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Composition, structure, and regeneration patterns in a gallery forest along the Tana River near Bura, Kenya

John K. Maingi [a,*], Stuart E. Marsh [b,1]

[a] Department of Geography, Miami University, Oxford, OH 45056, USA
[b] Arizona Remote Sensing Center, Office of Arid Lands Studies, The University of Arizona, 1955 E. 6th Street, Suite 205, Tucson, AZ 85719, USA

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Abstract

This study used classification and ordination techniques to characterize the composition and distribution of woody vegetation along the Tana River floodplain near Bura in eastern Kenya. Results obtained from cluster analysis of tree and shrub vegetation corroborated the results from non-metric multidimensional scaling (NMS), separating the forests into seven fairly well-defined assemblages of species. The primary vegetation gradient summarized by the ordination was significantly correlated (0.257–0.394, $p < 0.01$) with soil texture and soil carbon at depths of 50–120 cm. The secondary vegetation gradient was significantly correlated (0.480–0.483, $p < 0.01$) with indicators of river flood regime. Measured environmental variables, however, only partially explained observed vegetation patterns. Many overstory species were well represented in the regeneration layer of low-lying point-bar and oxbow forests, but were poorly represented in the higher elevation levee forests. There were significant correlations (0.278–0.320, $p < 0.01$) between the first ordination axis for the regeneration layer and flood regime of the river, and between the second ordination axis and soil texture (0.321–0.346, $p < 0.01$) in the top 20 cm where seedling roots are likely to be settled. *Spirostachys venenifera* and *Acacia elatior* had the widest environmental tolerance, occurring in 78% and 60% of all sample plots, respectively. *Populus ilicifolia* had the narrowest environmental tolerance, occurring in less than 1% of plots, all located on point-bars.

Keywords: Cluster analysis; Non-metric multidimensional scaling (NMS); Floodplain; Riparian; Diversity; Semi-arid

1. Introduction

Many studies on riparian ecosystems have demonstrated the significant influence of numerous abiotic factors such as hydroperiod (e.g., Wharton et al., 1982; Hupp and Osterkamp, 1985; Sharitz and Mitsch, 1993; Visser and Sasser, 1995; Townsend, 2001), floodplain geomorphic features (e.g., Hupp and Osterkamp, 1985; Hughes, 1988; Medley, 1992), soil properties (e.g., Jones et al., 1994; Robertson and Augspurger, 1999), climatic conditions (e.g., Wyant and Ellis, 1990; Medley, 1992), ecological influences such as competition, herbivory, and disease (Naiman and Decamps, 1997), and land-use history (e.g., Marsh, 1986; Medley, 1992; Stave et al., 2001). One of the most studied gallery forest in Kenya occurs along a 400 km stretch along the largest river in the country, the Tana, between Mbalambala and Kipini (Fig. 1). The forests are tall and lush, contrasting markedly with the semi-arid scrub that characterizes most of Tana River District where the river flows through. These gallery forests are dependent on ground water and exist as a mosaic of deciduous and evergreen trees rich in endemic species (Medley, 1992).

Most ecological studies along the Tana River floodplain have been conducted within the protected Tana River National Primate Reserve (TRNPR). This reserve occupies 16,900 ha and includes a 50 km stretch of the meandering river (World Bank, 1993). A majority of the studies conducted in the reserve have focused on primates (e.g., Allaway, 1979; Groves et al., 1974; Homewood, 1978; Marsh, 1978) and relationships between forest vegetation and primates (e.g., Marsh, 1986; Kinnaird, 1992; Medley, 1993; Wahungu et al., 2005).

Medley (1992) identified 175 woody species within the TRNPR and described the forests as belonging to four geographic affinities: the Zanzibar-Inhambane, Somali-Masai, Guinea-Congolian, and Zambezian floristic regions. Regional biodiversity of the forests is inadequately protected within the TRNPR because important species found in forests upstream

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* Corresponding author. Tel.: +1 513 529 5024; fax: +1 513 529 1948.
E-mail addresses: maingijk@muohio.edu (J.K. Maingi), smarsh@ag.arizona.edu (S.E. Marsh).
[1] Tel.: +1 520 621 8586; fax: +1 520 621 3816.

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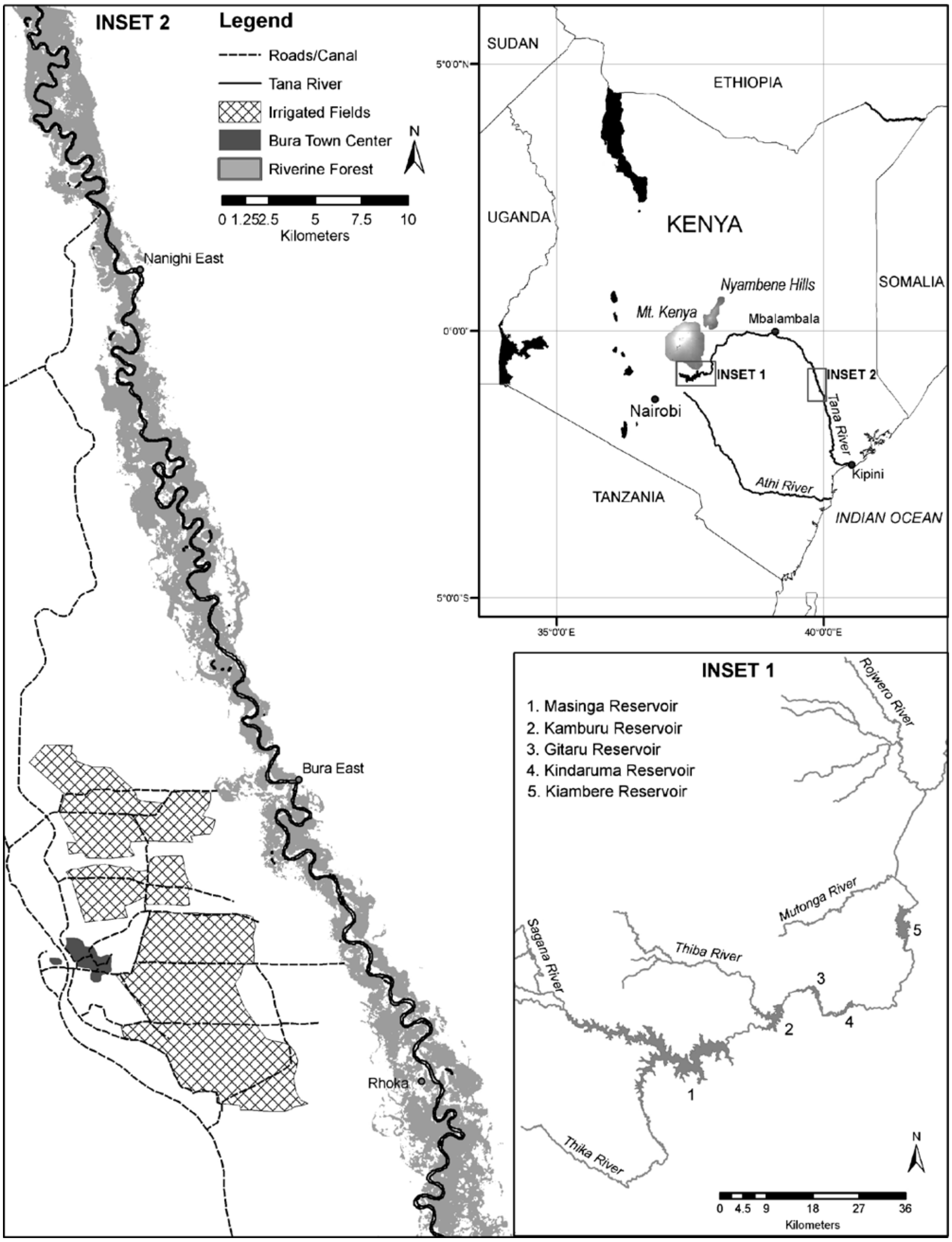

Fig. 1. Location of upstream dams, the Tana gallery forests, and the Bura Irrigation Scheme.

and downstream of the TRNPR are missing. Composition of the forests changes considerably from Bura downstream to the TRNPR and to the Wema forests (Fig. 2). Medley (1992) indicated that canopy-tree composition of the TRNPR forests was only 29% similar to that in Bura forests and that Bura forests were only 7% similar to Wema forests. Differences in forest composition from Bura to Wema were attributed to an increasing rainfall gradient, and to differences in floodplain complexity as meandering of the river decreased downstream with finer sediment transported, and larger areas inundated for longer periods. There are fewer well-drained sandy levees as the river progresses towards the delta, and grasslands are more common (Medley, 1992).

The only ecological study conducted outside the TRNPR was that by Hughes (1985). In that study, Hughes (1985) used vegetation plots sampled within the TRNPR and upstream Bura forests to characterize the forest types by linking them to geomorphological units and differentiated forest communities on the basis of their elevation above the river, flooding frequency and duration of inundation. Hughes' (1985) study was conducted shortly after the first of two large dams (the Masinga Dam) was completed (1981) in the upper river basin of the Tana River (Fig. 1). At about the same time, the large-scale Bura Irrigation and Settlement Project (BISP) established adjacent to the Tana River (Fig. 1) admitted its first settler farmers and government workers, subsequently doubling the local population by 1984. The Kiambere Dam is the second large dam completed in the upper river basin in 1988. Maingi and Marsh (2002) used Tana River hydrologic records (1941–1997) and field survey data to demonstrate that construction of

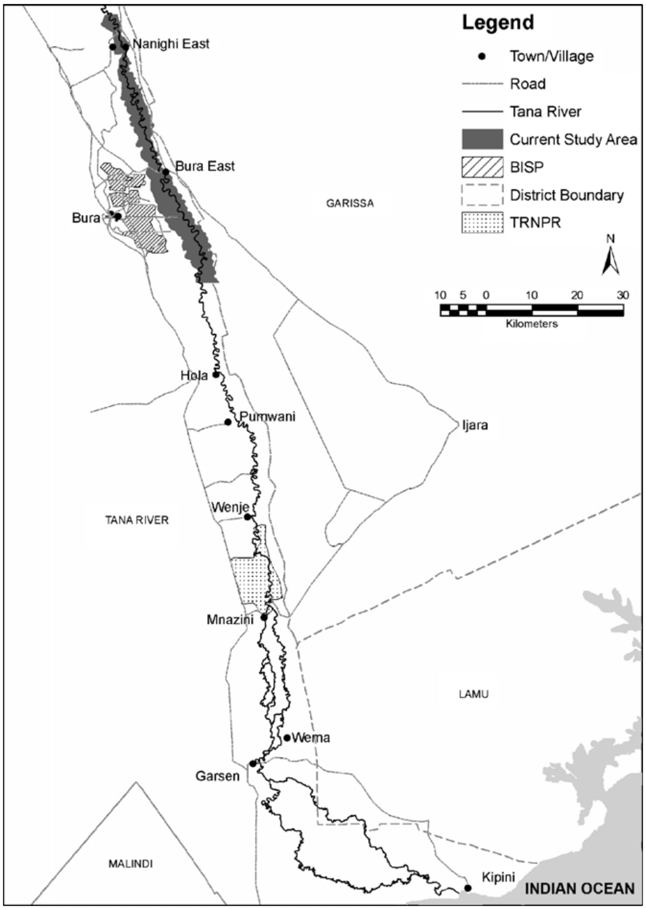

Fig. 2. Location of study area in Bura with respect to the Tana River National Primate Reserve (TRNPR) and Wema.

the two dams in the upper river basin had significantly augmented minimum river flows while reducing peak flows.

The Tana gallery forests are currently undergoing rapid depletion and fragmentation through clearing for agriculture, extraction of construction material, and forest die-back induced by increasingly xeric conditions associated with changes in river course and upstream dam construction (Maingi and Marsh, 2001; Suleman et al., 2001). Most studies on the forests have revealed a lack of regeneration which was attributed to various factors, among them, decreased peak flows (Marsh, 1976; Hughes, 1988; Medley, 1992). Currently, there is little information on the composition, structure, and regeneration patterns of the gallery forests outside the protected TRNPR. Information available from Hughes' (1985) study is essentially pre-dam and therefore the need for more current data in order to infer the future of these forests in the face of current and future planned river development projects and increasing human pressure.

The goal of the current study was therefore to describe the composition, structure and regeneration patterns of the upstream Tana gallery forests near Bura Irrigation Scheme (Fig. 1). This objective was achieved through classifications, ordinations, and ecological interpretation of woody vegetation data consisting of 101 species collected in 71 sample plots obtained by the transect method (McIntyre, 1953; Lindsey, 1955). The relative importance of environmental factors in determining community patterns was explored by correlating sample ordination scores with measured environmental variables. In addition, inferences on the regeneration status of the forests were made by examining the distribution of major tree species in the overstory, midstory, understory, and in the regeneration layer of the forests.

2. Study area

The study area is located in a semi-arid region near the Bura Irrigation and Settlement Project in southeastern Kenya, and includes a 60 km stretch of the Tana River (Fig. 1). Rainfall is highly variable and occurs in the March–May and the November–December seasons. Approximately 370 mm of rainfall is received annually, with slightly more rainfall falling in the November–December season. Mean annual temperature is 28.0 °C with February and July, the hottest and coldest, months, respectively.

The most prominent vegetation in the study area is the riverine forest found adjacent to the river and extending anywhere between 0.5 km and 3.0 km on either side of the river. The extent of the riverine forest is determined by the depth of the water table which drops off rapidly from the river's edge (Hughes, 1988). Rainfall received in this area is inadequate to support the forests, which must depend on annual floods and seepage from the river (Marsh, 1978). The Tana gallery forests have a high conservation value since they are home to two endemic subspecies of primate: the Tana River Red Colobus (*Colubus badius rufomitratus*, Peters) and the Tana River Mangabey (*Cercocebus galeritus galeritus*, Peters), both classified as endangered by the IUCN (2004). The Tana River poplar (*Populus ilicifolia*), is endemic, occurring in small patches along the Tana, Athi, and Ewaso-Nyiro river systems (Dale and Greenway, 1961). It is classified by the IUCN as endangered (IUCN, 2004).

A drought-deciduous bushland dominated by thorny shrubs with scattered annual grasses covers extensive areas away from the floodplain. This vegetation type has been described as an *Acacia-Commiphora* bushland and thicket (Pratt et al., 1966). Some trees will be found occurring along the Lagas (seasonal streams) and in some locations form patches of forest. Trees found dominating the lagas include: *Acacia tortilis*, *A. senegal*, *Berchemia discolor*, *Hyphaene compressa*, *Salvadora persica*, and *Dobera glabra* (Gachathi et al., 1987).

The Tana riverine floodplain is home to Malakote agriculturalists, a subgroup of the Pokomo people inhabiting most of the Tana River floodplain between Mbalambala and Kipini (Fig. 1). The Malakote grow bananas and mangoes along the banks of the river, and rice in the lower lying areas behind the fruit trees. Maize is grown in an area extending up to a kilometer from the rivers edge, depending on magnitude of the biannual floods. Rice is the most highly valued crop, but it can be grown only in the low-lying areas such as point-bars or oxbow lakes.

The pastoral Orma and Somali graze their animals in the extensive grasslands found in the outer edges of the floodplain.

During the dry season, the Orma and Somali move thousands of livestock to the floodplain for pasture and water, bringing them into conflict with the Malakote. In addition to these indigenous populations, there is a group of settler farmers in the Bura Irrigation Scheme that came from different parts of the country beginning in 1981. Census records indicate that population in the area increased from about 10,000 in 1979 to nearly 30,000 in 1999 (GOK, 1997). Agricultural activity within the Bura Irrigation Scheme came to a virtual stop in 1993 after the diesel-powered pumps failed. This left many settler farmers destitute and relying on food-aid. Some enterprising settler farmers joined hands with the Malakote to clear large patches of the riverine forests for irrigation using small diesel pumps. In addition, they embarked on commercial production of charcoal and timber from the riverine forests. The Malakote were eager to revive and expand their agricultural activity as this had been curtailed by diminishing floods since the first large dam in the upper river basin (Masinga Dam) was completed. This condition was exacerbated in 1988 when another large dam (Kiambere Dam) was completed.

Forest loss through clearing for farmland has been well documented in Tana gallery forests. Marsh (1976) used 1960 and 1975 aerial photography to document a 17% forest loss for an area between Wenje and Garsen (Fig. 2). Using a similar set of aerial photography, Medley (1993) found a 56% decrease in forest area in the TRNPR between 1960 and 1975. Wahungu et al. (2005) digitized topographic maps based on 1979 aerial photography and satellite images acquired in 2000 and found a 38% decline in forest area in the TRNPR. Maingi and Marsh (2001) used a pair of SPOT (XS) images acquired in 1986 and 1996 to document a 27% decline in forest area (approximately 2100 ha) in the upper gallery forests of Bura.

3. Methods

The sampling design adopted for this study was a modification of the transect method (McIntyre, 1953; Lindsey, 1955). Transects began on the bank of the river (or meander cut-offs) and ran perpendicular to the flow towards the edge of the forest. Each transect was deliberately placed to avoid areas close to the villages since most of the forest in these areas has been cleared for agriculture or been impacted heavily through cutting for fuelwood and building material. The length of each transect was therefore dependent on the width of undisturbed (continuous) gallery forest. We used aerial photographs acquired in 1989 at a scale of 1:20,000, and a 1:50,000 topographic map based on 1975 aerial photography, to locate 23 transects along levees of old meander cut-offs (inactive levees), active levees (cut-bank forests), point-bars, and oxbow lakes at various stages of in-fill. Each transect was then divided into 25 m segments and up to six segments were selected randomly. Each selected segment formed one side of a 25 m × 25 m square, the sampling unit we used for measuring trees and shrubs. We will refer to each selected segment as a plot hereafter. Most transects that began at the river's edge ran in a westerly direction but the exact direction depended on the direction of the river meanders and subsequent location of the widest stretch of "undisturbed" forest. We were unable to obtain 6 plots from each of the 23 transects because some segments showed too much disturbance (with many trees cut) or sometime the segments fell inside difficult to sample sites such as oxbow lakes. In total, 71 plots were located on various parts of the floodplain for sampling. Within each established plot, five subplots of 3 m × 3 m were randomly located to sample regenerating woody species.

Within each 25 m × 25 m plot, all tree and shrub species with a height of 1 m or more were identified by species, and diameter measurements at root collar (taken as 0.15 m above ground) and at breast height (1.3 m above ground) made using a diameter tape (for larger trees and shrubs) and calipers (for smaller plants). In addition, the height of each tree and shrub was measured using a graduated 10 m pole (for the shrub species) and a Suunto clinometer for taller trees. For each of the five randomly located 3 m × 3 m subplots, every regenerating species less than 1 m in height was identified and a count of each made by species.

Other measurements taken within a plot included plot location as determined by a global positioning system (GPS). The height of each plot above September (dry season) river flow at the nearest river section was determined using a David White Level (tilting dumpy level) and an accompanying leveling rod. Heights of plots above dry season river level had been used together with daily river discharge data for the Tana River, channel cross-sectional data, and the U.S. Army Corps of Engineers River Analysis System (HEC-RAS) developed by the Hydrologic Engineering Center (1995) to estimate frequency of flooding of each sample plot throughout the available hydrologic record. Channel cross-sectional data and reference surface elevations corresponding to flows of 150 $m^3 s^{-1}$ and 1025 $m^3 s^{-1}$ were available from river surveys by Sir McDonald and Partners Limited during the construction of the Bura Irrigation Scheme (NIB, 1979). These reference surfaces were used to calibrate the HEC-RAS simulation model after which the model was used together with daily river flows to determine the minimum river discharge necessary to inundate each sample plot. A detailed explanation on calibration of the HEC-RAS model and the estimation of frequency and duration of flooding, and flood pulse of sample plots is provided in Maingi and Marsh (2002). Richter et al. (1996) describe hydrologic pulses as periods within a year during which the daily mean water level either rises above the 75th percentile (high pulse) or drops below the 25th percentile (low pulse) of all daily discharge values.

Soil samples were obtained for each plot from one or more randomly located sampling points. One soil sample per plot was collected in areas where the soil appeared homogenous, but additional samples were obtained where there were obvious variations in the soil within a plot. Soil samples for each plot were obtained at the following depths: (1) the top 20 cm, (2) 50–70 cm, (3) 100–120 cm, and (4) 150–170 cm. No soil laboratory facilities were available at BISP and therefore all samples collected were sent to the Kenya Forestry Research Institute (KEFRI), Forest Soils Division for analysis. The soils were analyzed for texture, organic carbon, and soil pH.

Unfortunately, it was not possible to carry out macro-nutrient analysis because of problems with soil testing equipment.

4. Data analysis

Ecological data were analyzed using both classifications and ordinations. McCune and Grace (2002) recommend using hierarchical clustering techniques over the polythetic divisive TWINSPAN when dealing with heterogeneous data with complex underlying structure. The indirect gradient analysis technique, Non-metric multidimensional scaling (NMS), was chosen as the ordination technique because it is well suited to data that are non-normal or on arbitrary, discontinuous, or otherwise questionable scales (McCune and Grace, 2002). When using indirect gradient analysis techniques, environmental variables are not studied directly but are inferred from species composition data (Palmer, 1993). Indirect gradient analysis techniques are especially useful when it is uncertain that the most important environmental variables have been measured (Sagers and Lyon, 1997).

Vegetation data from the 71 sample plots were entered into a spreadsheet and basal areas of trees and shrubs were calculated. After individual tree basal areas were estimated, they were then summed and summarized by species and plot. Within each plot, relative densities, relative frequencies, and relative basal areas of all species were computed and then summed to calculate the importance value index (Curtis and McIntosh, 1950). The following formulae were used for each calculation:

$$\text{Relative density} = \frac{\text{number of plants by species in plot} \times 100}{\text{total number of plants of all species}}$$

$$\text{Relative frequency} = \frac{\text{number of species present in a plot} \times 100}{\text{total occurrence of all species in all plots}}$$

$$\text{Relative basal area} = \frac{\text{total basal area of all plants of a species} \times 100}{\text{total basal area of all plants}}$$

$$\text{Importance value (IV)} = \text{relative density} + \text{relative frequency} + \text{relative basal area}$$

Since no diameter measurements were made for the regeneration layer (trees less than 1 m in height), importance values were computed by summing up relative densities and relative frequencies. The Shannon diversity index H', and the evenness index E were also calculated for each plot (Magurran, 1988). Two sets of ordinations were produced: the first included IVs of all woody species, and the second used IVs for regeneration data. A cluster analysis was also performed using IVs of all woody species.

In order to explore vegetation relationships, all woody vegetation data were clustered using relative Sorensen distance measure and ordinated using NMS with relative Sorensen similarity index and varimax rotation. A Monte Carlo permutation test was performed on the NMS ordination in order to evaluate whether NMS was extracting stronger axes than expected by chance (McCune and Mefford, 1999). Regeneration data were ordinated using NMS with relative Sorensen distance and varimax rotation. Relationships between vegetation and environmental variables were examined by correlating NMS axes scores with environmental variables including hydrologic (plot height above river, frequency of flooding, duration of flooding, flood pulse, distance to river's edge) and soil variables (texture and organic carbon). There were problems with the handling of soil pH data and therefore it was omitted from analyses. Spearman's rank correlation analysis was used whenever variables were not normally distributed despite transforming the data.

The regeneration status of populations may be interpreted from time-specific analyses of stand structures (Daubenmire, 1968; Hett and Loucks, 1976). Stable species must be present as juveniles as well as adults and these species typically have a reverse-*J* curve of age distribution. The use of size class analysis to assess the regeneration status of the population requires a significant positive relationship between stem-size and age.

It has been shown for many tropical forest species that girth is not a reliable guide to ages of trees (Ogden, 1981; Swaine and Hall, 1986). Age estimates of trees have been made by calculating how long the average tree would take to pass through the various size classes leading to the present size of the tree (Ogden, 1981). Unfortunately, there can be great variation in the annual growth rates between individual trees of the same species even when the trees are growing within a stand with minimum micro-site differences. In such a situation, we can speculate that the diverse growth rates probably stem from genotypic differences. The slowest growth is usually found among the smallest trees, and therefore a large part of the age of many trees will be spent as seedlings and saplings. The absence of proven size–age relationship means that population size structures must be treated with caution when used to infer temporal patterns of regeneration. Interpretation of the regeneration status of a forest stand through the examination of species assemblages at different canopies, assumes that any tree in the overstory must have passed through the smaller sizes during growth to its present size, and that we may expect future canopy trees to be drawn from the existing population of smaller trees.

In order to obtain further insights into the recruitment of various tree species into different size classes in the Tana River gallery forests, each community type identified was stratified vertically and abundances of the species in different layers quantified. Thresholds for vertical stratification were determined by examining the frequency distribution of the heights of all woody vegetation sampled and subjectively identifying discontinuities in the distribution that could represent tall trees, tall shrubs, and low shrubs. The fourth vertical stratum was the regeneration layer. The definitions for the four categories were:

1. tall trees: height > 10.5 m (overstory);
2. tall shrubs: 4.5 m $<$ height ≤ 10.5 m (midstory);
3. lower shrubs: 1 m $\geq$ height ≤ 4.5 m (understory);
4. regeneration layer: height < 1 m.

Table 1
Woody species encountered in the Tana River gallery forests and their occurrence in the overstory, midstory, understory, and the regeneration layer

Species	Family	Overstory (%)	Midstory (%)	Understory (%)	Regeneration (%)
Sericocomopsis pallida Schinz	Amarantaceae			0.03	0.04
Cyathula coriacea Schinz	Amarantaceae			0.15	0.06
Sorindeia madagascariensis DC.	Anacardiaceae	1.53	0.13	0.12	0.62
Uvaria leptocladon Oliv.	Annonaceae		0.15	0.21	
Carisa edulis Vahl	Apocynaceae		0.22	0.52	1.13
Hunteria zeylanica Pichon	Apocynaceae	0.07	9.65	4.23	3.39
Rauvolfia mombasiana Stapf	Apocynaceae		0.66	1.60	0.61
Saba comorensis Pichon	Apocynaceae	0.73	0.62	0.82	0.44
Aristolochia bracteolata Lam.	Aristolochiaceae			0.01	0.08
Parquetina nigrescens Bullock	Asclepiadaceae		0.07	0.03	
Balanites rotundifolia Blatter	Balanitaceae		0.04	0.03	
Kigelia africana Benth.	Bignoniaceae	0.29	0.11	0.05	
Markhamia zanzibarica Engl.	Bignoniaceae	0.51	0.73	0.61	0.17
Ceiba pentandra Gaertn.	Bombacaceae	0.15			
Cordia goetzei Guerke	Boraginaceae	9.32	2.15	0.68	1.03
Cordia sinensis Lam.	Boraginaceae	10.99	7.23	1.06	0.28
Comiphora rostrata Engl.	Burse raceae			0.07	
Comiphora paoli Chiov.	Burse raceae		0.09	0.03	
Tamarindus indica L.	Caesalpiniaceae	1.53	0.09	0.20	0.50
Salacia madagascarensis DC.	Calast raceae	0.44	0.48	0.13	0.12
Cadaba farinosa Forssk	Capparaceae		0.04	2.59	1.19
Maerua subcordata De Wolf	Capparaceae		0.09	3.62	2.54
Thylachium thomansii Gilg	Capparaceae				0.03
Caparis tomentosa Lam.	Capparaceae	1.82	1.54	2.18	3.30
Maerua denhardtiorum Gilg.	Capparaceae			0.72	0.42
Boscia coriacea Pax	Capparaceae		0.31	2.29	0.86
Thylachium thomasii Gilg	Capparaceae			0.10	
Maerua triphylla A. Rich	Capparaceae		0.02	0.08	
Maerua macrantha Gilg	Capparaceae			0.02	
Cadaba farinosa Forssk	Capparaceae	0.15	0.04	0.03	
Mytenus heterophylla N. Robson	Celastraceae			0.01	
Hippocratea africana Loes.	Celastraceae	0.07	0.15	0.11	0.04
Maytenus senegalensis Excell	Celastraceae			0.14	0.02
Terminalia brevipes Pampan.	Combretaceae	5.82	5.93	2.36	1.64
Combretum constrictum Laws.	Combretaceae	0.07	0.18	0.19	
Combretum panniculatum Vent.	Combretaceae	0.36	0.37	0.13	0.01
Terminalia pervula Pampan	Combretaceae	0.22	0.13	0.35	0.06
Pluchea dioscoridis DC.	Compositae		0.09	1.26	
Blepharispermum fruticosum Klatt & Schinz	Compositae			0.25	
Hildebrandtia sepalusa Rendle	Convolvulaceae	1.02	0.53	1.19	1.62
Momordica trifoliata Hook. F.	Curcurbitaceae	1.02	0.13	0.35	0.21
Tapura fischeri Engl.	Dichapetalaceae		0.24	0.10	
Euclea natalensis A.DC.	Ebenaceae	0.73	3.32	4.41	5.64
Diospyros mespiliformis A.DC.	Ebenaceae	2.90	0.35	0.95	1.99
Diospyros abyssinica F. White	Ebenaceae	0.22	0.73	0.09	
Erythrococca kirkii Prain	Erythroxylaceae			0.10	
Securinega virosa Baill.	Euphorbiaceae		4.37	11.96	9.25
Acalypha echinus Pax & K.Hoffm.	Euphorbiaceae		0.79	1.83	0.29
Spirostachys venenifera Pax	Euphorbiaceae	24.96	13.43	1.88	7.07
Phyllanthus somalensis Hutch.	Euphorbiaceae			3.54	0.97
Antidesma venosum Tul.	Euphorbiaceae	0.66	1.01	0.01	
Phyllanthus guinensis Pax	Euphorbiaceae	0.15	0.15	0.20	0.06
Dry petes natalensis Hutch.	Euphorbiaceae		0.07	0.25	0.16
Oncoba spinosa Forssk.	Flacourtiaceae	1.09	2.35	1.01	2.39
Garcinia livingstonei T.Anders	Guttiferae	3.35	0.42	0.44	10.60
Oncella ambigua Van Tiegh	Loranthaceae			0.01	
Lawsonia inenvis L.	Lythraceae	0.66	0.51	0.60	0.05
Thespasia danis Oliv.	Malvaceae	0.07	2.73	2.54	3.23
Sida ovata Forssk.	Malvaceae			0.05	
Cocculus hirsutus Diels	Menispermaceae	0.29	0.15	0.20	0.30
Acacia elatior Brenan	Mimosaceae	6.70	0.99	0.38	0.47
Acacia robusta Burch.	Mimosaceae	1.46	0.15	0.05	0.14
Newtonia hildebrandtii Torre	Mimosaceae	0.29		0.01	0.14
Acacia zanzibarica Taub.	Mimosaceae		0.26	0.04	

Table 1 (*Continued*)

Species	Family	Overstory (%)	Midstory (%)	Understory (%)	Regeneration (%)
Acacia rovumae Oliv.	Mimosaceae	1.09	0.18	0.14	0.33
Acacia reficiens Brenan	Mimosaceae			0.14	
Acacia tortilis Hyne	Mimosaceae	0.29	0.22		
Albizia gummifera C.A. Sm.	Mimosaceae	0.22			
Ficus sycomorus L.	Moraceae	1.75	0.46	0.25	0.14
Ficus capreaefolia Del.	Moraceae	0.07	0.20	0.14	0.06
Ximenia americana L.	Olacaceae		0.02	0.07	0.08
Opilia campestris Engl.	Opiliaceae			0.04	
Phoenix reclinata Jacq.	Palmae	0.07	0.11	0.44	0.46
Hyphaene compressa H. Wendl.	Palmae	0.95	0.18	0.19	0.51
Indigofera schimperi Jaub. & Spach	Papilionaceae		0.07	2.56	1.05
Erythrina melanacantha Harms	Papilionaceae	0.15	0.04	0.01	
Paveta sphaerobotrys K. Schum.	Rubiaceae		1.45	3.08	2.77
Polysphaeria multiflora Hiern	Rubiaceae	0.15	8.33	7.58	7.45
Populus ilicifolia Rouleau	Salicaceae	3.20	0.46	0.85	0.38
Dobera loranthifolia Harms	Salvadoraceae	0.15	3.21	1.90	0.29
Salvadora persica L.	Salvadoraceae	0.15	1.91	1.58	1.96
Lecaniodiscus fraxinofolius Bak.	Sapindaceae	0.07	5.80	8.13	11.73
Lepisanthes senegalensis Leenh.	Sapindaceae	0.44	0.22	0.10	0.09
Deinbollia borbonica Scheff.	Sapindaceae	0.15	0.75	1.85	1.72
Allophylus rubifolius A.Rich.	Sapindaceae	0.15	0.11	1.80	1.17
Manilkaria mochisia Dubard	Sapotaceae	0.07	0.15	0.05	0.27
Mimusops obtusifolia A.DC.	Sapotaceae	3.93	1.01	1.10	0.82
Harrisonia abyssinica Oliv.	Simaroubaceae	1.60	3.16	0.84	2.34
Trichilia emetica Oliv.	Simaroubaceae	3.86	0.62	0.41	0.18
Sterculia appendiculata K. Schum.	Sterculiaceae	0.66	0.02	0.03	0.02
Tamarix nilotica Bunge	Tamaricaceae			0.07	
Grewia stuhlmanii K. Schum.	Tiliaceae		0.55	0.13	0.08
Grewia densa K. Schum.	Tiliaceae	0.80	4.73	1.46	1.07
Grewia villosa Willd.	Tiliaceae		0.02	0.13	
Grewia tenax Fiori	Tiliaceae			0.87	
Grewia tembensis Fres.	Tiliaceae			0.07	
Clerodendrum acerbianum Benth. & Hook.f.	Verbenaceae	0.36	0.29	2.26	0.88
Premna resinosa Schauer	Verbenaceae			0.26	0.18
Premna velutina Guerke	Verbenaceae	0.07	0.40	0.32	0.02
Rinorea elliptica O.Ktze	Violaceae		1.08	1.91	0.75
Ampelocissus africana Merr.	Vitaceae		0.04	0.04	0.05

Hughes (1985) also vertically stratified Tana River vegetation into the above four categories but there were some variations in the cut-off elevations: tall trees were considered greater than 10 m, tall shrubs were 3–10 m, low shrub 1–3 m, and regeneration layer was less than 1 m.

5. Results

5.1. Classification and ordination of woody vegetation data

Among the 15,538 stems of woody vegetation measured in 71 sample plots, 101 species belonging to 46 families were identified (Table 1). The families represented by the highest number of species were Capparaceae (11.9%), Mimosaceae (7.9%), Euphorbiaceae (6.9%), Apocynaceae (5.0%), and Tiliaceae (5.0%). On average, there were 19.3 species per plot. Six species of shrub were not identified.

5.2. Defining floodplain forest types

Defining groups using cluster analysis requires that the dendrogram be pruned at an appropriate level that represents a compromise between homogeneity of the groups and the number of groups (McCune and Grace, 2002). The Indicator Species Analysis (ISA) technique (Dufrene and Legendre, 1997) was used to choose an optimum pruning point for the dendrogram. This optimum point coincided with peak number of significant indicator species and the smallest *p*-value. The resulting cluster analysis dendrogram had 1.89% chaining, and was cut with 25% of the information remaining, resulting in seven forest groups (Fig. 3). The ISA was also used to identify statistically significant indicator species for each of the seven forest types delineated. Stronger indicator species have higher indicator values, indicating the faithfulness and exclusivity of a species to a particular group (McCune and Grace, 2002). The general characteristics of the seven forest types identified are summarized (Table 2) and described below. The description also includes composition of the different strata and regeneration patterns in each community type.

5.2.1. Group I: Tamarindus Forest

The four plots defining this group were all from inactive levees located some distance from the main river channel near the edge of the dry floodplain. The plots were dominated by

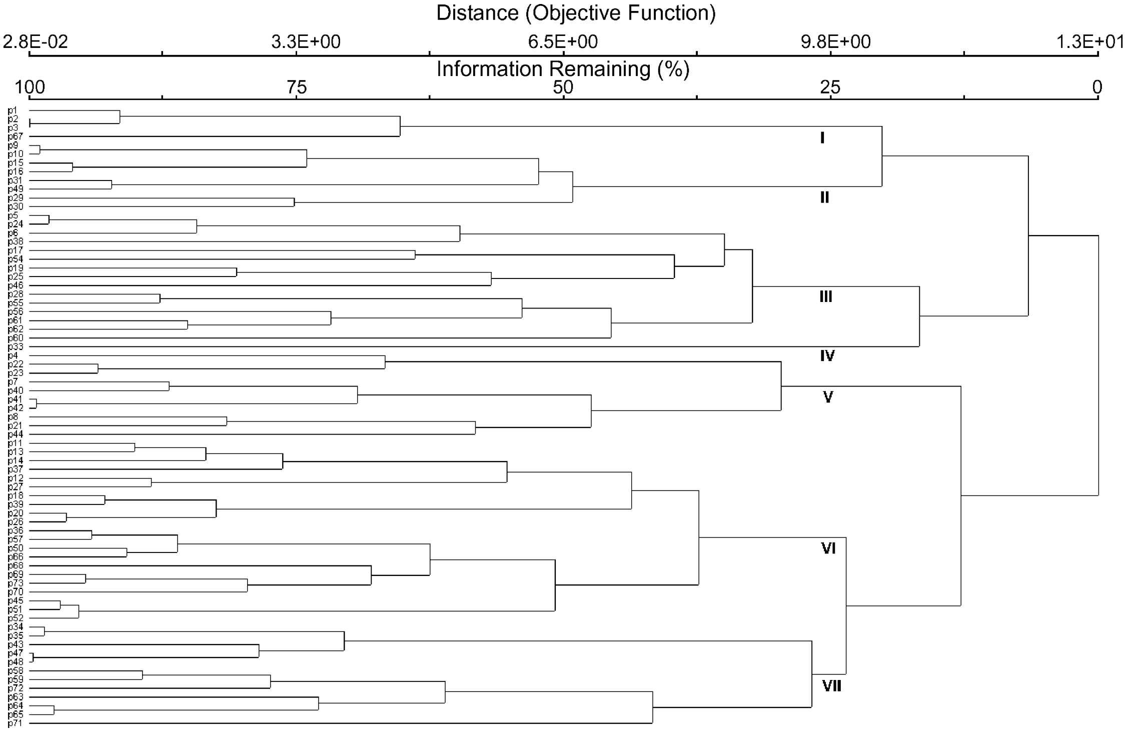

Fig. 3. Dendrogram resulting from a cluster analysis of 101 woody species in 71 sample plots located along the Tana River floodplain using relative Sorensen distance and the Flexible Beta Linkage group method.

Tamarindus indica, *Newtonia hildebrandtii*, and *Dobera loranthifolia* accounting for 73.4%, 11.6%, and 8.0% of the total basal area, respectively. There were 15.6 species observed per plot and these occurred at a density of approximately 3500 stems ha^{-1} and at an average height of 3.3 m. The overstory, which occurred at 18.3 m and a density of 104 stems ha^{-1}, consisted exclusively of *T. indica*, *N. hildebrandtii*, and *D. loranthifolia*. The midstory occurred at a mean height of 6.3 m and a density of 256 stems ha^{-1}, and was dominated by *Euclea natalensis*, *D. loranthifolia*, and *Hunteria zeylanica*. The understory occurred at mean height of 2.5 m and consisted of 41 species at a density of 3132 stems ha^{-1}. Dominant understory species included *Cadaba farinosa*, *D. loranthifolia*, *Maerua subcordata*, and *E. natalensis*. The only overstory species present in the understory were *D. loranthifolia* (752 stems ha^{-1}), *T. indica* (240 stems ha^{-1}), and *Acacia elatior* (16 stems ha^{-1}).

The regeneration layer consisted of 18 species at a density of 4098 seedlings ha^{-1}. *Lecaniodiscus fraxinofolius*, *Securinega virosa*, *M. subcordata*, and *E. natalensis* accounted for more than half of the regeneration. Overstory species observed in the regeneration layer included *S. persica* (3182 seedlings ha^{-1}), *T. indica* (2045 seedlings ha^{-1}), *A. elatior* (795 seedlings ha^{-1}), and *Garcinia livingstonei* (455 seedlings ha^{-1}). Overstory species such as *N. hildebrandtii* and *D. loranthifolia* were absent in the regeneration layer.

5.2.2. Group II: Acacia Forest

This group was defined by nine plots located mostly on levees. *A. elatior* was the dominant species accounting for 23.2% of the total basal area. Other species contributing approximately 55% of the basal area were: *Spirostachys venenifera* (12.8%), *Cordia sinensis* (9.9%), *D. loranthifolia* (8.4%), *S. persica* (5.9%), *Mimusops obtusifolia* (5.3%), *E. natalensis* (5.2%), *H. zeylanica* (4.0%), and *Cordia goetzei* (4.0%). On average, there were 14.9 species observed per plot, and these occurred at a density of approximately 3000 stems ha^{-1}, and had a mean height of 4.4 m. The overstory had a density of 87 stems ha^{-1} and occurred at a mean height of 19.9 m, making it the tallest among all forest groups. *A. elatior* accounted for nearly half of the basal area in the overstory. Other dominant species in the overstory included *M. obtusifolia*, *Acacia robusta*, *Diospyros mespiliformis*, and *S. venenifera*.

The density of the midstory was 823 stems ha^{-1} and consisted of 23 species at a mean height of 6.6 m. Dominant species included *S. venenifera*, *D. loranthifolia*, *C. sinensis*, *E. natalensis*, *S. persica*, and *C. goetzei*. The understory had a density of 2108 stems ha^{-1} and consisted of 35 species at an average height of 2.9 m. Dominant species included *S. persica*, *C. farinosa*, *L. fraxinofolius*, *S. virosa*, and *E. natalensis*.

The regeneration layer included 26 species at a density of 3748 seedlings ha^{-1}. Species with regeneration densities greater than 4000 seedlings ha^{-1} included: *S. venenifera*, *Maerua denharditiorum*, *Acalypha echinus*, *S. virosa*, *Thespasia danis*, *M. subcordata*, and *L. fraxinofolius*. The only overstory species with abundant regeneration was *S. venenifera* (22,159 seedlings ha^{-1}). Other overstory species occurred at below average densities in the regeneration layer: *S. persica* (2727 seedlings ha^{-1}), *G. livingstonei* (1500 seedlings ha^{-1}), *Mimusops fruticosa* (1364 seedlings ha^{-1}), *T. indica* (1023 seedlings ha^{-1}), *A. elatior* (1023 seedlings ha^{-1}), and *D. loranthifolia* (568 seedlings ha^{-1}).

Table 2
Forest types identified through classification and ordination of all trees and shrubs

Forest type identified by classification/ordination	Major constituent species	Indicator species	Associated geomorphic features	Species richness per plot (625 m^2)	Density (stems ha^{-1})	Mean evenness index	Mean Shannon's diversity index	Mean BA (m^2 ha^{-1})
Group I: Tamarindus Forest	*Tamarindus indica*, *Dobera loranthifolia*	*Tamarindus indica*, *Cadaba farinose*, *Maerua subcordata*, *Dobera loranthifolia*, *Hunteria zeylanica*	Inactive levee (4)	15.6	3500	0.989	2.673	36.8
Group II: Acacia Forest	*Acacia elatior*, *Spirostachys venenifera*, *Cordia sinensis*, *Dobera loranthifolia*, *Salvadora persica*, *Mimusops obtusifolia*	*Thespasia danis*, *Manilkaria mochisia*, *Clerodendrum acerbianum*	Inactive levee (5), active levee (3), oxbow (1)	14.9	3000	0.990	2.665	18.8
Group III: Point-bar Forest	*Spirostachys venenifera*, *Terminalia brevipes*, *Populus ilicifolia*, *Ficus sycomorus*, *Cordia sinensis*	*Terminalia brevipes*, *Indigofera schimperi*, *Pluchea dioscoridis*, *Spirostachys venenifera*, *Phyllanthus somalensis*	Point-bar (8), oxbow (3), active levee (2), backswamp (1)	16.3	3600	0.988	2.705	21.8
Group IV: Oxbow Lake Forest	*Spirostachys venenifera*, *Terminalia brevipes*, *Cordia sinensis*	N/A	Oxbow lake (1)	3.0	2200	0.995	1.093	13.2
Group V: Active Levee Forest	*Trichilia emetica*, *Cordia goetzei*	*Polysphaeria multiflora*, *Sorindeia madagascarensis*	Active levee (5), point-bar (1)	14.5	2800	0.990	2.642	37.7
Group VI: Levee Forest	*Cordia sinensis*, *Spirostachys venenifera*, *Acacia elatior*, *Trichilia emetica*, *Cordia goetzei*	*Cordia goetzei*, *Acacia robusta*, *Rinorea elliptica*, *Thespasia danis*	Active levee (12), inactive levee (10), point-bar (2), oxbow (1)	23.3	3400	0.891	3.094	37.1
Group VII: Backswamp Forest	*Mimusops obtusifolia*, *Diospyros mespiliformis*, *Hunteria zeylanica*, *Garcinia livingstonei*	*Mimusops obtusifolia*, *Boscia coriacea*, *Cadaba farinose*, *Hunteria zeylanica*, *Markhamia zanzibarica*	Backswamp (11), active levee (1)	22.8	3800	0.891	2.789	43.1

5.2.3. *Group III: Point-bar Forest*

A majority of the 14 plots belonging to this group were located on point-bars and inside meander scars. On average, there were 16.3 species per plot occurring at a density of 3600 stems ha^{-1} and a mean height of 5.7 m. *S. venenifera* was the most dominant species, accounting for approximately 22% of the basal area. *P. ilicifolia*, *Terminalia brevipes*, *C. sinensis*, *Ficus sycomorus*, and *G. livingstonei* contributed an additional 51% of the basal area.

The density of the overstory was 314 stems ha^{-1} and occurred at an average height of 16.5 m. Of the 23 species observed in this layer, *P. ilicifolia*, *G. livingstonei*, *S. venenifera*, and *F. sycomorus* were the most dominant in terms of basal area. The midstory occurred at a density of 1214 stems ha^{-1} and an average height of 7.4 m. Among the 45 species observed in the layer, *S. venenifera*, *C. sinensis*, *T. brevipes*, and *Grewia densa* were the most dominant. Overstory species represented in the midstory included *Trichilia emetica*, *P. ilicifolia*, *F. sycomorus*, *A. elatior*, and *Boscia coriacea*.

The understory consisted of 63 species, and occurred at an average height of 2.9 m and a density of 2039 stems ha^{-1}. Dominant species included *S. virosa*, *T. brevipes*, *S. venenifera*, *Polysphaeria multiflora*, *Indigofera schimperi*, and *Pluchea dioscoridis*. Overstory species found in the understory were *F. sycomorus*, *P. ilicifolia*, *A. elatior*, *T. emetica*, and *D. mespiliformis*.

There were 44 species observed in the regeneration layer and these occurred at a density of 5822 seedlings ha^{-1}. The most frequently encountered species were *Phoenix reclinata*, *S. venenifera*, *G. livingstonei*, *I. schimperi*, and *S. virosa*. Overstory tree species present in the understory included *P. ilicifolia* (4091 seedlings ha^{-1}), *D. mespiliformis* (3788 seedlings ha^{-1}), *M. obtusifolia* (3409 seedlings ha^{-1}), *S. persica* (2727 seedlings ha^{-1}), and *F. sycomorus* (2386 seedlings ha^{-1}).

5.2.4. *Group IV: Oxbow Lake Vegetation*

The only plot belonging to group was located on an oxbow lake. *S. venenifera*, *T. brevipes*, and *C. sinensis*, were the only species encountered and accounted for 77.1%, 13.4%, and 9.5%, of the basal area, respectively. There mean density and height for this group was 2200 stems ha^{-1} and 7.5 m, respectively. The oxbow lake was at a very early stage of in-fill and thus was frequently inundated with water.

The overstory was exclusively *S. venenifera* and occurred at a density of 544 stems ha^{-1} and a mean height of 14.7 m, making it the lowest among all forest groups. The midstory, at a density of 992 stems ha^{-1} and a mean height of 6.2 m was also dominated by *S. venenifera*. The only other species present in layer were *T. brevipes* and *C. sinensis*.

The understory consisted exclusively of *S. venenifera* and *T. brevipes*. The density of the understory was 896 stems ha^{-1} and occurred at a mean height of 3.6 m. At a density of approximately 668,000 seedlings ha^{-1}, regeneration within oxbow lake vegetation was the highest observed among all forest groups. Regeneration was 99.6% *T. brevipes* and

S. venenifera, with the former accounting for nearly 90% of the seedlings.

5.2.5. Group V: Active Levee Forest

Five of the six plots belonging to group were located on active levees. *T. emetica* and *C. goetzei* were the most dominated species, accounting for 31.5% and 14.7%, of the total basal area, respectively. *P. multiflora*, *Sorindeia madagascarensis*, and *S. venenifera* contributed an additional 26% of the basal area. On average, 14.5 species per plot were observed at a density of approximately 2800 stems ha^{-1} and these occurred at a mean height of 6.6 m.

The overstory consisted of 18 species and had a mean height of 16.2 m and a density of 405 stems ha^{-1}. Dominant species in layer were *T. emetica*, *C. goetzei*, *S. madagascarensis*, and *S. venenifera*. The density and mean height of the midstory was 1232 stems ha^{-1} and 6.5 m, respectively. Dominant species in layer included *P. multiflora*, *T. emetica*, *Oncoba spinosa*, *S. venenifera*, *L. fraxinofolius*, and *Harrisonia abyssinica*.

The mean height and density of the understory was 3.1 m and 1112 stems ha^{-1}, respectively. Dominant species included *P. multiflora*, *C. farinosa*, *S. venenifera*, *D. mespiliformis*, and *Paveta sphaerobotrys*. *G. livingstonei* was the only overstory species encountered in understory, albeit at below average density (32 stems ha^{-1}).

The regeneration layer consisted of 24 species and occurred at a density of 8988 seedlings ha^{-1}. The most frequently encountered seedlings were *P. multiflora*, *L. fraxinofolius*, *Rauvolfia mombasiana*, *O. spinosa*, and *S. madagascarensis*. Among the overstory species encountered, only *S. madagascarensis* occurred at above average density (9773 seedlings ha^{-1}). The remaining overstory species occurred at below average densities, e.g., *D. mespiliformis* (3636 seedlings ha^{-1}) and *G. livingstonei* (3409 seedlings ha^{-1}). Although *T. emetica* currently dominants this forest group, it was found regenerating at below average levels (1705 seedlings ha^{-1}). No seedlings of *S. venenifera* were encountered on active levee forests.

5.2.6. Group VI: Levee Forest

This group consisted of 23 plots and was ranked highest in species richness per plot (23.3), and in Shannon's diversity index (3.094). A majority of the plots were located on active and inactive levees. The most important species in terms of basal area were *C. sinensis* (14.1%), *A. elatior* (10.0%), *S. venenifera* (9.8%), *C. goetzei* (8.8%), *T. emetica* (8.7%), *T. brevipes* (5.2%), and *L. fraxinofolius* (4.6%). The density and height of all woody vegetation in group was 3400 stems ha^{-1} and 5.9 m, respectively.

The overstory occurred at a mean height of 17.5 m and at a density of 413 stems ha^{-1}. Among the 35 species found in layer, the most dominant were *C. sinensis*, *A. elatior*, *T. emetica*, *C. goetzei*, and *S. venenifera*. The midstory occurred at a mean height and density of 7.0 m and 1024 stems ha^{-1}, respectively. Dominant species among the 51 species observed in layer included *S. venenifera*, *L. fraxinofolius*, *G. densa*, *Antidesma venosum*, and *C. sinensis*. Overstory species observed in the midstory included *T. brevipes*, *M. obtusifolia*, *C. goetzei*, and *G. livingstonei*.

The density of the understory was 1967 stems ha^{-1}, and consisted of 70 species occurring at a mean height of 3.0 m. More than half of the basal area in this layer was accounted for by *L. fraxinofolius* and *S. virosa*. Overstory species present in the understory included *S. venenifera*, *C. sinensis*, *B. coriacea*, *Hyphaene coriacea*, *M. obtusifolia*, *D. mespiliformis*, *T. emetica*, *H. zeylanica*, *A. elatior*, and *G. livingstonei*.

The regeneration layer consisted of 46 species at a density of 6302 seedlings ha^{-1}. Species with highest regeneration rates included typical understory species such as *P. multiflora*, *P. sphaerobotrys*, *L. fraxinofolius*, *T. danis*, *Deinbollia borbonica*, and *Hildebrandtia sepalusa*. Several overstory species such as *G. livingstonei*, *P. reclinata*, *S. venenifera*, and *H. zeylanica* also had high regeneration rates (greater than 5000 ha^{-1}). Overstory species with below average regeneration rates included *S. madagascarensis* (3636 seedlings ha^{-1}), *M. obtusifolia* (4182 seedlings ha^{-1}), *D. mespiliformis* (3333 seedlings ha^{-1}), and *H. abyssinica* (3131 seedlings ha^{-1}). Other overstory species such as *C. goetzei*, *C. sinensis*, and *A. elatior* had even much lower regeneration rates (800–2700 seedlings ha^{-1}). *T. indica* though not currently present in the overstory, was present in the regeneration layer and occurred at a density of 682 seedlings ha^{-1}. *T. emetica*, a typical overstory species in levee forests, was however absent from regeneration layer.

5.2.7. Group VII: Backswamp Forest

A majority of 12 plots belonging to this group were located on backswamps or clay depressions behind levees. The group had the second highest mean number of species encountered per plot (22.8) and the second highest Shannon's diversity index (2.789). Six species accounting for approximately 60% of the basal area included *M. obtusifolia* (26.4%), *H. zeylanica* (9.6%), *D. mespiliformis* (9.4%), *S. venenifera* (7.4%), *G. livingstonei* (6.7%), and *C. goetzei* (1.9%). There were approximately 3800 stems ha^{-1} at a mean height of 5.1 m.

There overstory layer occurred at a mean height of 19.0 m and at a density of 275 stems ha^{-1}. Among the 25 species encountered in layer, *M. obtusifolia*, *D. mespiliformis*, and *G. livingstonei* were the most dominant. The midstory layer consisted of 44 species and occurred at a mean height of 6.5 m and at a density of 1211 stems ha^{-1}. Species dominating layer included *H. zeylanica*, *S. venenifera*, *M. obtusifolia*, *E. natalensis*, and *D. loranthifolia*. The understory layer had a density of 2535 stems ha^{-1} and occurred at a mean height of 2.6 m. Among the 68 species encountered in layer, *H. zeylanica*, *C. farinosa*, *Rinorea elliptica*, *S. virosa*, and *B. coriacea* were most dominant.

The regeneration layer had a density of 4787 seedlings ha^{-1} and consisted of 41 species. Overstory tree species found with regeneration rates greater than 3000 seedlings ha^{-1} included *G. livingstonei*, *B. coriacea*, *A. elatior*, and *S. persica*. Other overstory species were encountered at below average densities, e.g., *M. obtusifolia* (2273 stems ha^{-1}), *D. mespiliformis* (1250 stems ha^{-1}), *N. hildebrandtii* (1591 stems ha^{-1}), *Acacia rovumae* (1307 stems ha^{-1}), and *D. mespiliformis* (1250 stems ha^{-1}).

5.3. Ordination of all woody species

Forest types defined through cluster analysis were clearly recognizable as separate groups in the NMS ordination of all trees and shrubs. There were two NMS ordination axes because inclusion of a third axis resulted in only a minor reduction in minimum stress. A Monte Carlo test of 500 runs with randomized data indicated the minimum stress of a 2-D solution was lower than would be expected by chance ($p = 0.0132$). The final stress and instability of the 2-D solution were 22.60 and 0.00001, respectively. The first ordination axis (NMS1) captured 27.8% of the variability in the dataset and the second (NMS2) captured 42.9%, leading a cumulative 70.8% of variance in dataset explained (Fig. 4).

Results of correlation analyses between ordination scores and various abiotic factors are shown (Table 3). The first ordination axis (NMS1) was weakly correlated with various soil properties including soil organic carbon (SOC) and texture. NMS axis 1 had significant negative correlations with organic carbon in the 50–70 cm depth (−0.394, $p < 0.01$) and in the 100–120 cm depth (−0.271, $p < 0.05$), and significant negative correlations with percent clay in the 50–70 cm depth (−0.329, $p < 0.001$) and in the 100–120 cm depth (−0.339, $p < 0.001$). NMS axis 1 also had significant positive correlations with percent sand in the 50–70 cm depth (0.257, $p < 0.05$) and in the 100–120 cm depth (0.327, $p < 0.001$). NMS axis 2 represented a gradient of flooding, being negatively correlated with mean elevation of plot above dry season river level (−0.480, $p < 0.01$), and positively correlated with both percent days flooded (0.483, $p < 0.01$) and the duration of flooding (0.481, $p < 0.01$). Low-lying sample plots such as oxbow lakes and point-bars were the most frequently flooded while plots at

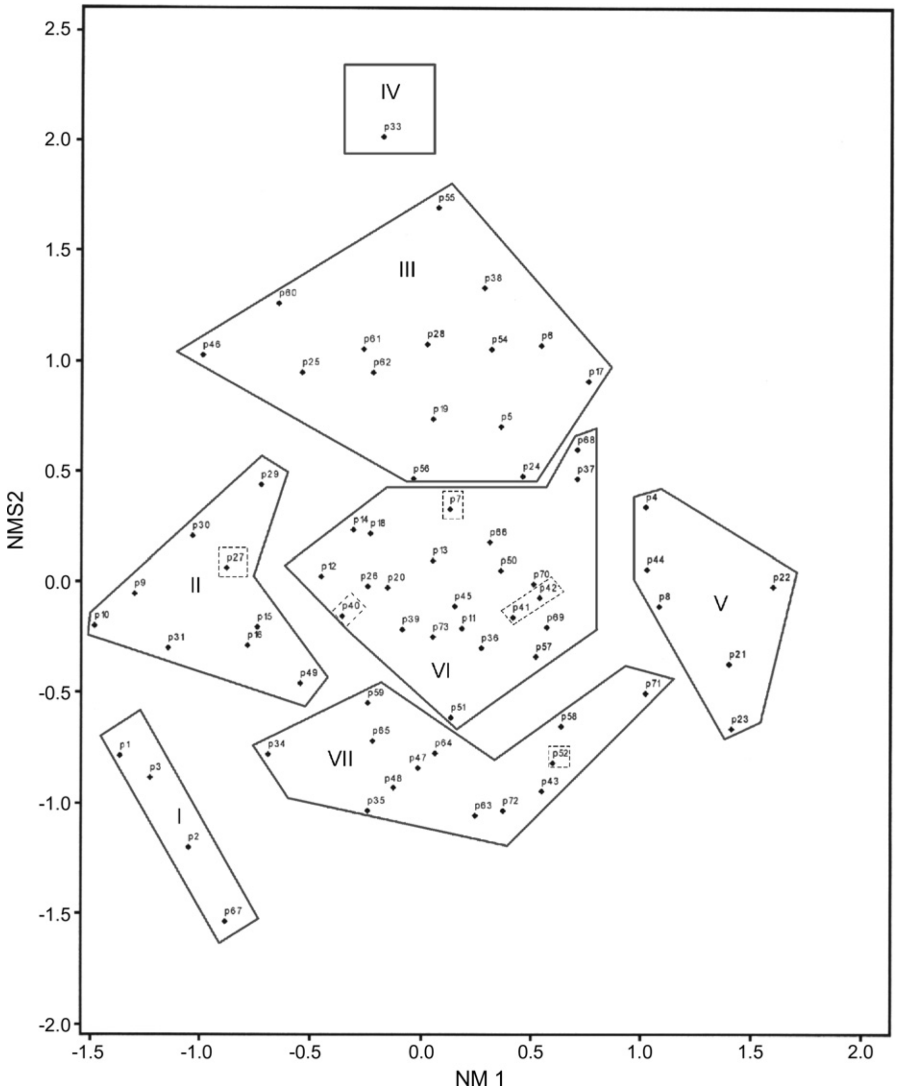

Fig. 4. NMS ordination of 101 woody species in 71 plots sampled along the Tana River gallery forests. Plot groupings obtained from cluster analysis of the same dataset are shown by solid-line polygons. Broken-line polygons indicates mismatches between cluster analysis and NMS ordination.

Table 3
Spearman's rank correlations between environmental variables and NMS ordination axes for all woody vegetation equal to or greater than 1 m in height

Variable	NMS axis 1 (*r*, *p*)	NMS axis 2 (*r*, *p*)
Flooding regime indicators		
Mean plot elevation above dry season river level	−0.066, 0.586	**−0.480**, 0.001
Percent days flooded	0.066, 0.587	**0.481**, 0.001
Duration of flooding	0.059, 0.627	**0.483**, 0.001
Distance of plot to river's edge	−0.152, 0.242	−0.176, 0.174
Percent soil carbon		
0–20 cm	−0.113, 0.382	−0.027, 0.837
50–70 cm	**−0.394**, 0.002	−0.199, 0.121
100–120 cm	**−0.271**, 0.036	−0.212, 0.061
150–170 cm	−0.084, 0.548	−0.225, 0.084
Percent clay		
0–20 cm	−0.102, 0.423	0.143, 0.259
50–70 cm	**−0.329**, 0.007	0.005, 0.970
100–120 cm	**−0.339**, 0.007	−0.078, 0.543
150–170 cm	−0.118, 0.368	−0.256, 0.058
Percent silt		
0–20 cm	−0.225, 0.074	0.200, 0.114
50–70 cm	0.013, 0.919	0.0001, 0.998
100–120 cm	−0.190, 0.137	−0.087, 0.497
150–170 cm	0.127, 0.333	−0.203, 0.119
Percent sand		
0–20 cm	0.135, 0.288	−0.237, 0.057
50–70 cm	**0.257**, 0.039	0.028, 0.826
100–120 cm	**0.327**, 0.009	0.071, 0.581
150–170 cm	0.105, 0.426	0.244, 0.061

Significant correlations are shown in bold.

higher elevations such as levees and inactive levees were flooded less frequently. These plots were located at opposite ends of the NMS axis 2 with the low-lying plots found on the high end of the axis and the higher elevation plots towards the bottom. None of the ordination axes were significantly correlated with distance of vegetation sample plots to the river's edge (Table 3).

5.4. Regeneration layer

5.4.1. Ordination of regeneration species

On average, 748 seedlings ha^{-1} were encountered in the 71 plots sampled. A total of 77 species belonging to 38 families were recorded. The families represented by the highest number of families included Celastraceae (10.7%), Euphorbiaceae (8.0%), Apocynaceae (6.7%), Mimoscaceae (5.3%), Sapindaceae (5.3%), Combretaceae (4.0%), and Verbanaceae (4.0%).

A 2-D NMS ordination was chosen for the regeneration data because the inclusion of a third axis resulted in only a minor reduction in minimum stress. A Monte Carlo test of 500 runs with randomized data indicated the minimum stress of the 2 axes NMS ordination were lower than would be expected by chance ($p = 0.0132$). The final stress and instability of the 2-D solution were 23.71 and 0.00001, respectively. The first ordination axis (NMS1) captured 41.9% of the variability in the dataset and the second (NMS2) captured 31.8%, leading a cumulative 73.7% of variance in dataset explained (Fig. 5).

Results from correlation analyses between ordination scores and various abiotic factors (Table 4) indicate that NMS axis 1 had significant negative correlation with mean plot elevation above dry season river level (−0.312, $p < 0.01$), and significant positive correlations with percent days flooded (0.320, $p < 0.01$), and with duration of flooding (0.278, $p < 0.01$). In addition, NMS axis 1 had significant positive correlations with percent clay in the top 20 cm (0.321, $p < 0.01$). The only significant correlation between NMS axis 2 and environmental variables was negative with percent sand in the top 20 cm (−0.346, $p < 0.01$). Ordination axes were not correlated to distance of sample plots from the river's edge (Table 4).

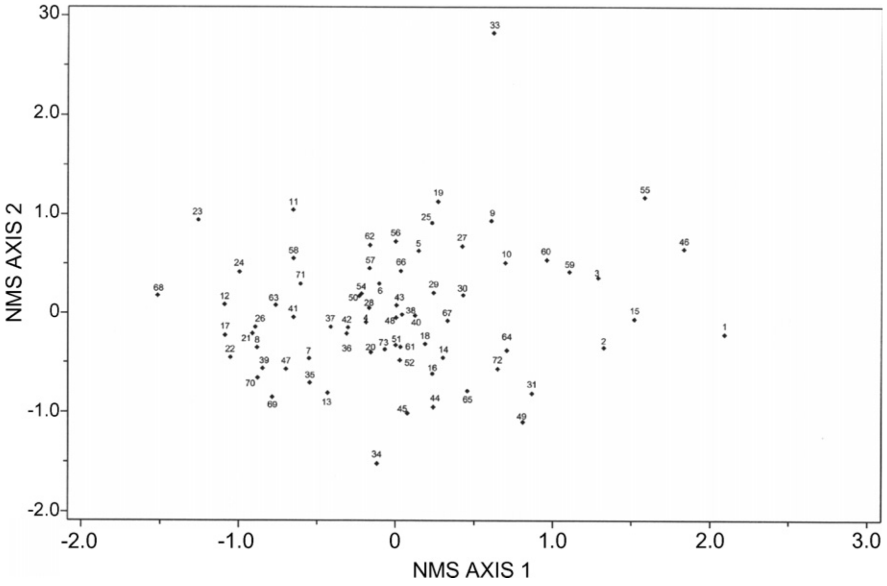

Fig. 5. NMS ordination of 77 regenerating woody species in 71 plots sampled along the Tana River gallery forests.

Table 4
Spearman's rank correlations between environmental variables and NMS ordination axes for forest regeneration data

Variable	NMS axis 1 (*r*, *p*)	NMS axis 2 (*r*, *p*)
Flooding regime indicators		
Mean plot elevation above dry season river level	−**0.312**, 0.008	0.004, 0.974
Percent days flooded	**0.320**, 0.007	−0.042, 0.726
Duration of flooding	**0.278**, 0.019	0.003, 0.980
Distance of plot to river's edge	−0.021, 0.872	0.246, 0.056
Percent soil carbon		
0–20 cm	−0.115, 0.375	0.171, 0.183
50–70 cm	−0.104, 0.421	0.240, 0.060
100–120 cm	−0.218, 0.094	0.170, 0.193
150–170 cm	−0.168, 0.228	0.106, 0.450
Percent clay		
0–20 cm	**0.321**, 0.009	0.185, 0.143
50–70 cm	0.219, 0.080	0.219, 0.080
100–120 cm	0.075, 0.559	0.233, 0.066
150–170 cm	−0.001, 0.995	0.115, 0.381
Percent silt		
0–20 cm	0.015, 0.908	0.148, 0.244
50–70 cm	0.137, 0.277	−0.043, 0.735
100–120 cm	−0.045, 0.726	0.035, 0.785
150–170 cm	−0.125, 0.342	−0.199, 0.128
Percent sand		
0–20 cm	−0.180, 0.154	−**0.346**, 0.005
50–70 cm	−0.052, 0.682	−0.176, 0.161
100–120 cm	−0.021, 0.871	−0.193, 0.130
150–170 cm	0.023, 0.863	0.002, 0.985

Significant correlations are shown in bold.

6. Discussion

6.1. Vegetation patterns and environmental gradients

Classification and ordination of trees and shrubs obtained in Tana gallery forests near Bura were used to define forest communities and to identify some of the underlying environmental gradients. Classification of vegetation data using cluster analysis tended to confirm NMS ordination results, separating the forests into seven fairly well-defined assemblages of woody species.

Correlation analyses performed between NMS ordination scores and measured environmental variables revealed that vegetation gradients identified in the ordination were correlated with the hydroperiod (as indicated by elevation of sample plot above river, percentage days flooded, and duration of flooding) of the Tana River, and that soil properties have important influences in community composition and abundance of trees and shrubs. These findings are in agreement with other studies that found river elevation a major influence on the distribution of vegetation within arid and semi-arid floodplains (e.g., Bennett et al., 1989; Hughes, 1990; Stave et al., 2005) and in temperate regions (e.g., Hupp and Osterkamp, 1985; Townsend, 2001).

In the current study, however, correlations between NMS ordination axes and measured environmental variables were only moderate (Table 3). There were significant ($p < 0.01$) negative correlation between NMS axis 1 and soil organic carbon (SOC), and with percent clay, and positive correlations with percent sand. Soil texture plays a key role in below ground carbon storage in forest ecosystems and strongly influences nutrient availability and retention (Silver et al., 2000). Soils with high clay content have a high water-holding capacity, high total porosity and a high cation exchange capacity. Soil organic carbon strongly influences important forest ecosystem processes such as nutrient recycling, cation exchange capacity, and soil water storage (Chen et al., 2005). No significant correlations were observed between vegetation gradients and distance to the river's edge. Several studies have demonstrated much stronger correlations between the main vegetation gradient and both elevation, and distance to river channel (e.g., Stave et al., 2005) than has been observed in the current study. Higgins et al. (1997), however, found these factors poorly correlated with vegetation patterns along the Nyl River floodplain in South Africa. Increasing distance from river channel represents a decreasing moisture gradient. In arid and semi-arid floodplains, locations farthest from the river may experience some desiccation when the water table drops beyond the reach of trees during low river flows. In complex floodplains such as the Tana, however, locations further from the main river channel may still experience higher moisture conditions than nearer ones when floodplain features such as relic meander scars become connected to the main river channel during the flood season thereby conveying floodwaters regularly to these locations much further from the main river channel. The choice of randomized rather than systematic design in the selection of sample plots resulted in a skewed distribution of distances to the river's edge and this may have hampered a more thorough evaluation of relationship between distance to river edge and vegetation gradients. Weaker than expected correlations between elevation and observed vegetation gradients may be explained by the inadequacy of plot elevation measurements to effectively capture micro-topographical differences within the sample plots. Mitsch and Gosselink (1993) indicated that even small differences in elevation (measured in centimeters), may lead to pronounced differences in hydroperiod and therefore community composition.

Correlations between NMS axis 2 and frequency and duration of flooding were moderate (Table 1), indicating that these environmental variables provided only a partial explanation for the ordering of vegetation along NMS axis 2. The most frequently flooded parts of the floodplain are oxbow lakes and depressions and these support species adapted to constant flooding and anaerobic soils. Along the Tana River, oxbow lakes in-filled with clay or sand contain flood-tolerant species such as *S. venenifera*, *T. brevipes*, and *C. sinensis*. Low-lying plots located on sandy point-bars are also frequently flooded and contain species such as *P. ilicifolia* and *P. dioscoridis*. Hughes (1994) indicated that although the Tana gallery forests are arranged in well-defined vegetation types associated with elevation, particular landforms and substrates, there is the inevitable overlap of species in different parts of the floodplain that can be attributed to species-specific environmental tolerances, and the lag-time between changed river position and associated site conditions. In the current study, forests with the highest biodiversity occurred along the well-drained levees, consistent with finding by Hughes (1988) and Medley (1992). Environmental factors that were not obtained in this study but have been found useful in explaining vegetation patterns include soil properties such as nitrogen content, soil moisture content, electrical conductivity, exchangeable Na^+, K^+, Ca^{2+}, and Mg^{2+}, and cation exchange capacity. Other important variables that could help explain observed vegetation gradients may include geomorphic history of the floodplain features and anthropogenic impacts on the vegetation.

As was the case with the analysis of woody vegetation with a height of 1 m or greater, the observed regeneration vegetation gradient was significantly correlated with measured indicators of flooding regime (elevation above river, frequency and duration of flooding), consistent with other studies (e.g., Robertson and Augspurger, 1999; Johnson, 2000) indicating that flooding is an important factor in regeneration patterns observed along floodplains. Among the soil variables measured, only percent clay and percent sand were correlated with regeneration vegetation gradients identified by NMS ordination (Table 4). These findings are consistent with suggestions by Turner et al. (2004) that local variation in soil properties were of greater importance for seedling establishment than for mature forest stands. It makes sense to find that seedling vegetation gradients are correlated with percent clay and percent sand in only the top 20 cm of the soil because this is zone where the bulk of seedling roots are found and therefore most likely utilizing. The findings in the current study indicate that the measured environmental variables explained only a small part of observed regeneration vegetation gradients and therefore warrant further study. Hall and Harcombe (1998) indicated that seedling growth and mortality may be influenced by light gradients within the forest. Several studies have found that seedling growth and survival is nearly always promoted by increased light within the forest, e.g., Coomes and Grubb (1998), Van der Meer et al. (1998), except at very high levels (Zagt and Werger, 1998). Unfortunately, availability of light in the forest floor was not measured in this study.

6.2. Stand Structure and regeneration status of some major forest species

In contrast to previous studies (e.g., Marsh, 1986; Hughes, 1988) that found a lack of regeneration in the Tana gallery forests, in the current study we found that a majority of forest species were regenerating. The highest regeneration rates were encountered in low-lying plots located on point-bars, oxbow lakes, and backswamps. Dominant overstory species in these sites were well represented in the lower canopy and in the regeneration layer. Regeneration of major canopy species in higher elevation inactive levee plots, however, was either absent or below average. On active levees, overstory species were well represented in the midstory and understory but major canopy species such as *T. emetica* and *C. goetzei* were either absent or had below average regeneration rates.

Hughes (1988) indicated that critical minimum flooding levels and frequency were necessary to permit successful germination and establishment of forest species, particularly in semi-arid regions. Maingi and Marsh (2002) found that all floodplain areas above 1.8 m above dry season river level (which includes all levee plots), experienced a 67.7% reduction in days flooded and that the duration of flood pulse had declined by 87.6% since construction of Masinga and Kiambere Dams in the upper river basin. Levees are the highest and least frequently flooded parts of the floodplain and also the best drained sites since they are mainly composed of sand (Hughes, 1994). It is therefore likely that reduced flooding of the Tana River resulting from dam construction is a contributing factor to the poor regeneration rates observed for some major overstory species that occur along levees.

Size distributions of some major species of the Tana gallery forests are shown (Fig. 6). *S. venenifera*, *C. sinensis*, and *T. brevipes* do not have a reverse-*J* size frequency distribution, as they have relatively fewer individuals in the smaller size class. The size frequency distributions of these species are typical of ‘‘sun’’ or ‘‘partial sun’’ species (Turner, 2001). Shade-tolerant species such as *M. obtusifolia* and *D. mespiliformis* have the reverse-*J* distribution with a large number of smaller size individuals relative to the larger sized individuals. Size distributions for *T. indica* and *A. robusta* indicate very few individuals of the species encountered, and suggest episodic establishment. Marsh (1986) regarded *A. robusta*, *Albizia gummifera*, and *F. sycomorus* as requiring high light intensity to achieve establishment to sapling size. Unfortunately, important factors affecting regeneration such as crown and gap sizes in forest stands were not measured in the current study, making it difficult to assess the effect of varying light availability on different sites influenced germination and establishment of seedlings. Crowns of taller trees reduce the amount of light penetrating onto crowns of shorter trees and subsequently, the growth rate and survival of the shorter trees as well as the rate of seedling recruitment (Kohyama, 1993). There did not appear to be a consistent trend between tree densities in the different forest types and seedling density, suggesting that other factors other than competition for resources may be more important in germination and establishment of different species among the seven forest groups (Table 2).

It is difficult to ascertain the successional status of Tana River forest species based on a one-time snapshot of the size distribution. Correlations between tree age and height must be established before we can reach further conclusions. In order to study stand dynamics effectively, it will be necessary to track changes in different forest stands by obtaining measurements regularly over decades. Alternatively, if tree species in Tana River prove to be useful for dendrochronology, tree rings could be used to reconstruct age-distributions at different times in the stand’s history.

S. venenifera showed the widest ecological tolerance by thriving in a variety of floodplain geomorphic features included in the 78% of all plots in which species was encountered (Table 1). *S. venenifera* was, however, absent in predominantly clayey plots located on backswamps and on inactive levees. Other species with wide ecological tolerance included *L. fraxinofolius* (70.4%), *C. sinensis* (64.8%), *A. elatior* (59.2%), and *C. goetzei* (53.5%). Although *A. elatior* was present in nearly 60% of all plots, its presence in the regeneration layer was limited to only 14% of plots, located mostly on backswamps. This observation is surprising and contradicts the suggestion by Hughes (1985) that the species would become more prevalent on many floodplain sites (especially around Bura) as a result of reduction in annual floods following the construction of Masinga Dam.

D. mespiliformis trees and saplings occurred in 45.1% plots, but seedlings were encountered in only 35.2% of plots. A majority of plots in which trees and saplings were present were located on active and inactive levees, and on backswamps. Other plots were located on oxbow lakes and on the back of point-bars. This observation indicates a wide ecological range for the species. *D. mespiliformis* seedlings were encountered in a variety of geomorphic units with the exception of oxbow lakes and drier inactive levees. The best regeneration was observed on active levees and on point-bars even though no trees and saplings were present in the latter. Distribution of *D. mespiliformis* seedlings suggests that adequate moisture levels are a condition for adequate germination and establishment of the species.

M. obtusifolia was present in 45.1% of plots located in a variety of geomorphic units, from in-filled oxbow lakes to

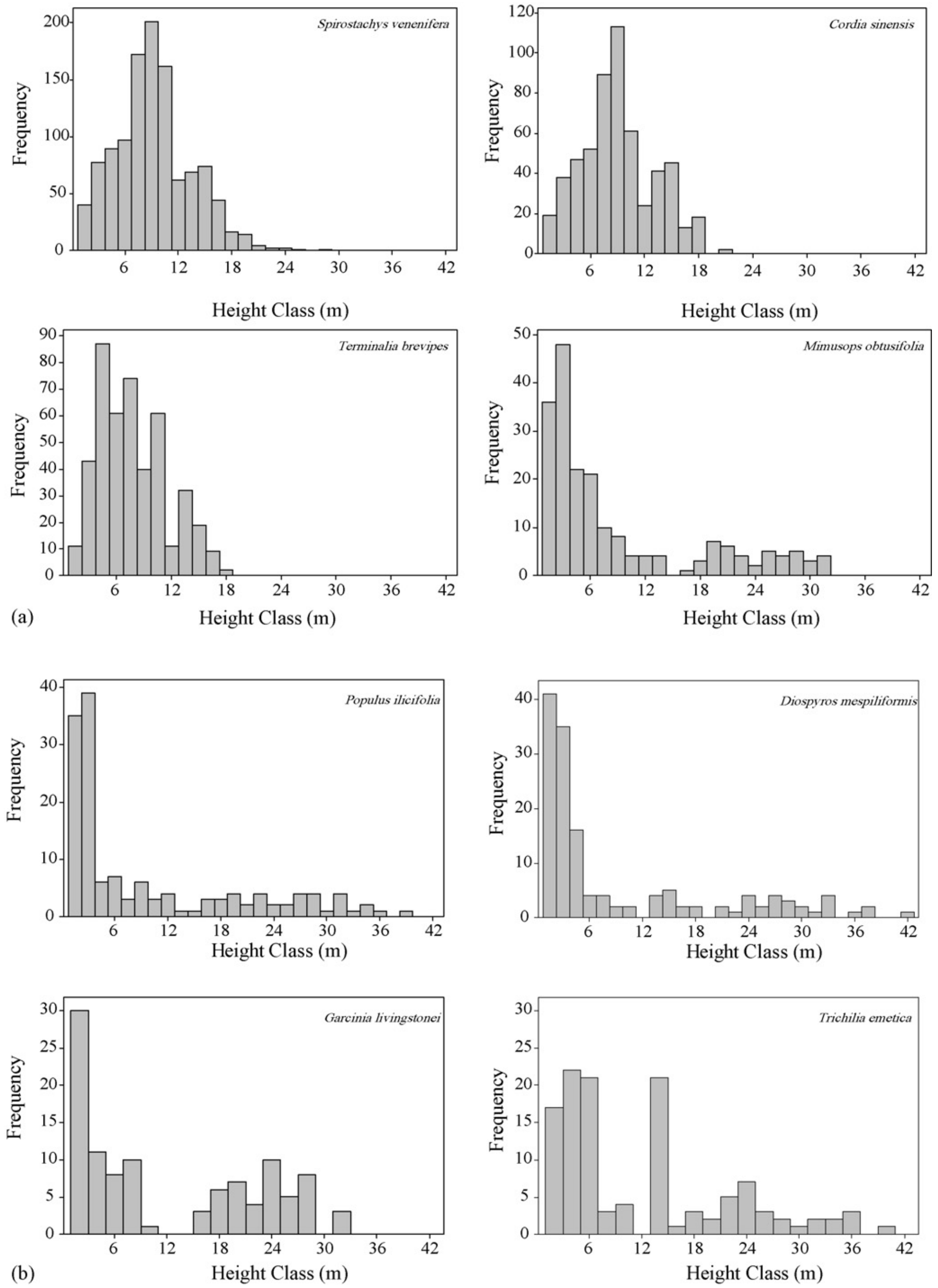

Fig. 6. (a–c) Height distributions for major tree species of the Tana River gallery forest. Note the different *y*-scales.

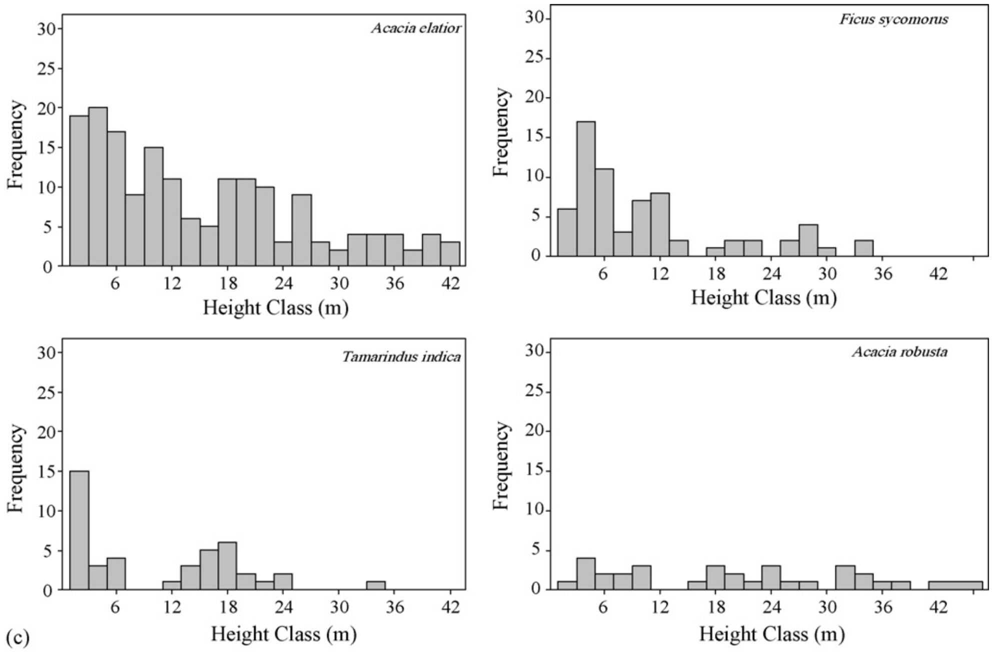

Fig. 6. (*Continued*).

active and inactive levees. In contrast, *M. obtusifolia* seedlings were observed in only 12.7% of the plots, a majority of which were located on point-bars and levees. *G. livingstoneia* occurred in 39.4% of all plots. These plots were located on backswamps, active and inactive levees, oxbow lakes, and on point-bars, an indication of a wide ecological tolerance of the species. *G. livingstoneia* was the most frequently encountered species in the regeneration layer, occurring in 77.5% of all plots.

T. emetica trees and saplings occurred in 30% of all plots, a majority of which were located on active and inactive levees. Seedlings were encountered in only 4.2% of the plots located on active levees. *T. emetica* seedlings were only observed on active levees, albeit at below average levels of regeneration for levees. These observations suggest a preference of the species to well-drained sandy levees and adequate moisture conditions for seedling germination and establishment. A better understanding of the dynamics of the species would help establish whether the poor regeneration observed for the species is part of the species normal dynamics or whether it should be attributed to reduced floods following dam construction in the upper river basin.

A. robusta and *Lepisanthes senegalensis* are well represented in all canopies and in the regeneration layer. *A. robusta*, however, consisted of 32 individuals in 14 plots, 12 of which were located on inactive levees. This observation suggests that the species has a preference for sites with specific ecological conditions. Inactive levee plots usually consist of a layer of clay overlaying levee sands and typically are flooded less frequently than levee forests (Hughes, 1990). *L. senegalensis* was represented by 26 individuals, all occurring on inactive levee plots. This also suggests a narrow ecological range for the species.

F. sycomorus consisted of 68 individuals in 13 plots that included point-bars, inactive and active levees, and on oxbow lakes. The presence of *F. sycomorus* in many stands despite having different ecological conditions suggests a wide ecological range for the species. Regeneration of *F. sycomorus* was observed in only two plots located on point-bars indicating a preference for sites that are regularly flooded but that also drain easily as the predominantly sandy levees.

T. brevipes is found mainly in the midstory and understory, although a few individuals make it to the upperstory. Although *T. brevipes* seedlings were found in far fewer plots compared to their occurrence in the midstory and understory, there were still an impressive number of seedlings encountered (over 3% of all seedlings observed). The wider distribution of *T. brevipes* in oxbow lakes, point-bars, and in active and inactive levees, suggest a wide ecological tolerance for the species. Its abundant presence in the midstory and understory of a variety of geomorphic units, suggests that ideal conditions for regeneration may have prevailed in the past. However, the narrower spatial distribution of *T. brevipes* seedlings in oxbow lakes and point-bars suggests that only these sites remain ideal for its regeneration. These sites, unlike the higher elevation levees, are some of the lowest-lying sites on the floodplain and therefore still experience flooding even after construction of dams in the upper river basin. As a result, these sites are also the preferred sites for flood recession agriculture for the Malakote people. It is likely that the continuing conversion of oxbow lake sites to agriculture may contribute to further declines in the regeneration of *T. brevipes*.

P. ilicifolia is a pioneer species that is shade-intolerant, adapted to well-drained sandy soils typical of point-bars and low levees (Medley and Hughes, 1996), and is short-lived with a lifespan of about 50 years (Maingi, 1998). *P. ilicifolia* has narrow ecological amplitude and is restricted to point-bars. There were only 43 individuals of the species encountered in the overstory of 5 plots. The midstory contained 21 individuals in 2 plots, and the understory had 77 saplings in 1 plot. There were only two sites in the study area that had significant numbers of *P. ilicifolia*. The first site, located in Aratole just to the south of Nanighi East (Fig. 1), consisted of mature and senescing individuals. Ghamano, just north of Bura East (Fig. 1) had healthy stands consisting of seedlings, saplings, and mature individuals. There was evidence of removal of the larger *P. ilicifolia* trees in Aratole as indicated by the presence of bench-saw stands and remnants of felled trees. *P. ilicifolia* trees are valued in construction of dug-out canoes. Regeneration of *P. ilicifolia* was restricted to three sample plots.

A. gummifera was the only tree species that occurred exclusively in the overstory. Furthermore, this species was represented by only three individuals in a levee plot located just north of Bura East (Fig. 1). Although *A. gummifera* is rare in the Bura forests, it is much more abundant in the TRNPR (Medley, 1990).

The role of browsing and trampling by domestic animals on the regeneration and establishment of gallery forest species has not been established. Although the Malakote agriculturalists do not keep livestock themselves, the Orma and Somali pastoralists occasionally bring their animals by the river to drink, and grazing pressure during the dry season or exceptional droughts can be severe. However, most of the livestock is found congregated around Bura Irrigation Scheme some 15 km from the river and watering of the animals frequently occurs along the numerous irrigation canals.

7. Conclusion

Classification and ordinations of woody vegetation in the Tana gallery forests near Bura indicated that there were fairly distinct species assemblages. Identified species assemblages were related to hydrologic regime of the river and soil properties. Measured environmental variables, however, did not account adequately for the observed vegetation gradients.

Examination of regeneration within defined forest groups indicated that many overstory species were regenerating. The best regeneration was observed in low-lying point-bar and oxbow lake sites. A lack of regeneration or below average regeneration was observed in some overstory species, particularly those located in higher elevation inactive levee plots. Altered hydrologic regime of the Tana River, resulting from dam construction in the upper river basin, and conversion of prime regeneration sites for agriculture by local people, were suggested as possible explanations for observed lack of regeneration in some of species.

Information on the age-structure of the Tana riverine forests is lacking, therefore constraining our ability to understand better the successional processes and the regeneration status of the forests. There is a need for long-term studies through permanent sample plots across a wide range of geomorphic sites in order to understand better the growth and stand dynamics of the Tana River species. Results obtained in study and descriptions made regarding the seven forest types identified could serve as a starting point to base future studies. Although the Tana gallery forests may not be as diverse as those in the TRNPR, regional biodiversity of the forests is inadequately protected within the TRNPR and therefore there is a need to set up more forest blocks for conservation with the active involvement of local people.

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