, LR 1214. RE.

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Delonix elata (L.) Gamble (tree). HM 76. X.
  Oxystigma msoo Harms (tree). KM 326. GC.
  Tamarindus indica L. (tree). KM 245. GC.
Capparaceae
  Capparis sepiaria L. var. subglabra (Oliv.) DeWolf. (wv). KM 270.
      SM.
  Capparis tomentosa Lam. (wv). KM 251, CM 37, HM 74. A.
  Maerua calantha Gilg (wv). JA 49, HM 84. SM.
  Maerua holstii Pax (wv). JA 51.
  Maerua micrantha Gilg (wv). KH s.n. SM.
  Maerua subcordata (Gilg) DeWolf (shrub). KM 362, KM 392. SM.
  Maerua triphylla A. Rich. var. triphylla (sc shrub). KM 412,
      LR 1209. SM.
  Maerua triphylla var. calophylla (sc shrub). CM 33. SM.
  Cadaba gillettii R.A. Grah. (wv). JA 52. SM.
  Cadaba glandulosa Forsk. (wv). JA 55. SM.
  Thylachium thomasii Gilg
Celastraceae
  Elaeodendron schweinfurthianum (Loes.) Loes. (shrub). LR 1205.
  Hippocratea africana (Willd.) Loes (wv). KM 358.
  Maytenus heterophylla (Eckl. & Zeyh.) N. Robson (shrub). KM 343,
      KM 240, KM 318, KM 322, LR 1177.
  Maytenus undatus (Thunb.) Blakelock (shrub). CM 34, KH s.n.
  Salacia erecta (G. Don.) Walp. (wv). KM 408, LR 1151.
  Salacia stuhlmanniana Loes (wv). KM 204, KH s.n., LR 1152.
Combretaceae
  Combretum cf. butryosum (Bertol. f.) Tul. (wv). KM 254, KM 241. ZI.
  Combretum constrictum (Benth.) Laws. (wv). KM 276, JA 39. ZI.
  Combretum hererense Schinz var. parvifolium Engl. (wv). JA 69.
  Combretum paniculatum Vent. (wv). KM 411. A.
  Terminalia brevipes Pampan. (st). KM 302, KM 357, KM 275, HM 37,
      KH 37. SM.
  Terminalia sp. (tree). KM 356.
Compositae
  Pluchea dioscoridis DC. (shrub). KM 405, JA 40, HM 1.
  Veronia hildebrandtii Vatke (wv). KM 304, HM 87, KH s.n.
Connaraceae
  Agelaea setulosa Schellenb. (wv). KM 351, KH s.n. ZI.
Convolvulaceae
  Merremia sp. = J.Ament & Magogo 132 (shrub). KM 369.
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Dichapetalaceae

Dichapetalum madagascariense Poir. (wv). KM 353. ZI. Dichapetalum sp. KH s.n. Tapura fischeri Engl. (st). KM 268, KM 256. GC.

Ebenaceae

Diospyros abyssinica (Hiern) F. White (tree). KH 91, RL 4600.
Diospyros consolatae Chiov. (st). KM 359, CM 36.
Diospyros ferrea (Willd.) Bakh. (tree). KM 378, LR 1170. GC.
Diospyros ?ferrea (Willd.) Bakh. (tree). KM 383, BD 17.
Diospyros kabuyeana F. White (tree). KM 274, KM 246, KM 325, KH 92.
ZI.
Diospyros mespiliformis A. DC. (tree). KM 239, BD 18, RL 4595. A.
Diospyros sp. KH 35, GK 19987.

Euclea divinorum Hiern (st). HM 60.

Erythroxylaceae

Erythroxylum fischeri Engl. (st). KM 298, KM 252a, JA 72, HM 48, RL 4585. ZI.

Euphorbiaceae

Acalypha echinus Pax & K. Hoffm. (shrub). KM 308, KM 249, KM 300, KM 335, JA 58, LR 119. ZI. Acalypha sp. nr. fruticosa Forssk. (shrub). KM 292. SM. Antidesma membranaceum Muell. Arg. (shrub). HM 47. A. Antidesma venosum Tul. (tree). KM 252, HM 72, LR 1203. A. Antidesma vogelianum Muell. Arg. (st). KM 212. A. Bridelia micrantha (Hochst.) Baill. (st). KM 282. Drypetes natalensis (Harv.) Hutch. var. leiogyna Brenan (st). KM242, KM 237, ?JA 59, HM 59, GK 19988. ZI. Erythrococca kirkii (Muell. Arg.) Prain (shrub). KM 334, KM 235, KM327, KH s.n., LR 1164. ZI. Erythrococca sp. = Rodgers 1689. KH s.n. Flueggea virosa (Willd.) Voigt subsp. virosa (shrub). KM 297, KM 248, KH 16, KH s.n., HM 41, HM 65. A. Phyllanthus guineensis (shrub). CM 28. A. Phyllanthus maderaspatensis L. (shrub). KM 368. A. Phyllanthus reticulatus Poir. var. reticulatus (shrub). LR 1173. A. Phyllanthus sepialis Muell. Arg. (shrub). KM 361. SM. Phyllanthus somalensis Hutch. (shrub). KM 319, KM 329. SM. Spirostachys venenifera (Pax) Pax (tree). KM 234, KM 296, KH 3, HM 4. ZI. Suregada zanzibariensis Baill. (st). KM 284, KM 350, JA 71. ZI.

Flacourtiaceae

Oncoba spinosa Forssk. (tree). KM 218, RL 4576. A.

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Flagellaria guinensis Shumach. (wv). HM 80, KH s.n. A.
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#### Guttiferae

Garcinia livingstonei T. Anders (tree). KM 200. GC.

#### Liliaceae

Asparagus ?africanus Lam. (wv). KM 354.

# Loganiaceae

Strychnos decussata (Pappe) Gilg (shrub). CM 24, HM 3?. ZI. Strychnos mitis S. Moore (st). LR 1160. Strychnos sp. KH 3.

#### Loranthaceae

Oncella ambigua (Engl.) Van Tiegh. (wp). KM 213, BD 11, RL 4580. Tapinanthus zanzibarensis (Engl.) Danser (wp). KM 384.

#### Lythraceae

Lawsonia inermis L. (tree). KM 221.

# Malvaceae

Thespesia danis Oliv. (st). KM 209, KH 12.

#### Meliaceae

Trichilia emetica Vahl (tree). KM 377.

## Menispermaceae

Anisocycla blepharosepala Diels subsp. tanzaniensis Vollenson (wv). KM 413, KM 376, LR 1202. RE. Cissampelos mucronata A. Rich. (wv). KM 372, LR 1169. Triclisia sacleuxii Diels (wv). LR 1201.

#### Mimosaceae

Acacia robusta Burch. subsp. usambarensis (Taub.) Brenan (tree). KM 403, KM 410, KH s.n. GC.
Acacia rovumae Oliv. (tree). KM 380, LR 1212, RL 4593. GC.
Albizia glaberrima (Schumach & Thonn.) Benth. var. glabrescens (Oliv.) Brenan (tree). KM 348, KM 226, BD 12, RL 4591. GC.
Albizia gummifera (J.F. Gmel.) E.A. Sm. var. gummifera (tree). BD 13. GC.

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Mimosa pigra L. (wv). JA 41. A.
Newtonia erlangeri (Harms) Brenan (tree). KM 388, KM 370, RL 4603,
KH 14. ZI.
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#### Moraceae

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Ficus ? bubu Warb (str). KM 323, BD 10. A (not including Central Africa).
Ficus bussei Mildbr. & Burret (tree). RL 4590. Z.
Ficus capreaefolia Del. (shrub). KM 342. A (not including Central Africa).
Ficus exasperata Vahl (tree). KM 382. A (not including Central Africa)
Ficus natalensis Hochst. (str). KM 307, BD 9, RL 4588, RL 4596.
A (not including Central Africa).
Ficus scassellatii (Pamp.) Stapf (str). KM 337. A (not including West Africa).
Ficus sp.- Mwangangi 1485. KH s.n.
Ficus sycomorus L. (tree). A (not including Central Africa).
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#### Ochnaceae

Ochna thomasiana (Engl.) Gilg (st). KM 395, KM 352, KH s.n.

# Palmae

Borassus aethiopum Mart. (palm). A (not including West Africa). Hyphaene compressa H. Wendl. (palm). RE. Phoenix reclinata Jacq. (palm). KM 219. A.

# Papilionaceae

Indigofera schimperi Jaub. & Spach var. schimperi (shrub). KM 215, CM 31, LR 1237. SM. Mucuna gigantea (Willd.) DC. subsp. quadrialata (Bak.) Verdc. (wv). KM 385. GC (to SE Asia).

# Rhamnaceae

Ziziphus pubescens Oliv. (tree). KM 253, RL 4577.

#### Rubiaceae

Canthium (-Keetia?) (wv). HM 49, HM55, HM 55b.
Catunaregam spinosa (Thunb.) Tirvengadum subsp. spinosa (st). KM 261, LR 1166. ZI.
Coffea sessiliflora Bridson subsp. sessiliflora (st). KM 347, KM 233, LR 1180. RE.
Gardenia volkensii K. Schum. (st). KM 355. SM.
Geophila repens (L.) I. M. Johnston (creeper). KM 360, LR 1157. A.
Ixora narcissodora K. Schum. (st). KM 321, KM 266, RL 4583.
Keetia zanzibaricum Klotzsch subsp. zanzibaricum (wv). KM 205, KM 290, JA 70, HM 52, HM 79, LR 1149. Kraussia kirkii (Hook.f.) Bullock (st). KM 401, HM 25, KH 25. ZI. Lamprothamnas zanguebaricus Hiern (st). KM 313, CM 26, HM 42. ZI. Pavetta sphaerobotrys K. Schum. subsp. tanaica (Bremek.) Bridson (st). KM 208, KH 8, ?HM 50, LR 1155, RL 4573. RE. Polysphaeria multiflora Hiern subsp. multiflora (st). KM 349 HM 68, KH 32. ZI. Polysphaeria parvifolia Hiern (st). KM 317, CM 27. SM. Psychotria punctata Vatke var. punctata (sc shrub). KM 341, KM 294, KH s.n. ZI. Psychotria schliebenii Petit. var. sessilipaniculata Petit. (sc shrub). KM 293, KM 232, KH s.n., LR 1165. ZI. Psychotria sp. (sc shrub). HM 26, KH 31, KH 26. Psydrax ?kaessneri (S. Moore) Bridson (wv). KM 414. Rytigynia = sp. 43 nr. parvifolia/celastroides complex. (shrub). KM 267, KM 289, HM 62, KM 320, KH 64. Uncaria africana G. Don. subsp. africana (wv). KM 404, KM 283. GC. Fagara sp. (shrub). KH 23, HM 66.

## Salicaceae

Populus ilicifolia (Engl.) Rouleau (tree). KM 220. RE.

#### Salvadoraceae

Azima tetracantha Lam. (wv). KM 301. Dobera glabra (Forssk.) Poir (tree). KM 385, KH 6. Dobera lorantifolia (Warb.) Harms (tree). KM 387. Salvadora persica L. var. persica (tree). KM 394, KH 11.

#### Sapindaceae

Allophylus alnifolius (Bak.) Radlk. (shrub). KM 265, KM 260, HM 27, HM 38, KH 27. ZI. Aporrhiza paniculata Radlk. (tree). KM 262, KM 244, JA 66, BD 16. Α. Blighia unijugata Bak. (tree). KM 339, KM 243b, BD 15, RL 4599. A. Chytranthus obliquinervis Engl. (st). KM 203, LR 1168, LR 1197. ZI. Chytranthus prieurianus Baill. subsp. longiflorus (Verdc.) Halle. (st). RL 4575. ZI. Deinbollia borbonica Scheff. (st). KM 273. ZI. Haplocoelum inoploeum Radlk. (tree). KM 366. ZI. Lecaniodiscus fraxinifolius Bak. subsp. scassellatii (Chiov.) Fries (st). KM 310, KM 247, KH 7, HM 83. ZI. Lepisanthes senegalensis (Poir.) Leenh. (tree). Majidea zanguebarica Oliv. (tree). KM 264, JA 65, BD 8, CM 32, RL 4594. ZI. Paullinia pinnata L. (wv). KM 363, KH s.n., RL 4579.

Sapotaceae

Manilkara mochisia (Bak.) Dubard. (tree). CM 35. Mimusops fruticosa A. DC. (tree). KM 250, KH 2, RL 4601. ZI. Pachystela msolo (Engl.) Engl. (tree). KM 216. GC.

# Simaroubaceae

Harrisonia abyssinica Oliv. (sc shrub). KM 214.

# Sterculiaceae

Cola clavata Masters. (tree). LR 1178, KH 13, KM 344. Cola minor Brenan (tree). KM 291, KH 9. Sterculia appendiculata K. Schum. (tree) ZI. Waltheria indica L. (suff. shrub). KM 303.

# Thymeliaceae

Synaptolepsis kirkii Oliv. (wv). KM 397.

#### Tiliaceae

Grewia ferruginea Hochst. ex A. Rich. vel aff. ehretioides Chiov. (wv). KM 257, HM 40, KH 29.
Grewia trichocarpa A. Rich. (st). KM 391, KM 375, KH 10.
Grewia densa K. Schum (st). KM 235, KM 236.
Triumfetta rhomboidea Jacq. (suff shrub).

# Ulmaceae

Celtis philippensis Blanco (-Celtis wightii) (tree). KM 331, KM 311, JA 73, BD 7, RL 4604. A. Trema orientalis (L.) Bl. (tree). KM 263. A.

# Verbenaceae

Clerodendrum acerbianum (Vis.) Benth. & Hook. f. (shrub). LR 1176. Premna velutina Guerke (sc shrub). KM 288, KH s.n., LR 1198.

#### Violaceae

Rinorea elliptica (Oliv.) O. Kuntze (st). KM 207, KH 30, KH 28, BD 12, RL 4575, RL 4602. ZI.

#### Vitaceae

Ampelocissus africana (Lour.) Merr. (wv). KM 255, KM 287, KH s.n., KH s.n., LR 1174. Cissus rotundifolia (Forssk.) Vahl (wv). KM 211. APPENDIX B

#### APPENDIX B

Local Pokomo Plant Names and Uses

The vernacular names and plant uses were compiled from local informants or from information compiled from earlier studies within the TRNPR (Homewood, 1976; Marsh, 1976; Geider, 1985). The list includes plant names and uses only recorded from the Pokomo population within the vicinity of the Reserve (the Gwano and Ndera locations). In some cases only the vernacular name was determined. Collections are filed at the East African Herbarium (EAH), with duplicates, as available, filed at Michigan State University (MSC), Royal Botanic Gardens, Kew (KEW), and Missouri Botanical Garden (MO). I have also listed plant species that were identified by the informants as unnamed and/or were not known to be used.

#### Alangiaceae

Alangium salviifolium (L.f.) Wangerin (KM 223). Mununae- choice wood for poles; furniture.

Anacardiaceae

Lannea schweinfurthii (Engl.) Engl. var. stuhlmannii (Engl.) Kokwaro (KM 224). Mhandarako- often rest beehives within its tree crown.

Sorindeia madagascariensis DC. (KM 217). Mniembembe- medicinal, roots boiled for stomach.

# Annonaceae

Monanthotaxis trichocarpa (Engl. & Diels) Verdc. (KM 281). Mndagoni- medicinal, leaves and roots boiled, burned.

Uvaria scheffleri Diels (KM 324). Mndagoni- medicinal, roots/leaves boiled, burned.

# Apocynaceae

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Carissa edulis (Forssk.) Vahl (KM 259, KM 280).
Mlalanche- medicinal, branch & root tips, malaria.
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Hunteria zeylanica Thw. var. africana (K.Schum.) Pichon (KM 231). Mchunguchungu- combs (shanua). Rauvolfia mombasiana Stapf (KM 225). Ufeke- milky sap used in eyes. Saba comorensis (Boj.) K. Schum. (KM 210). Maungo- rope; edible. Schizozygia coffaeaoides Baill. (KM 277). Ufeke mfupi- symbolic, protection from evil. Strophanthus courmontii Franch. (KM 312). Fimbo- used in making walking sticks. Asclepidaceae Parquetina nigrescens (Afz.) Bullock (KM 306). Mkungacheu- fibrous, used to tie winnowing baskets. Pergularia daemia (Forssk.) Gniov. (KM 333). Mumbwiga- strings obtained from small stem sections. Bignoniaceae Kigelia africana (Lam.) Benth. (KM 202, KM 243). Mbwoka- fruits used in making alcohol. Boraginaceae Cordia sinensis Lam. (KM 258). Mhali- aril used as a resin. Cordia goetzei Guerke (KM 269). Mdoko- poles, seed aril used as a resin. Cordia fauknerae Verdc. (KM 272). Seed aril used as a resin. Caesalpiniaceae Afzelia quanzensis Welw. (KM 299). Mgambakompfe- canoe, building; very hard. Caesalpinia volkensii Harms (KM 338). Msadeka- very hard round seeds used in the game Hesabu. Cassia abbreviata subsp. beareana (Holmes) Brenan (KM 305, KM 340). Mbaraka mtoni- medicinal, roots boiled for bilharzia; firewood. Cassia singueana Del. (KM 228). Mbaraka barabara.

Cynometra lukei Beentje (KM 222, KM 381, KM 409). Mpakata- canoes, furniture. Oxystigma msoo Harms (KM 326). Mucho- canoe. Tamarindus indica L. (KM 245). Mkwayu- aril used in cooking, drinks, porridge. Capparaceae Capparis tomentosa Lam. (KM 251). Mbutula- medicinal, roots boiled to drink or use topically. Maerua subcordata (Gilg) DeWolf (KM 362, KM 392). Mti wa maji- swollen tuber used to settle sediment in water (a flocculant). Maytenus heterophylla (Eckl. & Zeyh.) N. Robson (KM 240, KM 318, KM 322, KM 343). Mlalanche- medicinal. Salacia erecta (G. Don.) Walp. (KM 408). No known use or name. Salacia stuhlmanniana Loes (KM 201). Impo- wood burned to repel mosquitos. Combretaceae Combretum butyrosum (Bertol. f.) Tul. (KM 241, KM 254). Mkioa- rope, capable of pulling heavy objects (canoes). Combretum constrictum (K1.) Engl. (KM 276). Mkioa- fruit edible but will scratch the throat; rope for heavy pulling. Combretum paniculatum Vent. (KM 411). Muambo ngoma- dull recurved spines are used to attach animal skins to a hollowed log for a drum. Terminalia brevipes Pampan. (KM 275, KM 302, KM 357). Mkokole- poles. Terminalia sp. (possibly T. brevipes, but large and without thorns) (KM 356). Mualango- choice pole. Compositae Pluchea dioscoridis DC. (KM 405). Mnoynwe- medicinal, boil roots.

Veronia sp. (KM 304). Lufacho- medicinal, used for the stomach. Convolvulaceae Hewittia sublobata (L.f.) O. Kuntze (KM 286). Muviazi- tuber eaten; fruit, symbolic against evil. Cucurbitaceae Coccinia grandis (L.) Voight (KM 399). Mhombohombo- edible fruit. Kedrostis foetidissima (Jacq.) Cogn. (KM 328, KM 371). Kanuke- medicinal. Momordica trifoliolata Hook. f. (KM 204). Muchuraga; edible fruit. Ebenaceae Diospyros ferrea (Willd.) Bakh. (KM 378, ?KM 383). Mnwiza- poles. Diospyros kabuyeana F. White (KM 246, KM 274, KM 325). Muhino (Swahili), Mhero (Pokomo) - strong pole, firewood. Diospyros mespiliformis A. DC. (KM 239). Mkuru- canoes (good but will crack in the sun), furniture. Erythroxylaceae Erythroxylum fischeri Engl. (KM 252a, KM 298). Mluhe (Ndera location) - used for poles infrequently, weak. Euphorbiaceae Acalypha echinus Pax & K. Hoffm. (KM 249, KM 300, KM 308, KM 335). Mvundakiundu, Mgawabarisa- medicinal, leaves used in circumcision. Acalypha sp. nr. fruticosa Forssk. (KM 292). Use unknown, but cut heavily. Antidesma venosum Tul. (KM 252). Msasuzi- tool handles. Antidesma vogelianum Muell. Arg. (KM 212). Msasuzi- name given to the genus Antidesma. Bridelia micrantha (Hochst.) Baill. (KM 282). Mpuju (Ndera location) - soft wood of little value.

Drypetes natalensis (Harv.) Hutch. var. leiogyna Brenan (KM 237, KM 242). Munghadama- poles used in old-style thatch homes. Erythrococca kirkii (Muell. Arg.) Prain (KM 235, KM 334, KM 327). No name given or use known. Flueggea virosa (Willd.) Voigt subsp. virosa (KM 248, KM 297). Mkwamba- flexible branches used in fishing traps. Phyllanthus sepialis Muell. Arg. (KM 361). Mkambachana- possibly used in fishing traps. Phyllanthus somalensis Hutch. (KM 319, KM 329). Mnyambahi?- used in building grass homes (Orma, Wardei). Spirostachys venenifera (Pax) Pax (KM 234, KM 296). Mchalaka- milky sap is very poisonous. Suregada zanzibariensis Baill. (KM 284, KM 350). Mungombe? - confusion in local name. Tragia furialis Bojer (KM 406). Mgeni- with stinging hairs. Flacourtiaceae Oncoba spinosa Forssk. (KM 218). Mpuju- poles, infrequently selected; wood soft. Guttiferae Garcinia livingstonei T. Anders. (KM 200). Mchachozi- tree; Mpekecho- young sapling for stirring. Lamiaceae Ocimum suave Willd. (KM 271, KM 407). Uvumbani- flavoring in tea. Lecythidaceae Barringtonia racemosa (L.) Blume (KM 227). Mtole- firewood. Loranthaceae Oncella ambigua (Engl.) Van Tiegh. (KM 213). Mudawa- medicinal to reduce brain swelling in children. Tapinanthus zanzibarensis (Engl.) Danser (KM 384).

Munyuni- medicinal for children, heat sticks and touch to skin.

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Lythraceae
 Lawsonia inermis L. (KM 221).
     Muasimini (near farms); Msurua (forest); fragrant flowers used
        as perfume.
Malvaceae
 Abutilon mauritianum (Jacq.) Medic (KM 278).
     Mbalambala.
 Hibiscus micranthus L. f. (KM 206, KM 279).
     Mvunjahukumu- symbolic, for the prevention of punishment.
 Thespesia danis Oliv. (KM 209).
     Muoro- used for pounding tools; very hard wood.
Menispermaceae
 Anisocycla blepharosepala Diels subsp. tanzaniensis Vollenson
           (KM 413).
     Kivila kiangi- used to tie Hyphaene traps.
 Cissampelos mucronata A. Rich. (KM 372).
     Kivila bara- used to tie Hyphaene traps (not good).
Mimosaceae
 Acacia robusta Burch. subsp. usambarensis (Taub.) Brenan (KM 403,
           KM410).
     Munga.
 Acacia rovumae Oliv. (KM 380).
     Mungagowe.
 Albizia glaberrima (Schumach & Thonn.) Benth. var. glabrescens
           (Oliv.) Brenan (KM 226, KM 348).
     Mpumpe.
 Albizia gummifera (J. F. Gmel.) E.A. Sm. var. gummifera.
     Mchuchampili.
Newtonia erlangeri (Harms) Brenan (KM 370, KM 388).
     Mkame- pounding sticks, choice firewood, very hard wood.
Moraceae
 Ficus ?bubu (KM 323).
     Mhodole.
 Ficus bussei Mildbr. & Burret.
     Mvuli (Swahili), Chemeri (Pokomo)- furniture, pounding stools.
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Ficus capreaefolia Del. (KM 342).
     Msasa.
 Ficus natalensis Hochst. (KM 307).
     Mvuma.
 Ficus sycomorus L.
     Mkuyu- canoes; hollowed logs for beehives, drums.
Palmae
 Borassus aethiopum Mart.
     Mtalpa- wine, fruit edible.
 Hyphaene compressa H. Wendl.
     Mkoma- roof thatching; poles; fruit edible.
Phoenix reclinata Jacq. (KM 219).
     Mkindu- twine, mats, baskets; fruit edible.
Papilionaceae
 Indigofera schimperi Jaub. & Spach var. schimperi (KM 215).
     Mcharara- used in making brooms.
Rhynchosia viscosa (Roth.) DC. var. breviracemosa (Hauman) Verdc.
           (KM 285).
     Mchumbivi (seeds) - human food?
Rhamnaceae
 Ziziphus pubescens Oliv. (KM 253).
     Mpwame.
Rubiaceae
 Coffea sessiliflora Bridson subsp. sessiliflora (KM 233, KM 347).
    Mungombe? - confusion in local names.
 Gardenia volkensii K. Schum. (KM 355).
    Mpekecho bara- decussate terminal stem used in stirring.
 Geophila repens (L.) I. M. Johnston (KM 360).
     No name or use given.
 Ixora narcissodora K. Schum. (KM 266, KM 321).
    Mwano- fine branches used to make arrows.
Keetia zanzibaricum Klotzsch subsp. zanzibaricum (KM 205).
     No name given; not used.
Kraussia kirkii (Hook.f.) Bullock (KM 401).
   Mukuwano- small poles used in fish traps.
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Lamprothamnas zanguebaricus Hiern (KM 313). Mchome- poles. Pavetta sphaerobotrys K. Schum. subsp. tanaica (Bremek.) Bridson (KM 208). Mluhe (Gwano location) - infrequently used as a pole; not straight. Polysphaeria multiflora Hiern subsp. multiflora (KM 349). Mrora- choice tree for poles. Polysphaeria parvifolia Hiern (KM 317). Mnchancha. Psychotria punctata Vatke var. punctata (KM 294, KM 341). No name given. Psychotria schliebenii Petit. var. sessilipaniculata Petit. (KM 232, KM 293). No name or uses given. Uncaria africana G. Don. subsp. africana (KM 283, KM 404). Gora- medicinal, use bark with saliva to stop bleeding. Salicaceae Populus ilicifolia (Engl.) Rouleau (KM 220). Mlalahe- canoes, young trees used as poles, soft wood. Salvadoraceae Azima tetracantha Lam. (KM 301). Mughogho- medicinal. Dobera glabra (Forssk.) Poir (KM 386). Mkupha- pounding sticks, basins. Dobera lorantifolia (Warb.) Harms (KM 387). Mkupha- pounding sticks, basins. Salvadora persica L. var. persica (KM 394). Mswaki- small branches used for brushing teeth. Sapindaceae Allophylus alnifolius (Bak.) Radlk. (KM 260, KM 265). No name or use given. Aporrhiza paniculata Radlk. (KM 244, KM 262). Mubo (Ndera location) - firewood. Blighia unijugata Bak. f. (KM 243b, KM 339). Mubonyeuni (Ndera location) or Mubo (Gwano location) - canoes.

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Chytranthus obliquinervis Radlk. (KM 203).
   Mkondokondo- poor pole; specifically avoided as bad luck.
Haplocoeclum inoploeum Radlk. (KM 366).
   Mhumbe meusi- choice firewood, wood very dense.
Lecaniodiscus fraxinifolius Bak. subsp. scassellatii (Chiov.) Fries
          (KM 247, KM 310).
   Mhumbe meupe- choice firewood, tool handles.
Majidea zanguebarica Oliv. (KM 264).
   Mgankololo.
Paullinia pinnata L. (KM 363).
   Mkawa- used as a rope, especially in binding traps.
Sapotaceae
Mimusops fruticosa A. DC. (KM 250).
   Mnguvwe- choice canoe.
Pachystela msolo (Engl.) Engl. (KM 216).
   Mchambia- canoe paddles, spoons, canoes.
Simaroubaceae
Harrisonia abyssinica Oliv. (KM 214).
    Cheiwa- medicinal, roots are boiled and the solution is taken for
       the stomach.
Sterculiaceae
Cola minor Brenan (KM 291, KM 344).
    Mwanafankuku (Ndera) - good firewood.
Thymeliaceae
Synaptolepsis kirkii Oliv. (KM 397).
    Roots used medicinally.
Tiliaceae
Grewia stuhlmannii K. Schum. (KM 257).
   Mkirinkonko- used in tiing fishing traps.
Grewia trichocarpa A. Rich. (KM 375, KM 391).
   Mkole- poles; fibers stripped and used as a twine in baskets.
Ulmaceae
 Celtis philippensis Blanco (- Celtis wightii) (KM 311, KM 331).
   Mtarhe.
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Trema orientalis (L.) Bl. (KM 263).
    Mhahe, Mbarnbara- very soft wood.
Verbenaceae
 Premna velutina Guerke (KM 288).
     No name or use given.
Violaceae
 Rinorea elliptica (Oliv.) O. Kuntze (KM 207).
    Mwanafankuku (Gwano), Mrhigati (Ndera)- firewood.
Vitaceae
 Ampelocissus africana (Lour.) Merr. (KM 255, KM 287).
    Mchikichi- medicinal, tuberous root boiled for swollen legs or
       stomach.
 Cissus rotundifolia (Forssk.) Vahl (KM 211).
    Murhrabahaba- medicinal, boiled leaves used as a poultice.
 Cyphostemma sp. (KM 396).
    Mwengale- used as a tooth medicine; do not swallow (contains
       silicate or oxalate crystals).
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APPENDIX C

#### APPENDIX C

#### Forest Area Summaries

The following summary lists the woody plant species most important (based on relative densities), and the total number of species at three structural layers. Relative densities are listed in parentheses next to the plant name. Potential canopy trees (i.e., may obtain heights > 10 m) are identified by an asterisk (\*), and woody vines by a pound sign ( $\phi$ ).

Canopy Trees	Subcanopy Trees	Saplings
Mnazini South		
		Cola clavata (.0738)
Garcinia livingstonei (.175)	Acacia robusta* (.205)	Salacia stuhlmenniana# (.0528)
Mimusops fruticosa (.141)	Borassus aethiopum" (.123)	Azima tetrachantha (.0943)
Acacia robusta (.112)	Cola clavata* (.115)	Lecaniodiscus fraxinifolius (.0803)
Total species = 23	Total species = 23	Total species = 70
Mnazini Worth		
Pachystela msolo (.541)	Phoenix reclinata (.489)	Diospyros mespiliformis* (.041)
Alangium salviifolium (.123)	Alangium salviifolium* (.263)	Polysphaeria multiflora (.374)
Ficus sycomorus (.107)	Polysphaeria multiflora (.105)	Chytranthus obliquinervis (.050)
Total species = 13	Total species = 10	Total species = 31
Kitere West		
Pachystela msolo (.416)	Phoenix reclinata (.810)	Sorindeia madagascariensis* (.107)
Sorindeia madagascariensis (.289)	Polysphaeria multiflora (.050)	Polysphaeria multiflora (.407)
Diospyros mespiliformis (.099)	Alangium salviifolium* (.041)	Keetia zanzibaricum# (.102)
Total species = 12	Total species = 13	Total species = 28
Beomo South A		
Sorindeia madagascariensis (.249)	Phoenix reclinata (.72)	Polysphaerie multiflore (.167)
Ficus sycomorus (.210)	Ficus sycomorus* (.069)	Sorindeia madagascariensis* (.046)
Pachystela msolo (.156)	Spirostachys venenifera* (.057)	Dicspyros mespiliformis* (.03)
Total species = 21	Total species = 13	Total species = 52

# Appendix C (continued)

Canopy Trees	Subcanopy Trees	<u>Saplings</u>	
Beomo South B			
Pachystela msolo (.470) Sorindeia madagascariensis (.258) Antidesma venosum (.115)	Phoemix reclinata (.800) Saba comorensis# (.04) Pachystela msolo* (.04)	Polysphaeria multiflora (.25 Uvaria scheffleri# (.245) Diospyros mespiliformis* (.108)	
Total species = 12	Total species = 9	Total species = 34	
Baomo North			
Pachystels meolo (.234) Ficus sycomorus (.210) Mimusops fruticosa (.105) Total species = 17	Phoenix reclinata (.5812) Polysphaeria multiflora (.068) Spirostachys venenifera (.043) Total species = 20	Agalea setulosaf (.264) Polysphaeria multiflora (.219) Diospyros mespiliformis* (.057) Total species = 39	
Sifa West			
Byphaene compressa (.219) Sorindeia madagascariensis (.188) Garcinia livingstonei (.156)	Hyphaene compressa* (.543) Phoenix reclinata (.196) Rinores elliptica ((.087)	Polysphaeria multiflora (.205) Bumteria seylenica (.071) Riborea elliptica (.071)	
Total species - 12	Idtal species - 9	Iotal species = 25	
Congolani West			
Mimusops fruticosa (.174) Byphaene compressa (.123) Garcinia livingstonei (.110)	Hyphaene compressa* (.412) Borassus aethiopum* (.235) Hunteria seylanica (.088)	Arime tetracenthe# (.591) Cepparis sepiare# (.118) Selvedore persice (.038)	
Total species = 20	Total species = 10	Total species = 36	
Congolani Cantral			
Byphaene compressa (.273) Acacia robusta (.119) Garcinia livingstonei (.119)	Byphaene compressa* (.347) Phoenix reclinata (.251) Spirostachys venenifera* (.050)	Terminalia brevipes (.034) Barrisonia seylanica (.041) Rinorea elliptica (.034)	
Total species = 25	Total species = 22	Total species = 37	

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#### Appendix C (continued)

Canopy Trees	Subcanopy Trees	Seplings	
Mchelelo West			
Byphaene compressa (.278)	Phoenix reclinata (.593)	Polysphaeria multiflora (.206)	
Sorindeia madagascariensis (.146)	Alengium salviifolium* (.148)	Pavetta sphaerobotrys (.050)	
Dicepyros mespiliformis (.111)	Byphaene compressa* (.080)	Rinorea elliptica (.045)	
Total species = 26	Total species = 12	Total species = 46	
Guru South			
Alangium salviifolium (.133)	Phoenix reclinata (.287)	Anisocycla blepharosepala# (.105)	
Acacia robusta (.074)	Pavetta sphaerobotrys (.103)	Capparis tomentose# (.103)	
Ziziphus pubescens (.059)	Alangium salviifolium* (.097)	Harrisonia abyssinica (.058)	
Total species = 31	Total species = 31	Total species = 71	
Guru North			
Ficus sycomorus (.186)	Leceniodiscus freminifolius (.200)	Capparis tomentosa (.416)	
Acacia robusta (.124)	Terminalia brevipes (.18)	Ficus sycomorus* (.198)	
Dicepyros mespiliformis (.093)	Ficus sycomorus* (.16)	Pluches dioscoridis (.084)	
Spirostachys venenifera (.093)	Lawsonia inermis (.16)		
Total species = 16	Total species = 11	Total species = 20	

# 213

APPENDIX D

Appendix D

# Association Analysis Chi Square Results

Selected campy trees are listed across the top. Data columns are statistical results mesuring the association between the size classes of species listed by rows (ct = campy tree, set = subcampy tree, sep = septing, adl = seedling) to each of the campy-tree dominants.

	f leus syconorus	Pachystel a molo	Sor inde la madagascar iens is	Diospyros mespiliformis	Garcinia Livingstonei	Mimusops fruticosa	Acac i a robusta
	ct act sap adl	ct set sep sdl	ct act sap adl	ct sct sap sdl	ct sct sap sdl	ct sct sep sdl	ct sct sap sdl
icus sycomorus	• • •						•
achystele molo	•	• •	•		•	•	•
orindeia medegascariensis	•	• •	• •		•	•	•
iospyros mespiliformis	•	•	•	•	•	•	•
arcinia livingatonei	•	• •	•		* *		•
imusope fruticose		•	•	•		• <sup>•</sup>	
cecia robusta		•	•		٠		• •
ordia goetzi	•	•		•		•	•
ole clevate					•	• • •	
yphaene compressa					•		
pirostachys venenifera	•						
ilangium selviffoltum		•	•			•	• • •
cacia elation						•	
ibizia glaberrima	•					•	
intideama venoaum	•						
hoenix reclinata (palm)			•		•	•	
pporhiza peniculata		• • •					
iabe comprensis (vine)		•			•		
econicaliscue frexinifoliue				•	• •		•

Key to Table Codes: + significant positive association; - significant negative association; \* non-significant chi-square, but significant positive Speanaen correlation; # non-significant chi-square, but significant negative Speanaen correlation.

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APPENDIX E

#### APPENDIX E

#### Detailed Summary of Significant MANOVA Results

The results are taken from the SAS output (SAS, 1985). Only the results for the extraction of the first root are listed.

#### Species Distinction by Site Characteristics (Wilk's lambda = .451, probability = .0015)

Characteristic Root	Percent	FLOOD	MOISTURE	RIVDIST	EDGDIST	SAND
0.6426	64.79	-0.0035	0.0099	0.0003	0.0016	-0.0038

Species Distinction by Resources (Wilk's lambda = .683, probability = .029)

Characteristic Root	Percent	CANFOOD	SAPFOOD	SEEDFOOD
0.4615	99.77	0.0208	0.0089	-0.0005

Vigor Distinction by Compositional Characteristics (Wilk's lambda = .204, probability = .026)

Characteristic Root	Percent	CANSPP	SAPSPP	SDSPP .	VINEDEN	PHOEN IX
1.6982	71.08	-0.0156	0.0568	-0.0287	-0.0371	0.0374

APPENDIX F

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#### APPENDIX F

#### Forest Temporal Comparisons

An asterisk (\*) is used to reference species that occur in the forest, but have not been recorded in the plots. A zero indicates that the species is absent.

# a. Mnazini North

	Homewood	(unpubl, dat	a. 1973-1974)		<u>Medl<b>ey (1</b>9</u>	<u>88)</u>
	Density		Relative	Density		Relative
Tree Species	<b>∦</b> /ha	Frequency	Importance	#/ha	Frequency	Importance
Pachystela msolo	51,16	.209	1.292	31.74	.387	. 820
Majidea zanguebarica <sup>1</sup>	9.30	.023	.189	0	0	0
Diospyros mespiliformis	4.65	.023	.130	1.47	.097	.095
Mangifera indica	4.65	.023	.130	0	0	0
Alangium salviifolium	4.65	.023	. 130	7.22	.032	.146
Ficus depauperata <sup>1</sup>	4.65	.023	.130	0	0	0
Ficus sycomorus	*	*	*	6.28	.194	.247
Ficus natalensis	*	*	*	0.47	.032	.031
Antidesma venosum	0	0	0	2.41	.097	.111
Blighia unijugata	0	0	0	1.47	.097	.095
Garcinia livingstonei	0	0	0	0.47	.032	.031
Aporrhiza paniculata	0	0	0	5.28	.290	.299
Ficus bussei	0	0	0	0.47	.032	.031
Cola clavata	0	0	0	0.47	.032	.031
Cordi <b>a goetzei</b>	0	0	0	0.47	.032	.031
Kigelia africana	0	0	0	0.47	.032	.031
Totals	79.069	.324	2.001	58.665	1.386	1.999
Saba comorensis	13.95			119.05		
(vine)				11.52 1	arge	
Phoenix reclinata (palm)	186.047			184.33		

<sup>1</sup>Majidea zanguebarica and Ficus depauperata are probably the same species as Apporhiza paniculata and Ficus bussei, respectively, in my study.

#### Appendix F (continued)

#### b. Mnazini South

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	Homewood	(1976)		<u>Medley</u>	(1988)	
Tree Species	Density	Frequency	Relative	Density	Frequency	Relative
	#/ha		Importance	<b>#</b> /h <b>a</b>		Importance
Cola clavata	61.54	. 121	. 603	15.87	.462	. 410
Acacia robusta	19.78	. 138	. 334	7.79	.365	.256
subsp. usambarensis						
Mimusops fruticosa	10.99	.086	. 199	9.81	. 442	.315
Cordia goetzei	6.59	.052	. 120	5.43	.250	. 177
Lamprothamnus zanquebaricus	6.59	.052	. 120	0.35	.019	.012
Diospyros kabuyeana	6.59	.034	.094	0.70	.038	.025
Ficus sycomorus	4.40	. 034	.079	0.70	.038	.025
Diospyros mespiliformis	4.40	.034	.079	5.78	.003	.084
Sorindeia madagascariensis	4.40	.034	.079	1.67	.096	.062
Cassia abbreviata	6.59	.017	.070	1.04	.038	.030
subsp. beareana						
Dob <b>era gla</b> bra	2.20	.034	.064	1.04	.019	.023
Commiphora campestris	2.12	.017	.040	0	0	0
Cordia sinensis	2.20	.017	.040	0.35	.019	.012
Garcinia livingstonei	2.20	.017	.040	12.18	. 423	.342
Polysphaeria parviflora	2.20	.017	.040	0	0	0
Celtis philippensis	*	*	*	0	0	0
Grewia trichocarpa	*	*	*	*	*	*
Lecaniodiscus fraxinifolius	•	*	*	0.70	.038	.025
subsp. scassellattii						
Trichilia emetica	*	*	*	0	0	0
Hunteria zeylanica	*	*	*	0	0	0
var. africana						
Borassus aethiopum	*	*	*	1.32	. 058	.042
Mangifera indica	0	0	0	0.35	.019	.012
Alangium salviifolium	0	0	0	0.70	.019	.018
Lannea schweinfurthii	0	0	0	1.32	.058	.042
Kigelia africana	0	0	0	0.70	.038	.025
Ziziphus pubescens	0	0	0	0.35	.019	.012
Markhamia zanzibaricus	0	0	0	0.35	.019	.012
Cynometra lukei	0	0	0	0.70	.038	.025
Spirostachys venenifera	0	0	0	0.35	.019	.012
Totals	142.79	.704	2.001	69.55	2.537	1.998
Saba comorensis (vine)	30.76			112.18		
only > 10 cm $\sim$				6.90		

Phoenix reclinata was not recorded within the compared area

Borassus < 10 m in height 29.21 25.76

# Appendix F (continued)

c. Congolani West.

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	<u>Marsh (1978)</u>	<u>Medl<b>ey (1</b>988)</u>
Tree Species	Density (#/ha)	Density (#/ha)
Mimusops fruticosa	5.67	6.60
Acacia rovumae	5.56	2.53
Diospyros mespiliformis	2.33	1.03
Garcinia livingstonei	1.89	2.53
Acacia robusta subsp. usambarensis	1.00	4.07
Albizia gummifera	1.00	0
Cynometra lukei	0.78	1.03
Cordia goetzei	0.78	3.04
Sorindeia madagascariensis	0.67	2.53
Cola clavata	0.56	0
Celtis philippensis	0.44	0
Oncoba spinosa	0.33	0
Albizia glaberrima var. glabrescens	0.22	0
Ficus sycomorus	0.22	0.51
Hyphaene compressa	0.22	4.54
Borassus aethiopum	0.11	0
Lannea schweinfurthii var. stuhlmannii	0.11	1.03
Ficus bussei	0.11	0.51
Cordia sinensis	0	1.03
Hunteria zeylanica var. africana	0	0.51
Majidea zanguebarica	0	1.03
Alangium salviifolium	0	0.51
Ziziphus pubescens	0	2.01
Afzelia quanzensis	0	0.51
Salvadora persica var. persica	0	1.03
Populus ilicifolia	0	0.51
Dead tree, standing	0	2.53
Totals	22.00	39.62

APPENDIX G

# APPENDIX G

# Ecological Attributes of Three Forest Corridors

a. Mnazini Forest Corridor.

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Large Trees (> 10 m)	Belt transect 10 m wide (3300 $m^2$ )					
Tree and Palm Species	# ind	Density #/ha	Coverage m <sup>2</sup> / ha			
Mangifera indica	4	12.12	14.004			
Borassus aethiopum	20	60.61	34.765			
Ficus sycomorus	1	3.03	14.170			
Lannea schweinfurthii var. stuhlmannii	2	6.06	0.976			
Alangium salviifolium	2	6.06	0.557			
Pachystela msolo	1	3.03	1.600			
Aporrhiza paniculata	1	3.03	0.291			
Total		93.94	66.363			
Phoenix	2	6.06	3.386			

Small Trees and Palms (3-10m)	Belt	transect 8m m	: 330 m (2640m <sup>2</sup> )
Tree species	# ind	Density	Coverage
Diospyros kabuyeana	1	3.79	0.060
Drypetes natalensis var. leiogyna	1	3.79	0.016
Chytranthus obliquinervis	2	7.58	0.014
Diospyros mespiliformis	1	3.79	0.014
Borassus aethiopum	10	37.88	23.413
Pavetta sphaerobotrys			
subsp. tanaica	2	7.58	0.143
Aporrhiza paniculata	1	3.79	0.003
Acacia robusta subsp. usambarensis	s 1	3.79	0.003
Alangium salviifolium	1	3.79	0.829
Polysphaeria multiflora	2	7.58	0.039
Thespesia danis	1	3.79	0.018
Sorindeia madagascariensis	1	3.79	0.008
Caesalpinia?	1	3.79	0.399
Cordia sinensis	1	3.79	0.060
Antidesma venosum	1	3.79	0.027
Total		102.31	25.046

# Appendix G (continued)

b. Mchelelo Camp to Mchelelo West Corridor (Mchelelo North)

Trees and Palms > 10 m in height	Belt	transect 10m	<b>x</b> 275m (2750 m <sup>2</sup> )
Tree and Palm Species	# ind	Density #/ ha	Coyerage m <sup>2</sup> / ha
Celtis philippensis	1	3.64	0.499
Sorindeia madagascariensis	1	3.64	0.686
Spirostachys venenifera	1	3.64	0.153
Mimusops fruticosa	1	3.64	0.604
Hyphaene compressa	1	3.64	1.028
Total		18.20	2.970

Small Trees and Palms 3-10 m	Belt	transect 4m x 2	75m (1100m <sup>2</sup> )
Tree and Palm Species	# ind	Density	Coverage
Ziziphus pubescens	5	45.46	0.441
Rinorea elliptica	3	27.27	0.268
Oncoba spinosa	2	18.18	0.356
Antidesma vogelianum	2	18.18	0.018
Polysphaeria multiflora	1	9.09	0.006
Hyphaene compressa	12	109.09	13.344
Grewia trichocarpa	4	36.36	1.336
Flueggea virosa	1	9.09	1.086
Drypetes natalensis var leiogyna	1	9.09	0.067
Harrisonia abyssinica	3	27.27	87.583
Cordia goetzei	2	18.18	2.182
Thespesia danis	1	9.09	0.016
Acacia rovumae	1	9.09	0.008
Total		345.44	106.711
Phoenix reclinata		54.54	474.809

# Appendix G (continued)

c. Mchelelo West to Congolani Central Corridor (Mchelelo South)

Trees and Palms > 10 m in height Belt transect 6 m x 464m ( $2784m^2$ )

Tree and Palm Species	# ind	Density #/ ha	Coverage m <sup>2</sup> / ha
Markhamia zanzibarica	1	3.59	0.083
Acacia rovumae	6	21.55	0.365
Acacia robusta ssp usambarensis	1	3.59	0.113
Garcinia livingstonei	1	3.59	0.353
Trichilia emetica	1	3.59	0.057
Populus illicifolia	3	10.78	0.811
Hyphaene compressa	3	10.78	2.509
Ficus sycomorus	1	3.59	10.684
Sterculia appendiculata	1	3.59	7.821
Total		64.65	22.796

Small Trees and Palms 3-10 m Belt transect 6 m x 464 m (2784 m<sup>2</sup>)

Tree and Palm Species	# ind	Density	Coverage
Phoenix reclinata	13	46.70	46.959
Hyphaene compressa	38	136.49	74.363
Chytranthus obliquinervis	7	25.14	0.027
Rinorea elliptica	1	3.59	0.021
Harrisonia abyssinica	9	32.33	0.203
Polysphaeria multiflora	4	14.37	0.159
Acacia rovumae	4	14.37	0.051
Markhamia zanguebarica	2	7.18	0.196
Soriendia madagascariensis	2	7.18	0.075
Ficus sycomorus	1	3.59	0.034
Spirostachys venenifera	1	3.59	0.343
Grewia trichocarpa	17	61.06	0.927
Cassia abbreviata ssp beareana	1	3.59	0.065
Pluchea discorides	11	39.51	0.082
Rauvolfia mombasiana	2	7.18	0.046
Acalypha echnis	1	3.59	0.005
Albizia gummifera	1	3.59	0.003
Antidesma vogelianum	2	7.18	0.075
Alangium salviifolium	1	3.59	0.002
Hunteria zeylanica var africana	2	7.18	0.039
Oncoba spinosa	1	3.59	0.0203
Pavetta sphaerobotrys ssp tanaica	2	7.18	0.116
Cordia goetzei	1	3.59	0.006
Total		445.36	123.800

APPENDIX H

Tree Species	Seed Collection	# Trials	Germination <b>X</b>	Germination Time	Seedling Vigor
Sorindeia madagascariensis	before short and long rains; best before short; fruits ripe but not dry	4 (n-49, n-20, n-17, n-140)	10 <b>%</b> (fruits dry) to 76 <b>%</b>	l4 days approx.	very good, 100% survival after 6 months
Pachystela msolo	before short and long rains; best before short seeds destroyed when consumed?	2 (n=25, n=39)	80% to 87.5%	21 days; staggered	slov growth, high survival
Ficus sycomorus	aseasonal; fruits must be ripe; dry and scatter seeds (or select with lens)	2 (n=40, 40) seeds selected	23 <b>7</b>	7 days; staggered	delicate; must harden by increasi sunlight;
<u>Ficus bubu, F. natalensis,</u> <u>F. scasselattii</u>	similar techniques and succ	ess as with Ficus sy	comorus		growth slow
Phoenix reclinata	before short and long rains (September good)	2 (n=15, n=35)	83%	18 days; staggered	good; growth very slow
Diospyros mespiliformis	after long rains (July); many seeds bad (54X)	2 (n=18, n=40)	7.5% at 8 wks	50 days; staggered	
<u>Acacia</u> robusta	near short rains; high oil content; easily infested	2 (n <del>-</del> 40, n-12)	7.5 to 25%	7 days	low seedling survival

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Appendix H

Nursery Propagation of Tree Seedlings

	:	,			
Tree Species	Seed Collection	f Trials	Germination <b>X</b>	Time	Seedling Vigor
Mimusops fruticosa	prior to long rains; removed seeds from fruit	2 (n=21, n=10)	70 to 76 <b>%</b>	17 to 48 days	49 days before first leaf; high survival
Garcinia livingstonei	before short and long rains; seeds large	3 (n=18, n=20, n=26)	22 to 73 <b>%</b>	48 to 90 days or more; staggered	slow growth; high survival
Majidea zanguebarica	before long rains; seed coat very hard, resistant, good storage	3 (n-31, n-21. n-13)	69.2 to 86 <b>%</b>	10 to 12 days; not staggered	fast growth; high survival
Acacta rovumae	seeds collected from ground; many insect infested	2 ( <b>n=</b> 12, n=30)	33-40%	7-14 days; not staggered	fast growth; harden by limiting water
Oncobe spinose	fruit black and hard when ready; many small seeds; scatter, then transplant	2 (n-120, n-20)	50-78%	7 days; staggered	vill mildew with overwatering
Kauvolfia mombasana	fruits orange when seed is ready; year- round production	1 (n=80)	24%	21 days	slow growth; not ready to transplant after 5 months
Cordia goetzei	careful collection of only ripe fruits	2 (n=36, n=80)	2.7 <b>%</b> seeds not ready	21 days; staggered	
<u>Saba comorensis</u>	fruits must be very ripe (orange); no storage	<b>1 (n=</b> 20)	60 <b>X</b>	35 days	

Appendix H (continued)

223

LIST OF REFERENCES
## LIST OF REFERENCES

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