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FOREST REGENERATION IN THE TANA RIVER PRIMATE NATIONAL RESERVE, KENYA

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ABSTRACT

This paper examines forest regeneration in the Tana River Primate National Reserve, using data on the size-class abundances and site conditions of major canopy tree species. Forests vary from those dominated by *Pachystela msolo* to mixed forests of greater species richness with *Sorindeia madagascariensis* and *Diospyros mespiliformis* or with *Garcinia livingstonei* and *Mimusops obtusifolia*. The low occurrence of saplings and narrow range of soil conditions supporting mature individuals project a relative decline for *P. msolo* in the study area. Size-class associations between six major canopy trees show a successional tendency toward greater species diversity but a decline in the regeneration of primate resources. Significant differences in the environmental conditions of *Ficus sycomorus*, *P. msolo* and *S. madagascariensis* document possible causal changes in the physical environment. The effects of riverine changes on the regeneration of primate habitat and its persistence potentially jeopardises long-term conservation in this small reserve.

INTRODUCTION

The lower floodplain of the Tana River, Kenya, provides a groundwater regime suitable for a narrow corridor of tropical forest, up to 30 m in stature, in an otherwise thorn-scrub environment. Riverine forest patches persist in isolation from the rain forests of Central Africa and the Indian Ocean coast (Lind & Morrison, 1974). Along the Tana River, as in other riverine systems, the distribution of forests and their composition are determined by the groundwater-hydrologic regime (Hughes, 1988) and the dynamics of a meandering river system (*cf.* Brinson, 1990; Salo and Räsänen, 1989). Floodplain disturbances are primary factors influencing forest dynamics in this region.

The Tana River Primate National Reserve was established in 1976 to preserve the best remaining riverine forest along the Tana River and important habitat for the endangered Tana River red colobus (*Colobus badius rufomitratus*) and crested mangabey (*Cercocebus galeritus galeritus*) (Marsh, 1976). The riverine forest mosaic provides an isolated refuge for plant and animal species adapted to a moist climatic regime (Andrews *et al.*, 1975). A regional examination of the flora and structural characteristics of floodplain forests along the Tana River suggests that river meanders, erosion, and deposition result in a high diversity of land forms and forest types in the TRPNR vicinity (Medley, 1992).

Irrigation projects, upstream and downstream from the Reserve, jeopardise regional conservation of riverine forest along the Tana River (Hughes, 1987, Ledec, 1987, Medley *et al.*, 1989), and argue for stewardship activities in the protected area. The Reserve, however, is one of the smallest in East Africa (171 km^2) and the forest area is fragmented and much smaller (9.5 km^2 in approximately 26 areas). A primate survey conducted in 1985, ten years after the establishment of the Reserve, showed population declines equal to 80% for the red colobus and 25% for the crested mangabey (Marsh, 1986). Marsh (1986) reported that the sharp decline in their populations may be attributable to a corresponding decline in forest habitat, primarily through the loss of important canopy-tree food resources. Furthermore, Hughes (1988) concluded from a study of forests between Bura and the Reserve that pioneer forest areas were absent, and that tree regeneration levels were low at all sampling plots. These findings, while providing an overview of forest condition at locations along the Tana River, support the need for a detailed examination of regeneration in the protected area. Preservation of primate habitat depends on understanding, and potentially managing for, vegetation change in a small land area (*e.g.*, White and Bratton, 1980).

Based on field research conducted between 1987–1988 in the Reserve (Medley, 1990), I address three questions concerning forest regeneration: (1) what is the current status of tree-species establishment; (2) do significant associations exist among the size classes of major canopy trees that may reflect species preferences or successional tendencies; and (3) do sites near three tree species, important as primate food resources (*sensu* Decker, 1989 and Kinnaird, 1990; see Medley, 1993a), differ significantly in their environmental conditions and potential for forest regeneration? The overall objective is to quantify the current status of forest regeneration through an examination of the ecology and successional tendencies of important riverine trees. Although an absence of long-term data on the vegetation and floodplain land forms limits successional projections, the results should show several key patterns of forest regeneration within this region, especially as it may be related to establishment and change in primate habitat. The study thereby provides a basis for further research in this region.

STUDY AREA

The Tana River flows from the humid highlands near Mt Kenya and the Aberdare Mountain Range, through an arid-semiarid floodplain between Garissa and Garsen, and to the Indian Ocean north of Malindi (fig. 1). At Hola (1° 30' S, 40° 2' E; 100 m), approximately 40 km upstream from the Reserve, annual minimum and maximum temperatures average 21.4 °C and 33 °C, respectively (Muchena, 1987). The climate is anomalously dry with an annual mean precipitation of 470 mm, no months with greater than 100 mm precipitation, and a growing season of 40 days occurring coincident with the short rains (October–December) (FAO 1984). The life zone is thorn woodland (*sensu* Holdridge 1967).

Evergreen-semi-evergreen forest vegetation along the floodplain is groundwater-dependent and its lateral extent is determined sharply by access to the groundwater with distance from the river (Hughes, 1988). Furthermore, forest community types correspond with particular flooding frequencies (Hughes, 1990) and land forms (Hughes, 1988, Medley, 1992), emphasising the close relationship between river dynamics, floodplain development, and the mechanisms of forest succession (Hughes, 1994). Given the dynamics of a meandering stream (Medley and

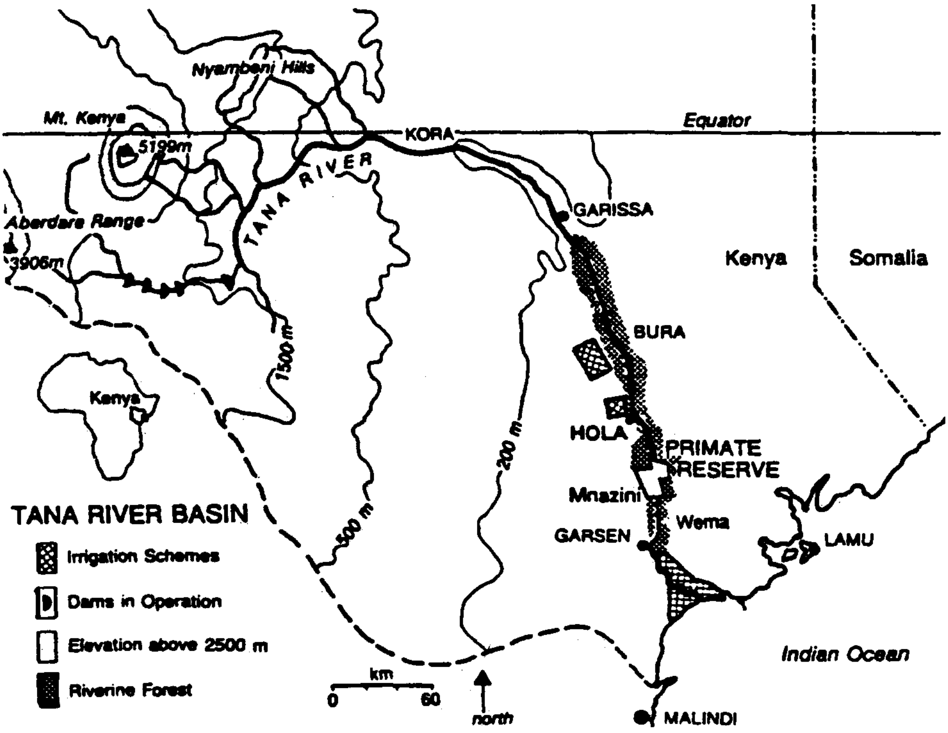

Figure 1. The Tana River basin, Kenya (modified from Medley 1992).

Hughes, in press), human land use activities (Medley, 1993b), and large mammal populations (Allaway, 1979; Marsh, 1976), riverine forest occurs as a patch mosaic (fig. 2).

METHODS

Status of tree-species establishment

I selected twelve forest areas in the Reserve that were representative of the forest-community types in this region. They varied in tree-species composition and primate abundances (Fig. 2; Medley, 1993a). In each forest, sample points were located at 50 m distances along transects placed approximately 100 m apart, and quadrats or plots were randomly orientated from each point centre. The number of transects and points per study area varied, depending on the size of the forest. In total, 363 points were used to document intraforest variation in the Reserve, as well as differences among the twelve forest study areas in tree-species composition and levels of regeneration.

Vegetation data were collected from four structural layers at each sample point, using point-centred quarter sampling for large trees (>20 cm dbh) and nested rectangular plots for the sub-canopy (10–20 cm dbh in 8 x 14 m plots), sapling (>1 m in height and < 10 cm dbh in 4 x 6 m plots), and seedling (.03–1 m in height in 2 x 2 m plots) layers. Species that obtain heights greater than 10 m were considered canopy trees, and their size-class abundances were derived from point frequencies, total densities, and relative densities. Data analyses focused on major canopy species that were most abundant as large trees in the study areas. A geographic information system (GIS) was used to show spatial patterns in the occurrences of the major tree species in

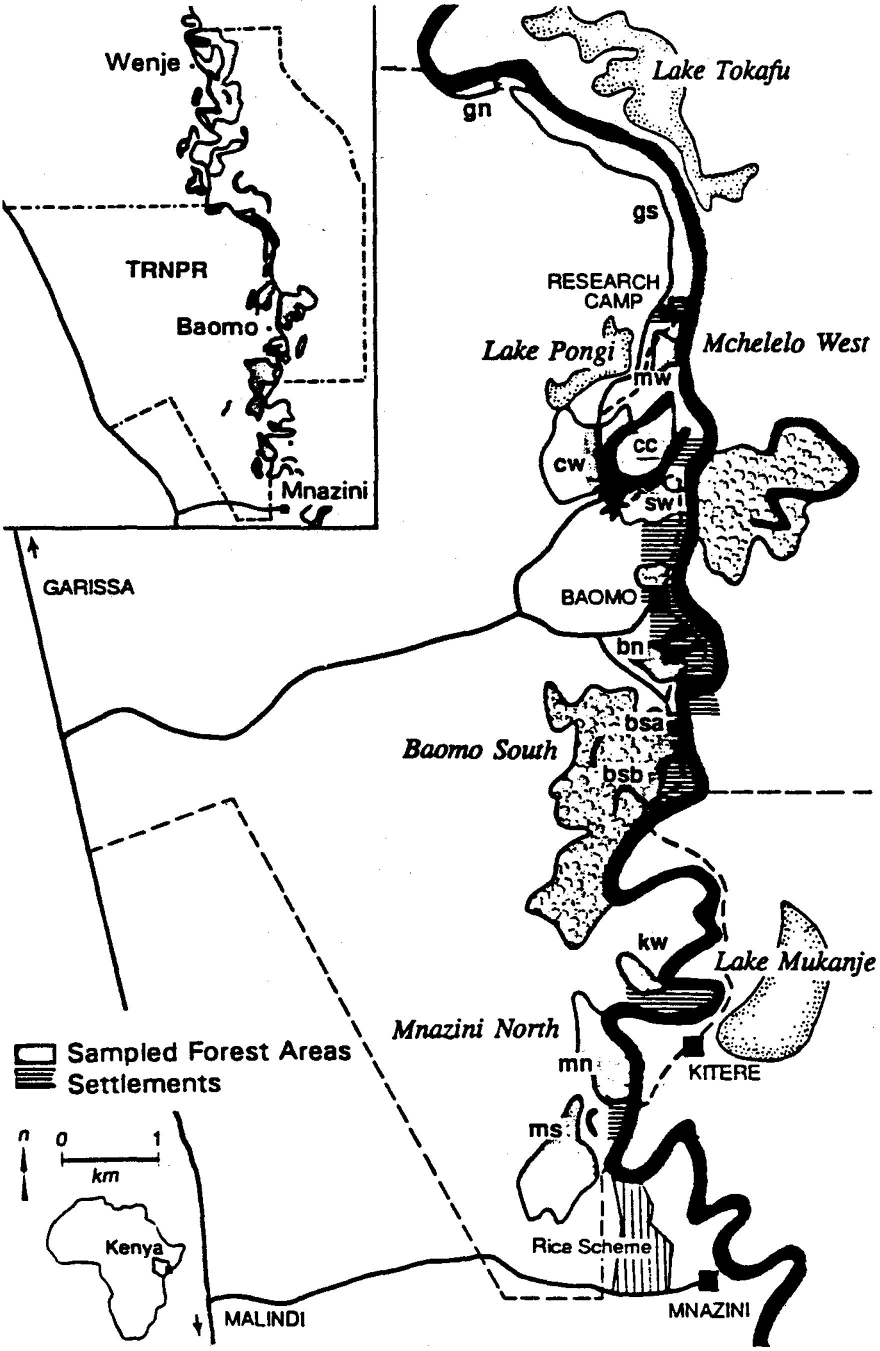

Figure 2. The study area located in the south-central sector of the Reserve. The twelve forest areas include: Guru North (gn), Guru South (gs), Mchelelo West (mw), Congolani Central (cc), Congolani West (cw), Sifa West (sw), Baomo North (bn), Baomo South A (bsa), Baomo South B (bsb), Kitere West (kw), Mnazini North (mn), and Mnazini South (ms). The top inset shows the reserve boundary and riverine forest (shaded) (reprinted from Medley, 1992).

the study forest areas by extrapolating from the sample points.

Associations among major forest canopy tree species

Successional tendencies between important riverine trees were investigated using the inter-associations among species size classes (Pielou, 1977, Zedler and Goff, 1973). Spearman correlations were computed to determine the direction and significance of associations between abundances in the large-tree size class of each major canopy tree species and abundances in their respective size classes (*i.e.*, seedlings, saplings, sub-canopy trees, and large trees).

Three associations with the large-tree size class of a major canopy species by another species were possible: (1) Invader: positive correlation for the sub-canopy, sapling, and/or seedling size-class; (2) Associate: positive correlations for the large-tree size class or all size classes; and (3) Nonassociate: negative correlations with all size classes. Negative correlations between the abundances of a canopy species and its sapling size class, but positive correlations with the sapling size class of other canopy species, suggest a change in forest composition. If a successional pathway is evident, one would expect a canopy tree species to enter (invade), associate, and decline (nonassociate) according to a particular sequence. Negative correlations between the large-tree size class of one canopy species and the sapling size classes of all canopy species indicate low forest regeneration.

Site and plant community characteristics near three canopy tree species

Ficus sycomorus, *Sorindeia madagascariensis*, and *Pachystela msolo* are highly used food resources for the endangered primates (Decker, 1989, Homewood, 1978, Kinnaird, 1990, Marsh, 1981), were identified as common components of suitable primate habitat (Medley 1993a), and appeared representative of different forest communities and/or stages of development (Hughes, 1988, Medley, 1992). Working in the same 12 forest areas, I selected 16 mature *F. sycomorus*, 15 *P. msolo*, and 10 *S. madagascariensis* trees for a comparative study of their site conditions and evidence of forest regeneration. Three individuals of *P. msolo* were selected from a large open area of the Baomo South forest that had experienced stand-level death of this species after a major flood in 1969.

Circular plots (radius = 15 m; 707 m^2) were established around each tree and divided into four quadrats (A, B, C, D) along a random orientation. Soil texture, subsurface soil moisture, and flood heights were compared as three attributes directly related to the flooding regime and moisture characteristics of the floodplain environment (see Hughes, 1990, 1994). Composite soil samples were collected in each circular plot at 30 cm in depth, and soil textures were determined by the Soil Testing Laboratory at the National Agricultural Laboratories, Kenya Ministry of Agriculture. Soil moisture percentages were determined by taking initial and dry weight measurements from samples collected at 1.5 m. Samples were collected from all plots during a 26.5 hour period in order to limit moisture differences attributable to a fluctuating water table. After a flood event in May 1988 (fig. 3), I measured the maximum water height as evidenced by the high-water markings on each selected tree and the depth of newly deposited sediments. The species richness and abundances of tree saplings, greater than 1 m in height and less than 10 cm dbh, were measured in quadrat A (177 m^2).

RESULTS

Status of tree-species establishment

Compositional differences are evident among the twelve forest areas, based on the densities of

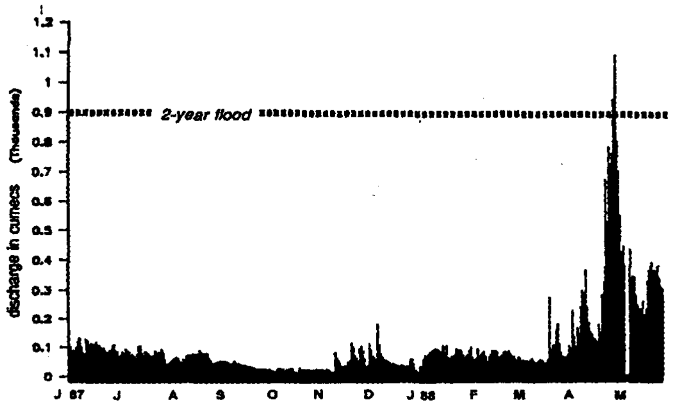

Figure 3. Tana River discharge measured daily at the Garissa station gauge. Data obtained from the Hydrology Department, Kenya Ministry of Water Development. Discharge is measured in cubic meters per second (cumecs) and the recurrence interval for the flood in May 1988 is derived from long-term data for the basin (see Hughes, 1990).

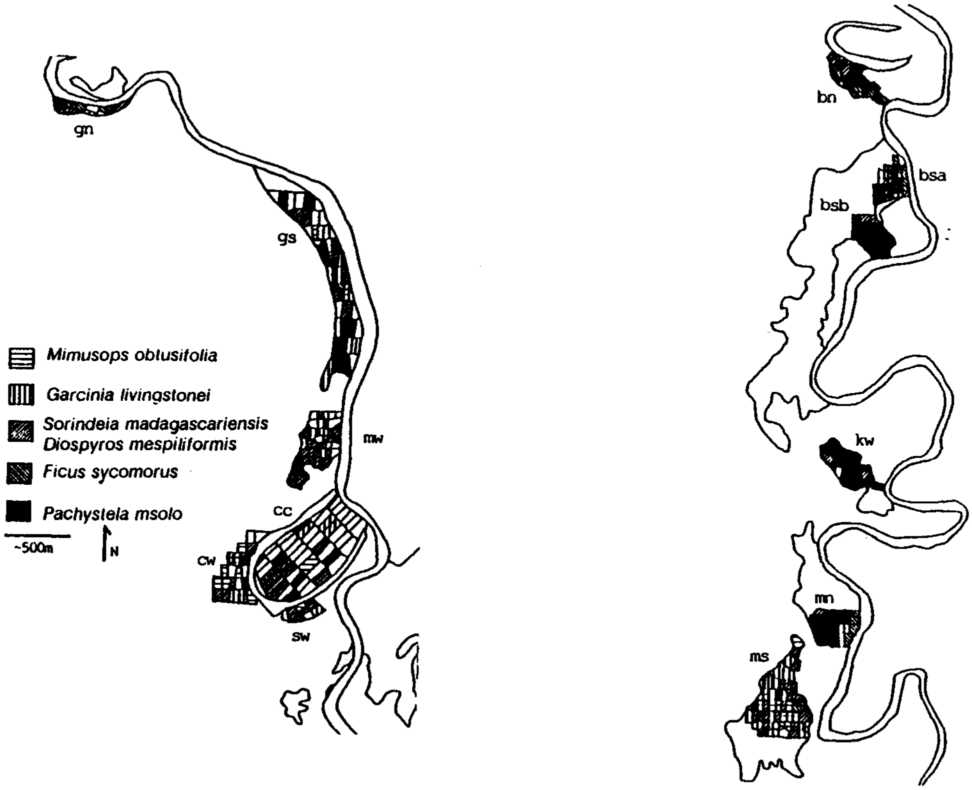

Figure 4. Spatial distribution of the six major canopy-tree species in the forest study areas. Forest names are provided in figure 2. Note that Mimusops obtusifolia *was formerly identified as* Mimusops fruticosa *and that* Pachystela msolo *is now called* Synsepalum msolo *by Pennington (1992) in the* Genera of Sapotaceae *(see Turrill et al., 1952)*

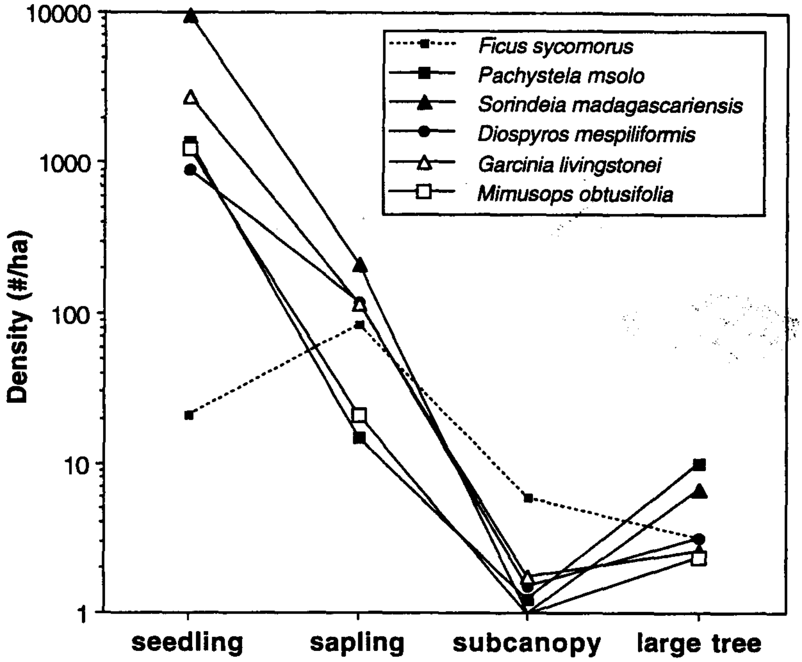

Figure 5. Densities of the six major canopy-tree species at four forest layers.

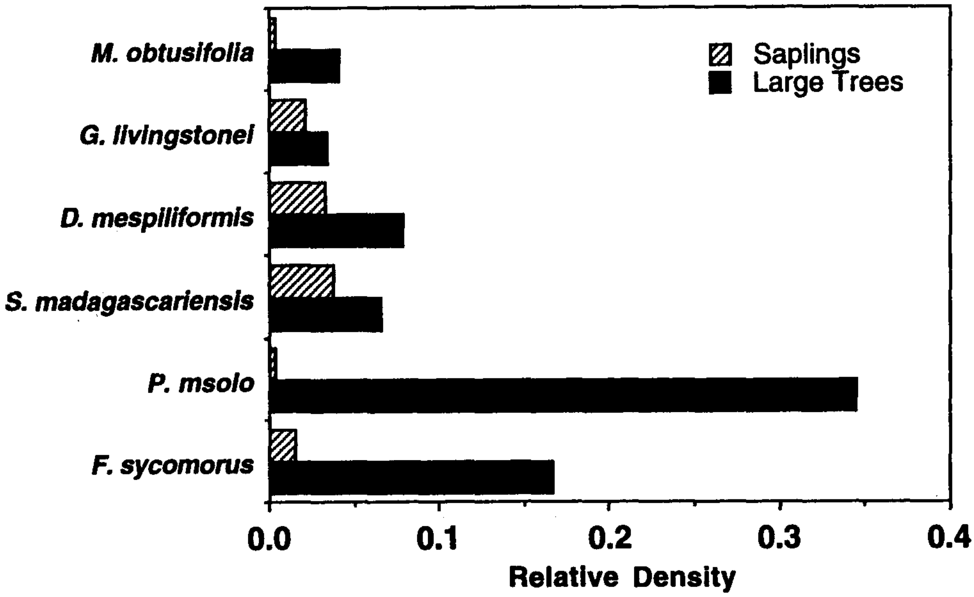

Figure 6. Relative densities of the six major canopy-tree species in the large-tree and sapling size classes.

canopy trees (table 1). *Pachystela msolo*, identified in earlier Tana River research as *P. brevipes* (see Homewood, 1978; Hughes, 1988; Marsh, 1976) and now listed as *Synsepalum msolo* by Pennington (1992) in the Genera of Sapotaceae (see Turrill *et al.*, 1952), is the most abundant tree in four forest areas, accounting for approximately 23–54% of the total large-tree density in each area. The rest of the forests have a mixed composition with *Sorindeia madagascariensis*, often in association with *Diospyros mespiliformis*, or with *Mimusops obtusifolia*, identified in earlier research as *M. fruticosa*, and *Garcinia livingstonei*. The density of *Ficus sycomorus* is high in several forests, mostly in association with *P. msolo*. Based on their densities in the twelve forest areas, these six trees (*F. sycomorus*, *P. msolo*, *S. madagascariensis*, *D. mespiliformis*,

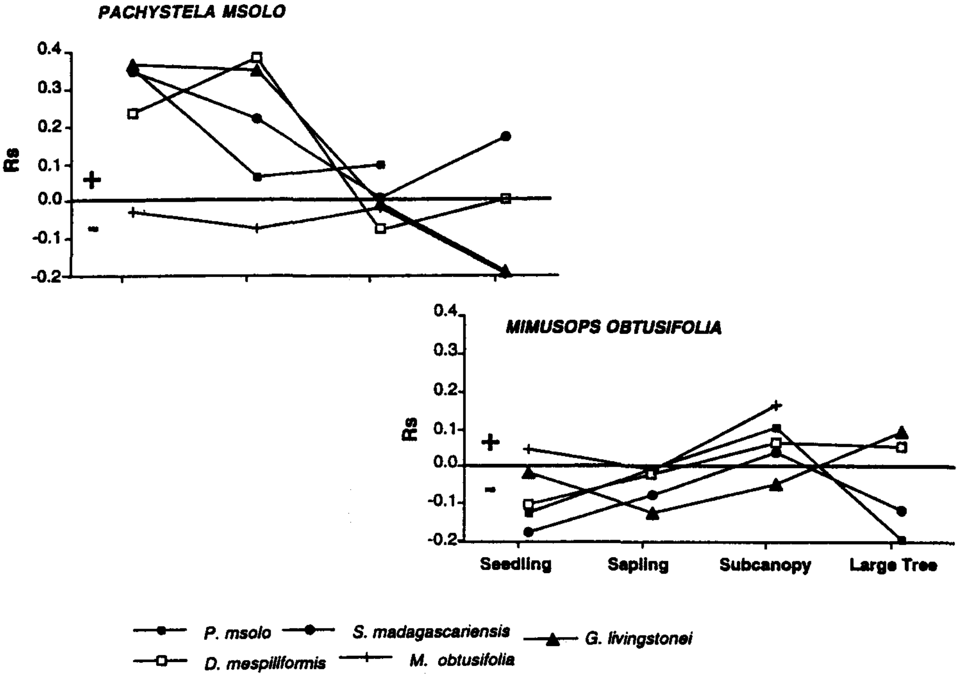

Figure 7. Spearman correlations (Rs) between the size classes of five canopy trees and the large-tree size class of Pachystela msolo *(top graph) and* Mimusops obtusifolia *(bottom graph).*

G. livingstonei, and *M. obtusifolia*) are identified as the most important canopy-tree species. Their current distribution in the study area appears non-random, especially evident by the clustered distribution of *P. msolo* in the southern forests (except Mnazini South) and the concentration of *F. sycomorus* along the river (*e.g.* Guru North, Baomo South A, and Mnazini North; fig. 4).

Levels of establishment by these six trees vary from relatively low densities in the seedling and sapling classes (*Ficus sycomorus*) to a nearly bimodal distribution pattern with lowest densities in the sub-canopy size class (fig. 5). In the large-tree size class, *Pachystela msolo* is the most abundant tree, representing nearly 35% of all the canopy-tree individuals (fig. 6). The tree occurs as the single dominant species (relative density >0.4) in three forest patches (table 1). At the sapling layer, however, *P. msolo* is among the least abundant of the canopy species (fig. 6). Saplings were recorded at only seven points out of 363, and the low number of individuals at those points resulted in a low overall density (fig. 5).

Table 1. Density (No/ha) of canopy trees recorded in the large-tree size class (>20 cm dbh). The twelve forest areas include: Mnazini North (mn), Baomo South b (bsb), Kitere West (kw), Baomo South a (bsa), Baomo North (bn), Mchelelo West (mw), Guru South (gs), Guru North (gn), Congolani Central (cc), Congolani West (cw), Sifa West (sw), and Mnazini South (ms) (see Fig. 2). Forests are arranged according to their similarity to Mnazini North, as measured by the relative abundances of all co-occurring canopy species and the six most important canopy trees are identified in bold print.

Tree species	mn	bsb	kw	bsa	bn	mw	gs	gn	cc	cw	sw	ms
Pachystela msolo	31.7	39.7	27.7	6.8	8.5	0.6	1.8		0.4			
Alangium salviifolium	7.2	1.3	3.7	1.0		3.8	5.1		0.2	0.5		0.7
Ficus sycomorus	6.3	2.5	2.2	9.2	7.7	0.9	1.0	3.9	1.7	0.5	1.3	0.7
Apporhiza paniculata	5.3	2.5	0.7	0.7	1.3	0.9						
Antidesma venosum	2.4	1.3		4.1	0.9				0.6			
Blighia unijugata	1.5					0.9	1.0		0.2			
Diospyros mespiliformis	1.5	9.0	6.6	2.7	3.0	4.7	1.6	1.9	0.4	1.0		5.8
Cordia goetzii	0.5		0.7		2.6	1.2	0.4	1.3	0.4	3.1		5.4
Cola minor	0.5			0.4								15.9
Ficus bussei	0.5									0.5		
Ficus natalensis	0.5						0.4					
Garcinia livingstonei	0.5	1.3		0.4	0.4	1.2	1.0	0.6	1.7	2.5	6.7	12.2
Kigelia africana	0.5						0.4				1.3	0.7
Sorindeia madagascariensis		21.8	19.2	10.9	2.6	6.1	3.4	1.3	1.9	2.5	8.1	2.0
Coffea sessiliflora		1.3										
Hunteria africana		1.3					0.8			0.5		
Lepisanthus senagalensis		1.3										
Mimusops obtusifolia		1.3	0.7		3.8	0.3	1.2	1.3	0.4	6.6	2.7	9.8
Phoenix reclinata			2.9	0.4		0.6						

Tree species	mn	bsb	kw	bsa	bn	mw	gs	gn	cc	cw	sw	ms
Albizia glaberrima			0.7	0.4	0.4	0.6	0.8		0.2			
Ixora narcissodora			0.7									
Oxystigma msoo			0.7		1.3							
Mangifera indica				2.7					1.0			0.4
Acacia robusta				0.7	1.7	0.9	2.8	2.6	4.4	4.1	1.3	7.8
Bridelia micrantha				0.7								
Lannea schweinfurthii				0.7		1.5	0.4	0.6	0.6	1.0		1.3
Acacia rovumae				0.4	0.4	0.3	1.2		2.3	2.5	1.1	
Borassus aethiopum				0.4								1.3
Polysphaeria multiflora				0.4								
Spirostachys venenifera				0.4	0.9	0.3	1.4		2.5			0.4
Sterculia appendiculata				0.4		0.9	0.2		0.2			
Trema orientalis				0.4		0.3						
Albizia gummifera					0.4	2.0	1.8		0.2			
Diospyros kabuyeana					0.4							
Thespesia danis					0.4							
Hyphaene compressa						11.7	3.7	0.6	10.0	4.6	9.4	
Majidea zanguebarica						0.9	1.6			1.0	1.3	
Diospyros ferrea						0.3	0.2	0.6				
Markhamia zanzibarica						0.3	0.6					0.4
Oncoba spinosa						0.3	0.2					
Pavetta sphaerobotrys						0.3	0.4					
Tamarindus indica						0.3						
Ziziphus pubescens							2.3	0.6		2.0	1.3	0.4

Tree species	mn	bsb	kw	bsa	bn	mw	gs	gn	cc	cw	sw	ms
Celtis occidentalis							1.0	1.9				
Populus ilicifolia							0.4		1.0	0.5		
Afzelia quanzensis							0.2		1.2	0.5		
Dobera glabra							0.2					1.0
Ficus scasselatii							0.2					
Cynometra lukei								0.6	0.2	1.0	2.7	0.7
Haplocoelum inoploeum								0.6				
Lecaniodiscus fraxinifolius								0.6				0.7
Terminalia brevipes									1.5			
Cassia abbreviata									0.4			1.0
Lawsonia inermis									0.2			
Cordia sinensis										1.0		0.4
Salvadora persica										1.0		
Lamprothamnas zanguebaricus												0.4
Total Density (# trees/ha)	**58.9**	**84.6**	**66.5**	**44.2**	**36.7**	**42.1**	**37.7**	**19**	**33.8**	**36.9**	**37.2**	**69.4**
Number of Tree Species	**13**	**12**	**12**	**21**	**17**	**26**	**31**	**15**	**25**	**20**	**11**	**22**
Sample Points	**31**	**17**	**23**	**37**	**23**	**41**	**52**	**10**	**47**	**21**	**9**	**52**

Table 2. Size-class association analyses. Data columns show significant (+) and negative (-) Spearman correlations (alpha <0.05) between the size classes of species listed by rows (sd = seedling, sp = sapling, sc = sub-canopy, and c = large tree) and the large-tree size class of six major canopy tree species.

	Large-Tree Size Class of Six Major Canopy Tree Species																							
Plant species (rows) and their size classes (columns)	*Ficus sycomorus*				*Pachystela msolo*				*Sorindeia madagascariensis*				*Diospyros mespiliformis*				*Garcinia livingstonei*				*Mimusops obtusifolia*			
	sd	**sp**	**sc**	**c**	**sd**	**sp**	**sc**	**c**	**sd**	**sp**	**sc**	**c**	**sd**	**sp**	**sc**	**c**	**sd**	**sp**	**sc**	**c**	**sd**	**sp**	**sc**	**c**
Ficus sycomorus	+	+	+	+												-				-				
Pachystela msolo		+			+		+	+	+			+					-			-	-		+	-
Sorindeia madagascariensis		+			+	+		+	+		+	+					-	-			-			-
Diospyros mespiliformis				-	+	+			+				+			+		-			-			
Garcinia livingstonei				-	+	+		-	+	+									+	+		-		
Mimusops obtusifolia								-				-			+								+	+

Associations between major forest canopy tree species

Spearman correlations between the size classes of five canopy species and the large-tree size class of *Pachystela msolo* and *Mimusops obtusifolia* show two contrasting patterns (fig. 7). Seedlings and saplings of most species are positively associated with large trees of *P. msolo* (except *M. obtusifolia*) and negatively associated with *M. obtusifolia* (except *M. obtusifolia*). Although self-replacement (*i.e.*, positive association with its saplings) is non-significant, other canopy species are established under the *P. msolo* canopy. In contrast, *M. obtusifolia* shows a negative relationship with those size classes, or an absence of invading species. *P. msolo* and *M. obtusifolia* are nonassociates as large trees. Significant positive and negative associations between the respective size classes and the large-tree size class of the six major canopy species (table 2), coupled with field observations and summaries for the twelve forest areas, illustrate some relative preferences and successional tendencies. *P. msolo* and *S. madagascariensis* invade beneath *F. sycomorus* and occur as positive associates at the canopy layer. The co-occurrences between these two trees and *Diospyros mespiliformis* at the canopy (e.g., Kitere West and Baomo South; table 1 and fig. 4), and the significant invasion of *S. madagascariensis* and *D. mespiliformis* under *P. msolo* indicate a successional tendency toward a mixed-forest composition. *Garcinia livingstonei* and *Mimusops obtusifolia* are significant invaders under *Sorindeia madagascariensis* and *Diospyros mespiliformis*, respectively, but show a negative or non-significant association with these species as large trees. Community differences are greatest between *Pachystela*-dominated forests (e.g., Mnazini North) and *Mimusops-Garcinia* forests (e.g., Mnazini South; see table 1). *Ficus sycomorus*, *Pachystela msolo*, and *S. madagascariensis* show negative correlations with large trees of one or both of these species. These trees either decline upon this change in canopy-species dominance, or segregate to different sites (*sensu* Hughes, 1988) irrespective of their preferences as saplings.

Site conditions and forest regeneration near three canopy tree species

Individuals of *Ficus sycomorus*, *Pachystela msolo*, and *Sorindeia madagascariensis* show significant differences in their site conditions and evidence of sapling establishment (fig. 8). *Ficus sycomorus* shows an adaptation to a wide range of sand percentages (mean = 35.9; sd = 21.1; range = 14–86%), in contrast to the greater sand content of soils associated with *Sorindeia madagascariensis* (mean = 53.6; sd = 19.2; range 24–86%) and the low percentages of sand associated with *Pachystela msolo* (mean = 26.5; sd = 10.9; range = 2–48%). These differences correspond with those observed for soil moisture percentages at 1.5 m in depth. Soil moisture is highest and least variable under *P. msolo* (mean = 22.3; sd = 1.72; range = 14.3–31.4%). Whereas highest flooding heights (92 cm) and sediment deposits (8 cm) are measured for *F. sycomorus* plots, 11 of the 15 *P. msolo* plots flooded (up to 56 cm) and the mean sediment depth (1.4 cm) exceeds that recorded for *F. sycomorus*.

Highest species richness at the sapling layer occurs in the *Sorindeia madagascariensis* plots (mean = 14; sd = 2 spp.). The mean value closely approximates that measured for *Pachystela msolo* (mean = 14; sd = 5 spp.), which is especially high for individuals in the area of stand-level death (mean = 23 spp.). Primate food resources show an opposite relationship. They are most abundant in the *Ficus sycomorus* plots (mean =210; sd = 120/ha), decline in the *P. msolo* plots (mean = 128; sd = 162), and are significantly lower in the *S. madagascariensis* plots (mean = 78; sd = 58/ha).

DISCUSSION

The twelve forest areas studied in the Reserve vary in composition from those dominated by

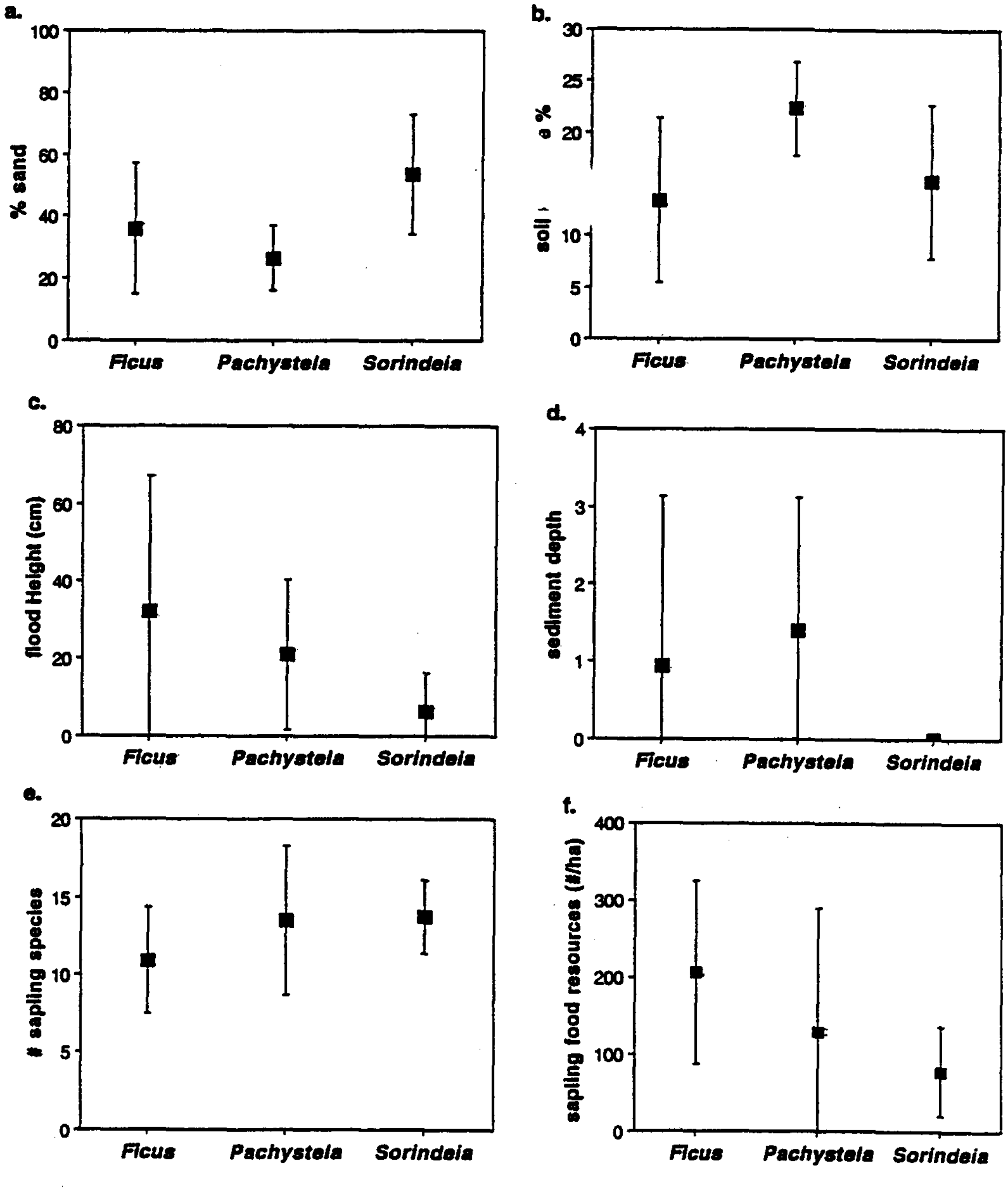

Figure 8. Site and regeneration characteristics of the plots centered on Ficus sycomorus *(n=16),* Pachystela msolo *(n=15), and* Sorindeia madagascariensis *(n=10). The graphs show the means and standard deviations for the following attributes: a) percent sand in soils collected at 30 cm in depth; b) percent soil moisture measured at 1.5 m in depth; c) maximum water height during the May 1988 flood; d) depth of sediments deposited during the May 1988 flood; e) number of species measured as saplings (>1m ht and < 10 cm dbh) in 177 m^2 plots; and, f) density of primate food resource trees (*Ficus *spp.,* Diospyros mespiliformis, S. madagascariensis, P. msolo, *and* Acacia robusta *subsp.* usambarensis*).*

Pachystela msolo, with *Ficus sycomorus*, to mixed forests of greater species richness dominated by *Sorindeia madagascariensis* and *Diospyros mespiliformis* or by *Garcinia livingstonei* and *Mimusops obtusifolia*. Studies of community diversity in this region by Marsh (1976), Homewood (1978), Hughes (1988), Medley (1992), and Njue (1992) concur that the forest types represented by these trees vary with major floodplain land forms: flooded low-levees (e.g., Mnazini North), well-drained high levees (e.g., Mchelelo West), and clay-backwater swamps (e.g., Mnazini South; fig. 8). Some of the study areas contain a mosaic of these forest types as represented by the distribution of canopy trees in the sample quadrats, documenting a heterogeneity of site conditions over small (<200 m) distances (fig. 4; see Guru South, and Baomo South a).

Forest regeneration, as it may influence change in these community types, directly relates to the levels of establishment and potential for recruitment by the major canopy tree species. *Ficus sycomorus* shows pioneer growth characteristics, with low abundances at the seedling and sapling layers in the forest study areas (fig. 5) and a large number of individuals near the river edge (fig. 4). Other studies show a record of invasion on point bars (with *Populus illicifolia*) and cleared openings and a record of high mean growth rates at geater than1 cm dbh/year (Hughes, 1988; Medley, 1994; Kahumbu, 1993). In contrast, *Sorindeia madagascariensis* appears more shade tolerant, with high levels of regeneration in the forest study areas.

Low abundances of major canopy species in the sub-canopy layer suggest a delay will occur in the closure of the canopy following the death of large trees. This size structure may be explained by episodic establishment (*sensu* Hughes, 1994; Wissmar and Swanson, 1990), continuous regeneration with a low number of species reaching the sub-canopy size-class (Webb *et al.*, 1972), or recruitment dependent on fast growth through the sub-canopy size class in canopy gaps (Hartshorn, 1980; Salo and Kalliola, 1991). Large-magnitude floods that occur infrequently may change the status for regeneration and initiate a new successional cycle. Earlier studies by Marsh (1976) and Allaway (1979) document a more open riverine forest, attributable mostly to disturbances imposed by large mammal populations. The recent population crash in elephants along the Tana River and local extinction of the black rhino have allowed for greater establishment and growth in the forest understory (Marsh, 1986). Both regional (e.g., river flows) and local (e.g., animal populations) environmental changes may partially explain the profound differences in the abundances of trees at the sapling and sub-canopy layers, and the overall size-class structure of the forests.

Pachystela msolo, which is presently most abundant in the large-tree size class and occurs in nearly mono-dominant stands (e.g., Mnazini North), shows a low abundance at the sub-canopy size class (Fig. 5) and the lowest relative abundance in the sapling size class (Fig. 6). Areas of significant regeneration by *P. msolo* were not measured or observed. Furthermore, stand-level death of mature individuals is documented in the Congolani and Baomo South forests (Marsh, 1986; Medley, 1990). These observations question the persistence of this species, at least in the short-term, as the most abundant canopy tree in the Reserve. The flooding and/or geomorphological conditions that promote the establishment of a new cohort of trees are not clearly documented.

Significant associations between the size-classes of the six major canopy species show successional tendencies among the forest communities in which they dominate (Fig. 9). *Ficus sycomorus* is a riparian pioneer tree; it is not found invading significantly under mature trees of any other major canopy species. In contrast, *Pachystela msolo* and *Sorindeia madagascariensis* both invade under *F. sycomorus* canopies. While the occurrence of mono-dominant stands of *P. msolo* is an obvious feature in some forest patches, its low level of regeneration complicates any understanding of conditions necessary for establishment. From the association analyses,

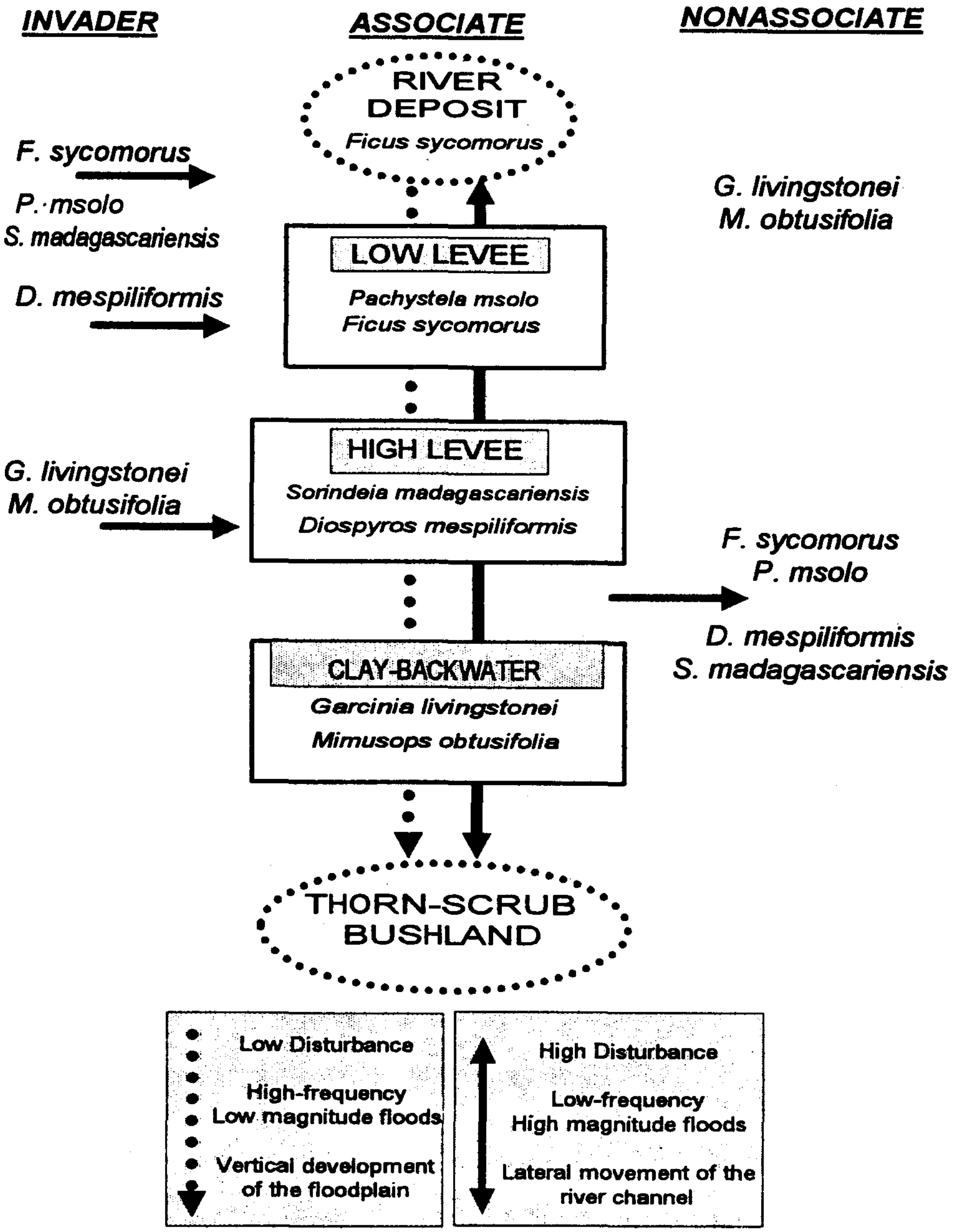

Figure 9. Model showing the site preferences and successional tendencies of the six major canopy tree species in the riverine forest communities. A primary successional pathway is shown along the dotted line in association with vertical development of the floodplain through high-frequency, low magnitude floods. The solid line shows disruption of the pathway, attributable to low-frequency, high magnitude floods and lateral movement of the river channel.

it appears that *P. msolo* establishes and dominates at the transition toward a high-levee forest with *S. madagascariensis* and *Diospyros mespiliformis*. In view of the low regeneration recorded for *P. msolo*, I hypothesise a trend toward greater dominance by these other two species.

Along this section of the Tana River, the upland vegetation is thorn-scrub. Forest is confined to a narrow band with environmental factors determining its expansion on either edge. With the exception of *F. sycomorus*, none of the major canopy species has a significant association with its saplings, identifying a low level of self-replacement in the studied forests. Forest community establishment and persistence appears dependent on the destabilising influence of river meanders, floods, and the continual development of new sites for colonisation. Riverine forest is necessarily sensitive to changes in the hydrologic regime, such as those associated with upstream dam construction (see Hughes, 1987; Njue, 1992). At present, five dams are constructed in the upper basin of the Tana River (Masinga, Kamburu, Gitaru, Kindaruma, and Kiambere). The much larger Three Forks Dam proposed for construction at Mutonga and Grand Falls is projected to drop groundwater levels, decrease the sediment load, and reduce seasonal flooding patterns. Unless mitigation measures, such as controlled water releases from the reservoir, are a part of the final plan, the impacts on riverine forest could be devastating (Butynski, 1995).

A comparative study of *Ficus sycomorus*, *Pachystela msolo*, and *Sorindeia madagascariensis* further documents the ecological differences among the forest communities where these species dominate. Together, they represent the range in conditions characteristic of high-quality primate habitat (Decker, 1989; Kinnaird, 1990; Medley, 1993a). Soils vary from sandy loam under *S. madagascariensis* to predominantly clay soils under *P. msolo*, with corresponding differences from low to relatively higher moisture availability at depth. Flooding conditions also differ significantly between the three trees. After the flood in May 1988, with a predicted two-year recurrence interval, floodwater heights varied from mean levels above 30 cm for *F. sycomorus* to low mean heights (6.2 cm) or an absence of flooding for six of the ten *S. madagascariensis* plots. Greater site variability in *F. sycomorus* may be attributable to relatively longer life spans and changing environmental conditions. In contrast, *P. msolo* shows the narrowest range of site conditions.

Greatest species richness at the sapling layer occurs in association with *S. madagascariensis*, but the regeneration of primate food resources is highest under *F. sycomorus*. These results support a trend toward greater species richness from low-levee to high-levee forest communities. The regeneration of primate habitat corresponds with riverbank to low-levee positions, consequently dependent on active deposition and flooding from the river channel. Primates, through their high use of fruits from these tree species, may be important in the dispersal of seeds between the community types. Again, regional changes in the deposition of new sites for early colonisation, a predicted outcome of dam construction, and local human needs for agricultural lands will reduce the potential for early-forest development and the establishment of high-quality primate habitat.

A mosaic of forest communities is represented in the Tana River Primate National Reserve. Other studies have shown a correspondence between the distribution of forest types and the characteristics of the floodplain disturbance regime (Hughes, 1988, 1990). This study quantifies regeneration patterns for the major canopy species, which vary in their relative abundances in different forests, and identifies some possible successional tendencies. The overall mechanisms of forest change and/or persistence are complicated by the coupling of allogenic (riverine), and autogenic (species establishment and recruitment) factors (Medley and Hughes, in press). A projection of community change based on current patterns of regeneration necessarily assumes no major shifts in the river position or hydrologic regime (Fig. 9). Forest community change progresses along the projected pathway in accordance with vertical floodplain development through high-frequency and low magnitude floods, as represented by the flood that occurred in May 1988. Community change would be notably disrupted by a major shift in the river position associated with low-frequency and high magnitude events (*cf.* Hughes, 1994). The relative abundances of tree species and their size-class structures documented in this study should provide a basis for comparative studies of change through time in the Reserve. Turner (1989) states that a dynamic landscape may exhibit a stable mosaic of community types at one spatial scale, but not at another. Along the Tana, the spatial scale at which a stable mosaic of all forest communities is maintained, or at best a sustainable distribution of primate habitat, is not yet predictable.

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