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MANGROVE LITTER BIOMASS INPUT IN A FOREST IMPACTED BY HUMAN PHYSICAL DISTURBANCE, GAZI BAY, KENYA

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Abstract. This study investigated the impact of human physical disturbance on litter yield in a mangrove forest by comparing amount and composition of litterfall between disturbed and relatively undisturbed sites in Gazi mangrove forest. Litter was trapped using littertraps suspended from trees at the upper and lower intertidal zones of the four sites. Litterfall material was collected fortnightly from October 2001 to June 2003, and dry weight of components determined and compared using ANOVA. Physical disturbance reported from the forest include tree cutting, digging for bait, and trampling by man and vehicles which were more prevalent at the disturbed sites than comparable undisturbed sites. Annual litter production in the Gazi forest was 4.3 t ha^{-1} yr^{-1} and was dominated by leaves of *Rhizophora mucronata*, which constituted 39% of litter components. Disturbed sites recorded significantly lower litterfall than corresponding undisturbed sites (ANOVA, $P < 0.01$), an increase (10%) in litter yield of *Avicennia marina* leaves, and 20% and 30% declines respectively in *R. mucronata* leaf and flower productivity. The decline in litter biomass and its changing composition were attributed to changes in predominant mangrove species as a result of size, site, and species selection by harvesters and the competitive ability of regenerating and uncut trees.

Keywords: *composition, harvesting, litterfall, selectivity, species change.*

INTRODUCTION

Mangrove forests are important to inhabitants of coastal communities as a prime source of construction material, fuel-wood, tannins, dyes, and medicine throughout the tropics (Kokwaro 1985, Farnsworth & Ellison 1997, Taylor *et al.* 2003). They are also important as nursery and feeding grounds for fish and crustaceans (Krumme 2003, Crona & Ronnback 2005), and their spatial extent has been correlated to marine fisheries yields (Alongi 2002). Diop (1993) estimated mangrove forests to provide goods and services valued at US$ 10 000 ha^{-1} yr^{-1} and put the global economic value of mangrove forest at US$ 1.6 billion per year.

However, human-induced stresses, as a result of physical, chemical and biological disturbance, threaten the existence of this important ecosystem. Human disturbance has reduced global mangrove forest cover by between 30 and 50% in the last decade due to conversion to agriculture or aquaculture enterprises, overexploitation, and pollution by organic and inorganic wastes (Farnsworth & Ellison 1997, Valiela *et al.* 2001). Conversion of mangrove areas into agricultural, aquaculture, and salt production facilities is more common in forests of South-East Asia than in Africa (Farnsworth & Ellison 1997, Valiela *et al.* 2001). Biological and chemical pollution by sewage, solid waste, and oil spill are more commonly reported in mangrove forests adjacent to urban centers. In East Africa, such pollution has been reported from Mombasa and Dar es Salaam (Semesi 1998, Abhuodha & Kairo 2001). Deforestation and overexploitation of mangrove forests due to harvesting of timber products by local communities is however widespread in tropical regions throughout the world and is probably as old as coastal settlements themselves.

Overexploitation of mangrove forests has been measured using remote sensing techniques in Kenya (Gang & Agastiva 1992, Kairo *et al.* 2002, Dahdouh-Guebas *et al.* 2004) and elsewhere. A number of studies have implicated mangrove deforestation and overexploitation as an important factor influencing mangrove flora (Gang & Agastiva 1992, Allen *et al.* 2001, Walters 2003, Dahdouh-Guebas *et al.* 2004) and fauna (Schrijvers *et al.* 1995, Fondo & Martens 1998, Ashton *et al.* 1999, Skilleter & Warren 2000, Khalil 2001) also in Kenya and elsewhere. These

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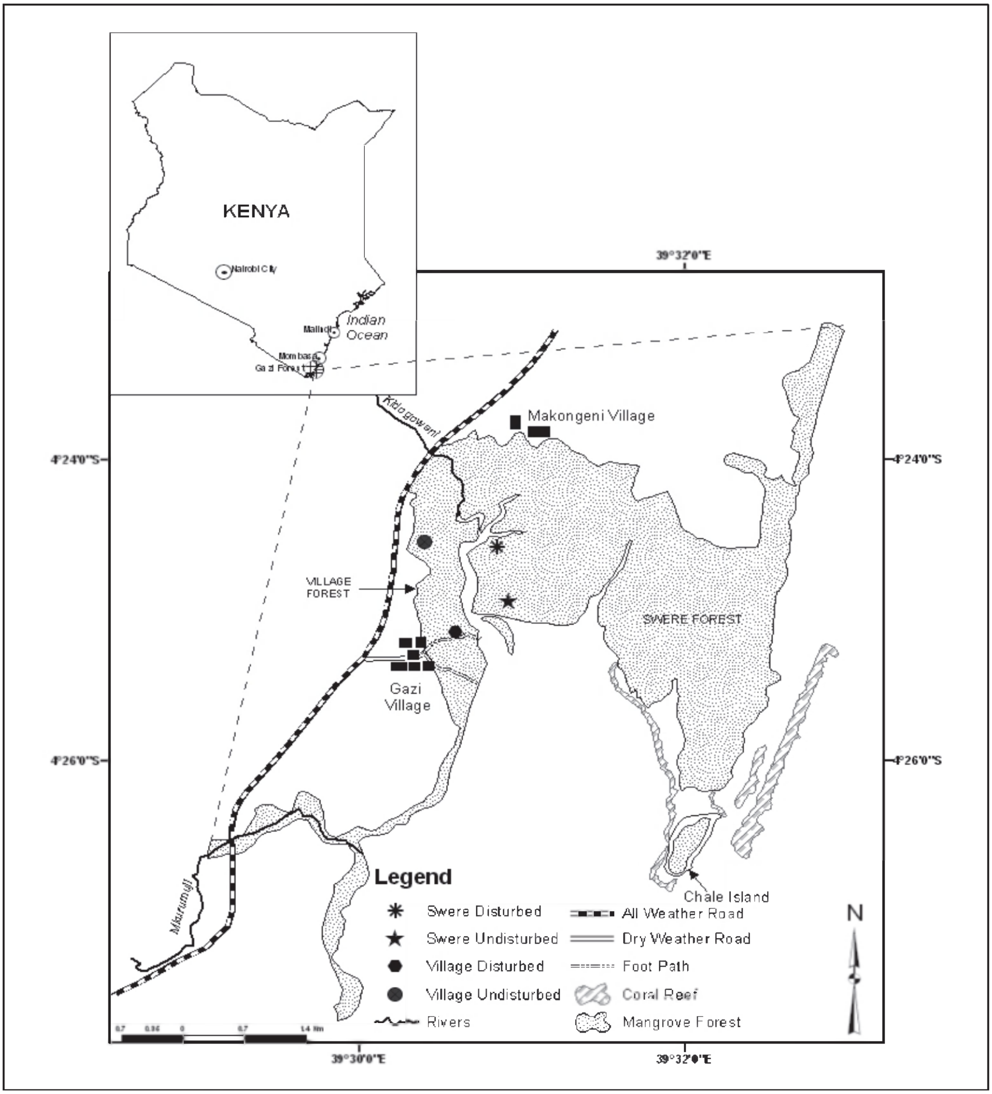

FIG. 1. Map of Kenya showing location of Gazi Bay and a detailed map of the Gazi Bay mangrove forest showing the location of the study sites.

studies have reported changes in floral and faunal abundance and diversity as a result of human physical disturbance, but none has directly related such changes to variations in litterfall input into the forest floor. Such basic knowledge is essential in understanding and explaining the impacts of deforestation on forest functioning described in some of the above studies, and hence the present study. The sampling design adopted was comparison of patterns of litter biomass input at disturbed and undisturbed sites with comparable species composition, identified during a preliminary survey of the forest.

MATERIALS AND METHODS

Study area. The study was conducted at Gazi Bay mangrove forest (4°25'S, 39°30'E), located in Kwale District, approximately 50 km south of Mombasa city along the Kenyan coastline (Fig 1). Chale Peninsula and a fringing coral reef shelter the bay from incoming oceanic waves. The bay occupies an area of about 1500 ha, consisting of mangrove forest (615 ha), creek (25 ha), intertidal mud and sandflats (300 ha), and 500 ha of subtidal seagrass beds. The forest experiences semidiurnal tides with a tidal amplitude of between 1 and 4 m. Freshwater input into the forest and bay is from groundwater seepage and two seasonal rivers, Kidogoweni and Mkurumuji. The Kidogoweni River bisects the forest and divides it into the Village and Swere forests (Fig. 1).

Gazi and Makongeni villages border the forest to the west and northwest respectively, and have populations estimated at between 3000 and 5000 persons. Small scale subsistence agriculture and also plantations of cashew nuts, coconuts, mangoes, and citrus fruits occur on land adjacent to the forest. However the main economic activity of communities adjacent to the forest is fishing using baited line, unmotorized canoes and dhows.

Two sites on either bank of the Kidogoweni River were used during the data collection. The Village undisturbed site (4°24.780'S, 39°30.595'E) was situated to the west of Kidogoweni Creek; (Fig 1). This site corresponds to the *Ceriops* plot used by Slim *et al.* (1996). The site experienced flooding for approximately 2.1 hr day^{-1} and had extremely high water (EHW) estimated at 0.66 m. The site was dominated by *Ceriops tagal* – *Rhizophora mucronata* at the seaward edge and *Avicennia marina* – *C. tagal* association at the landward edge.

The Village disturbed site (4°25.148'S, 39°30.670'E) was closest to the Gazi village being less than 1 km from the village to the west of Kidogoweni Creek. The site was the most accessible to villagers with four footpaths and two roads passing through the forest (Fig. 1). This site corresponds to the disturbed site used by Schrijvers *et al.* (1995), Fondo & Martens (1998), Bosire *et al.* (2004), and Huxham *et al.* (2004), and was chosen to represent a disturbed site at the village forest. The site received tidal inundation for an average of 1.5 hr day^{-1} and had EHWS of 0.55 m. The site was dominated by *C. tagal* – *R. mucronata* at the seaward edge and *A. marina* at the landward margin.

The Swere undisturbed site (4°25.173'S, 39°30.911'E) was situated to the east of Kidogoweni Creek (Fig. 1). This site corresponds to the virgin habitat described by Slim *et al.* (1996) and Huxham *et al.* (2004). The site received tidal inundation for approximately 9.6 hr day^{-1} with tidal water during EHWS reaching 0.90 m. The site was dominated by *R. mucronata* – *Sonneratia alba* – *Bruguiera gymnorhiza* at the seaward edge and *C. tagal* at the land margin.

The Swere disturbed site (4°25.173'S, 39°30.911'E) was situated to the east of Kidogoweni Creek (Fig. 1). This site was chosen to represent a disturbed site on Swere forest. The site received tidal inundation for approximately 10.2 hr day^{-1} with tidal water during EHWS reaching 1.03 m. The site was dominated by *R. mucronata* – *Sonneratia alba* – *Bruguiera gymnorhiza* at the seaward edge and *C. tagal* at the land margin.

Data collection. Human disturbance was evaluated by estimation of tree-cutting intensity, abundance of harvestable trees (long straight poles with stem diameter above 2 cm), and observation of human activity such as roads, footpaths, and digging for fish bait at the sites. Tree cutting and forest attributes were evaluated from line transects laid from the seaward edge to land at each of the sites. Tree stumps and harvestable trees were counted on 5 x 5-m plots at intervals of 10 m along two transects at each of the site. Temperature and pH of the substrate was also determined at the sites.

At each of the sites in the Village and Swere forest (Village undisturbed and Village disturbed, Swere undisturbed and Swere disturbed) identified during the preliminary survey, four sampling stations were set up. Two sampling stations were allocated to each of the lower and upper intertidal zones corresponding to the *C. tagal*- and *R. mucronata*-dominated areas respectively. A set of random numbers was used to determine positioning of the sampling plot at each of the stations.

Litter traps to collect falling litter material were constructed of welded metal rings (0.8 m diameter) and a nylon mesh cloth (1-mm^2 mesh), attached to the metal rings to form a conical pocket-like trapping surface at the base. Five traps were allocated to each sampling station at the landward and seaward edge at the four sampling sites. The traps were suspended from appropriate trees. Traps were mounted below the lowest tree branch but above highest inundation level.

Litter accumulating in the traps was collected fortnightly, and transported to the laboratory from October 2001 to June 2003. In the laboratory, samples were dried to constant weight, sorted to components (leaf species, flower, seeds, and wood) and dry weight determined. Ash-free dry weight was determined by combustion of sub-samples of each litter component in the sample at 500°C for 5 hours in a muffle furnace. The data was used to calculate composition and amounts of litter input (g m^{-2} day^{-1}) for the sampling sites within the forest. Mean litterfall figures were compared between sites by ANOVA test, significant differences detected were separated using Tukey's Honest Significant Difference test (SPSS 1992, Zar 1999).

RESULTS

The Gazi Village disturbed and undisturbed sites were closer and more accessible to local communities, being less than 2 and 5 km from the village respectively. The Swere forest sites were less accessible since they required traversing the village forest through available footpaths and then undertaking a 20- to 30-min boat or canoe ride across the creek.

Tree cutting, trampling by man and vehicles, and digging for bait were the major human activities recorded at the sites in Gazi forest. Tree cutting was significantly different (ANOVA, F = 4.7, $P < 0.01$) between the undisturbed Swere site and the disturbed Village site. Other sites had intermediate but similar cutting intensity (Table 1). Roads, footpaths and digging for bait were common evidence of human activities at the disturbed sites of Village forest. Substrate temperature was significantly (ANOVA, F = 3.26, $P < 0.05$) different between the undisturbed Swere site (27.0°C) and the undisturbed Village forest site (28.1°C); the other sites had intermediate but similar temperatures (Table 1). Substrate pH was lowest (6.3) at the disturbed site of Village forest; other sites had significantly higher pH (Table 1; ANOVA, F = 6.07, $P < 0.05$). Harvestable tree abundance was considerably and significantly lower at disturbed sites than at the corresponding undisturbed sites (Table 1; ANOVA, F = 4.9, $P < 0.01$). Harvestable tree abundance at the undisturbed Swere site was five times higher than that at the disturbed Village forest site.

Results indicated that dry weight litterfall at Gazi mangrove forest was 1.19 ± 0.01 g m^{-2} day^{-1}, equivalent to an annual litter productivity of 4.34 t ha^{-1} yr^{-1}. The litter had an organic matter content averaging about 88.7%. The litterfall material was dominated by leaves from the four mangrove species *Rhizophora mucronata*, *Ceriops tagal*, *Avicennia marina*, and *Bruguiera gymnorhiza*, which together constituted an average of 0.95 g m^{-2} day^{-1} of the litterfall (Table 2). Non-leaf material in litterfall consisted of reproductive components (fruits and flowers) and woody debris (including leaf stipules), which together contributed 20% of total litterfall (Table 2).

R. mucronata yielded most leaves at Gazi forest, with 0.46 g m^{-2} day^{-1} of litter, and together with *C. tagal* (0.32 g m^{-2} day^{-1}) contributed over 65% of the litter that entered the forest floor, while *A. marina* and *B. gymnorhiza* were least productive (Table 2). Generally, leaves had lower organic matter content

TABLE 1. Forest attributes at the disturbed and undisturbed sites of Gazi Bay mangrove forest, Kenya.

Parameter	Village undisturbed	Village disturbed	Swere undisturbed	Swere disturbed
Forest character:				
Cutting intensity m^{-2}	3.25 ± 0.78_{ab}	4.98 ± 1.06_{b}	0.69 ± 0.64_{a}	2.31 ± 0.87_{ab}
Tree density m^{-2}	24.6 ± 13.4	5.75 ± 18.3	50.40 ± 11.0	40.82 ± 15.0
Harvestable trees m^{-2}	2.53 ± 0.8_{b}	1.04 ± $1,1_{c}$	5.24 ± 0.6_{a}	3.42 ± 0.9_{b}
Human activity:				
Roads / paths	Few	Common	Absent	Rare
Bait digging	Little	Common	Absent	Absent
Substrate profile:				
Temperature	28.08 ± 0.28_{b}	27.73 ± 0.29_{ab}	27.02 ± 0.24_{a}	27.26 ± 0.24_{ab}
pH	6.63 ± 0.07_{b}	6.32 ± 0.08_{a}	6.68 ± 0.06_{b}	6.70 ± 0.06_{b}

Column means (± standard error (SE) with similar letters a, b, c, or d attached are not significantly different (ANOVA test, Tukey Honest Significant Difference (HSD) test, $\alpha = 0.05$)

TABLE 2. Contribution of various mangrove litterfall components in litter reaching the forest floor at Gazi Bay, Kenya (values are means of pooled data).

Component	Dry weight g m^{-2} day^{-1}	AFDM g m^{-2} day^{-1}	Organic matter in components (%)	Percent of component in sample
Leaves:				
Ceriops	$0.32 \pm 0.01_b$	0.27 ± 0.02	86.7	26.9
Rhizophora	$0.46 \pm 0.01_a$	0.40 ± 0.02	86.2	38.7
Avicennia	$0.08 \pm 0.01_d$	0.07 ± 0,02	85.1	6.70
Bruguiera	$0.09 \pm 0.01_d$	0.08 ± 0.02	85.9	7.60
Non-leaf:				
Flower	$0.12 \pm 0.01_c$	0.11 ± 0.02	95.2	10.0
Fruit	$0.10 \pm 0.01_d$	0.09 ± 0.02	91.4	8.40
Wood	$0.02 \pm 0.01_e$	0.02 ± 0.02	90.4	1.70

Column means (± SE) with similar letters a, b, c, or d attached are not significantly different (ANOVA test, Tukey HSD, $\alpha = 0.05$), AFDM-ash free dry mass

(85-87%) than non-leaf litter components such as flowers, fruits and wood. Among the non-leaf litter components, flowers, which contained over 95% organic matter, also occurred more frequently than either fruits or woody debris (Table 2).

Significant differences in the rates of litterfall were detected among the sampling sites under different levels of human disturbance in the Gazi forest (ANOVA F = 108.05, df = 3, $P < 0.001$). The undisturbed Swere forest site recorded the highest rate of litterfall, the disturbed site in the Village forest the lowest (Table 3). Disturbed sites recorded between 35 and 45% lower litterfall than corresponding undisturbed sites at the Village and Swere forest sites respectively (Table 3). The sequence in rates of litterfall among the sites was Swere undisturbed > Swere disturbed = Village undisturbed > Village disturbed (Tukey HSD, $\alpha = 0.05$).

TABLE 3. Quantities of dry weight mangrove litterfall components (g m^{-2} day^{-1}) at sampling sites under different levels of human disturbance in Gazi forest.

Component	Village undisturbed	Village disturbed	Swere undisturbed	Swere disturbed	F-value
Leaves:					
Ceriops	$0.33 \pm 0.01_b$	$0.13 \pm 0.01_d$	$0.26 \pm 0.01_c$	$0.58 \pm 0.01_a$	110.60***
Rhizophora	$0.52 \pm 0.01_b$	$0.13 \pm 0.01_d$	$0.95 \pm 0.01_a$	$0.32 \pm 0.01_c$	11.58**
Avicennia	$0.05 \pm 0.01_b$	$0.23 \pm 0.01_a$	$0.04 \pm 0.01_b$	$0.03 \pm 0.01_b$	120.65***
Bruguiera	$0.06 \pm 0.01_b$	$0.09 \pm 0.01_a$	$0.10 \pm 0.01_a$	$0.10 \pm 0.01_a$	5.11**
Non-leaf:					
Flower	$0.13 \pm 0.01_b$	$0.04 \pm 0.01_c$	$0.21 \pm 0.01_a$	$0.10 \pm 0.01_b$	88.79***
Fruit	$0.05 \pm 0.01_c$	$0.06 \pm 0.01_c$	$0.17 \pm 0.01_a$	$0.09 \pm 0.01_b$	35.12***
Wood	$0.01 \pm 0.01_{ab}$	$0.02 \pm 0.01_{ab}$	$0.03 \pm 0.01_a$	$0.01 \pm 0.01_b$	3.47*
Total	1.15	0.70	1.76	1.23	
Mean	$0.15 \pm 0.01_b$	$0.10 \pm 0.01_a$	$0.22 \pm 0.01_c$	$0.16 \pm 0.01_b$	108.05**

Row means (± SE) with similar letters a, b, c, or d attached are not significantly different (Tukey HSD, $\alpha = 0.05$), ANOVA, F-value significance; * - $P < 0.05$, ** - $P < 0.01$, and *** - $P < 0.001$

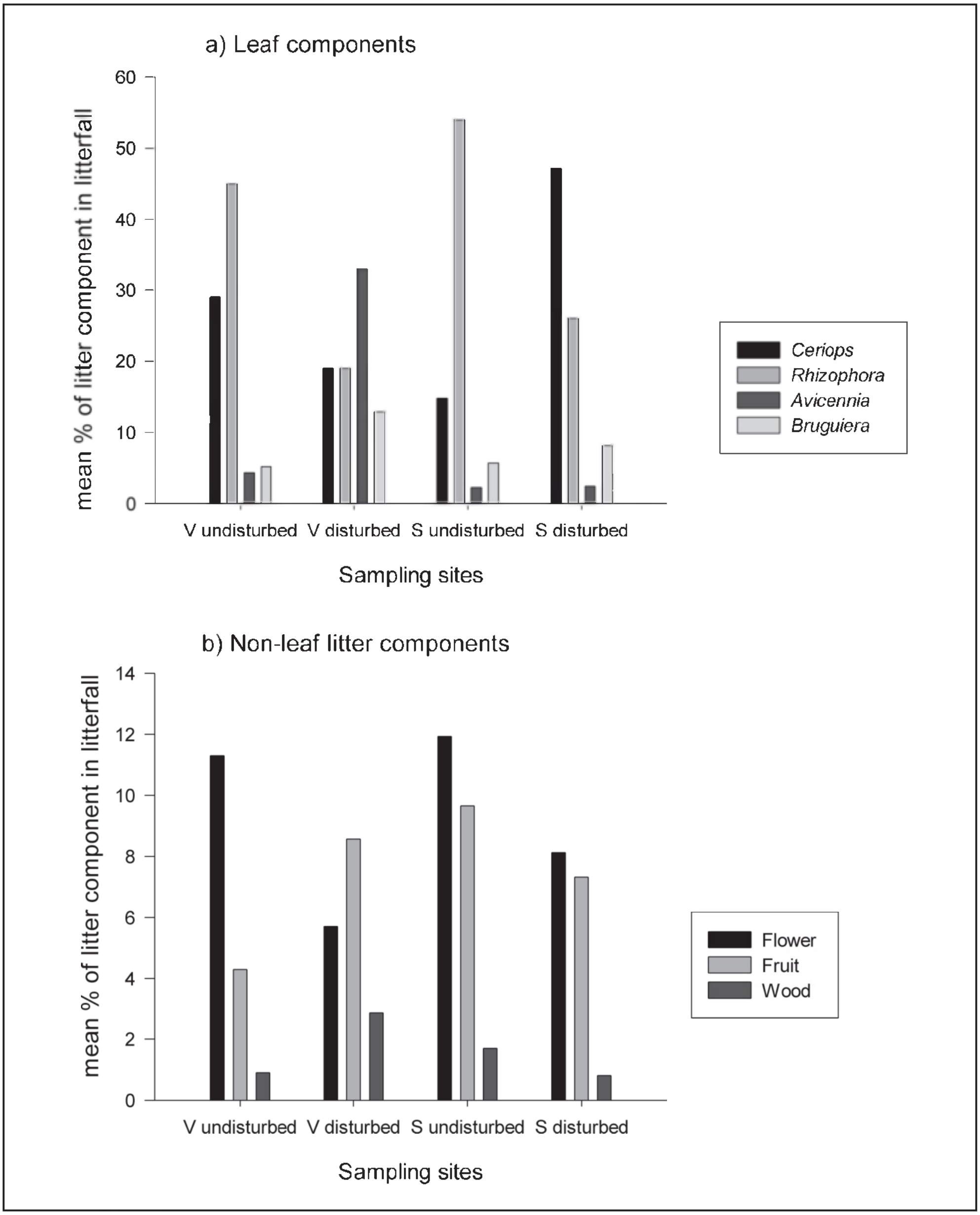

FIG. 2. Variations in composition of mangrove (a) leaf and (b) non-leaf components of litterfall at undisturbed and disturbed sites of Village (V) and Swere (S) at Gazi Bay (Values are pooled means for the site).

R. mucronata leaf fall was significantly lower at disturbed sites in Swere and Village compared with corresponding undisturbed sites (Table 3). On the other hand, increased leaf yields were observed for *C. tagal* at Swere site and *A. marina* and *B. gymnorhiza* at Village disturbed site (Table 3). Among non-leaf litter components, human disturbance had a greater influence on flower production than on either fruit or wood debris production (Table 3). Disturbed sites always had lower flower production than corresponding undisturbed sites (Tukey HSD, $\alpha = 0.05$).

Figure 2 shows the contribution of leaf and non-leaf litter components of litterfall at the sampling sites under different levels of disturbance. The results indicated that dominance of *R. mucronata* leaves in samples from undisturbed sites declined with human disturbance (from 45 to 20% and 55 to 28% at Village and Swere sites respectively), while that of *A. marina* (from 5 to 30% and 5 to 5%), *C. tagal* (from 28 to 18% and 14 to 48%), and *B. gymnorhiza* (from 5 to 10% and 5 to 8% at Village and Swere sites respectively) either increased or remained the same with disturbance (Fig. 2a). Among the non-leaf litter components, flower productivity declined with disturbance at both Village and Swere sites. However, fruit and wood production declined with disturbance at Swere while it increased at Village sites (Fig. 2b).

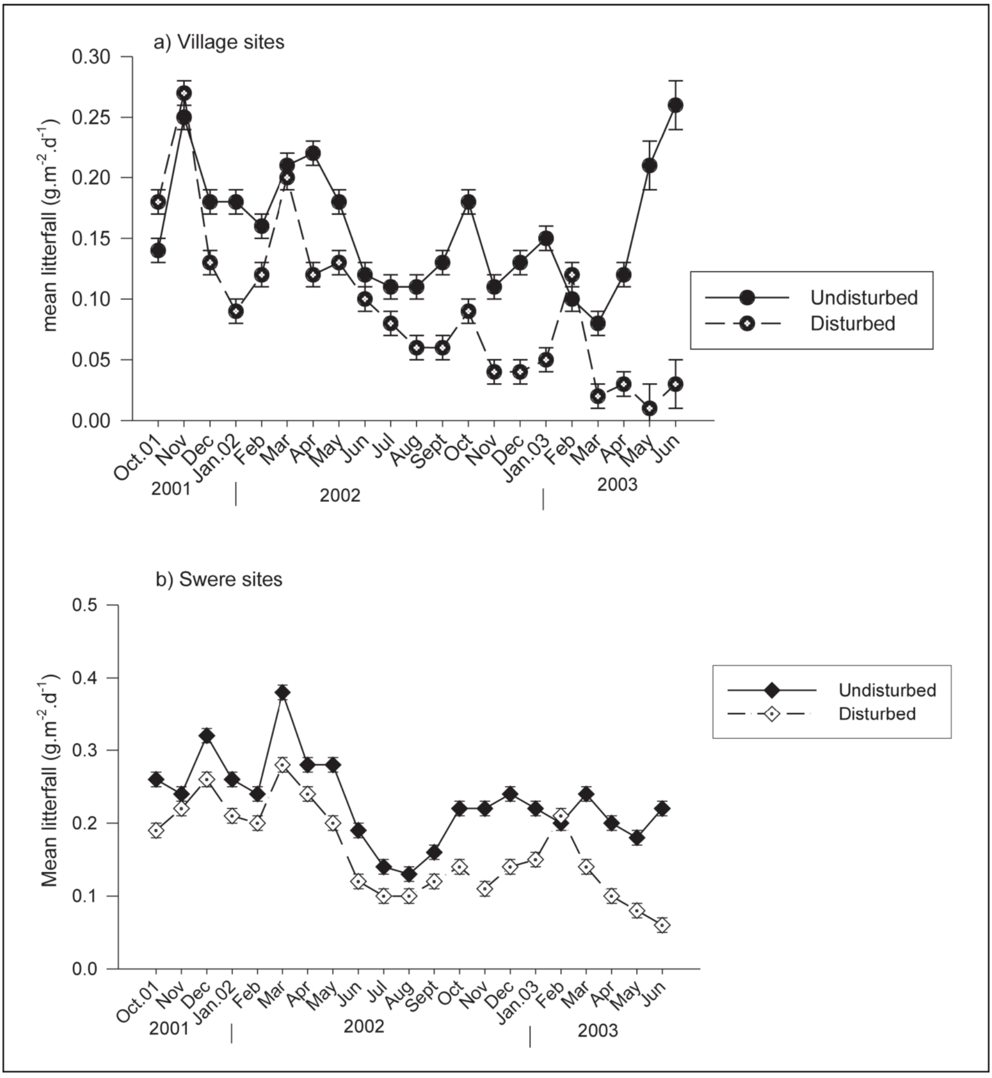

FIG. 3. Monthly fluctuations in mean litterfall on the forest floor of undisturbed and disturbed sites at (a) Village and (b) Swere within the Gazi mangrove forest (values displayed are mean (± SE) litterfall per month).

Temporal patterns of litterfall were generally similar between the disturbed and corresponding undisturbed sites in the Village and Swere forest (Fig. 3a, b). However, disturbed sites always had lower litterfall than the corresponding undisturbed sites, especially during the wet months that received above 10 mm rainfall (November, December, March, April, and May) at Swere and dry months (February, August, and September) at both Village and Swere forest (Fig. 3a, b).

DISCUSSION

The rate of mangrove litter production of 4.34 t ha^{-1} yr^{-1} reported for Gazi forest in this study is comparable to rates reported by Twilley *et al.* (1986) for basin mangrove forests (5.21 t ha^{-1} yr^{-1}) in Florida USA, but higher than that reported for *Avicennia*-dominated forests in Mexico and Australia (Table 4). The rate reported here is lower than that reported by Slim *et al.* (1996) at the same forest (Table 4). However, Slim *et al.* (1996) used only two sites, *C. tagal* and *R. mucronata* plots, corresponding to the undisturbed Village and Swere forest sites in this study. These sites were dominated by tall mature trees and experienced limited human disturbance. Their litterfall figures may therefore be overestimates and cannot be extrapolated to the whole forest, since the site suffers differing levels of human disturbance, as has been shown in this study. Reliable estimates of litterfall in mangrove forests impacted by human disturbance should include estimates from both disturbed and less disturbed sites.

Litter that became part of the Gazi mangrove forest floor as litterfall was dominated by leaves especially of *R. mucronata*, which formed over 50 % of the leaves. *A. marina* and *B. gymnorhiza* were the least productive mangrove species. However, human disturbance influenced both litterfall composition and productivity at the Gazi mangrove forest. Changes

TABLE 4. Annual litter production (t ha^{-1} yr^{-1}) in selected regions of the world.

Region / Country	Species	Litterfall t ha^{-1} yr^{-1}	Source
America			
Fort Myers, Florida (USA)	A & R	6.1	Twilley *et al.* (1986)
Tabasco, Mexico		6.1	Lopez-Portillo & Ezcurra (1989)
Braganza, Brazil	A & R	13.0	Mehlig (2001)
Guayas River, Ecuador		10.6	Twilley *et al.* (1997)
California Gulf, Mexico	A	1.8	Arreola-Lizarraga *et al.* (2004)
Asia & Pacific			
Goa, India	R	11.7	Wafar *et al.* (1997)
Ca Mau, Vietnam	R	11.0	Clough *et al.* (2000)
Australia & New Zealand			
Darwin harbour, Australia	Mix	16.0	Woodroffe *et al.* (1988)
Jervis Bay, Australia	A	3.7	Clark (1994)
Tuff Crater (NZ)	Mix R	7.7	Woodroffe (1985)
Africa			
Richards Bay (SA)	R	8.5	Steinke & Ward (1988)
Mgeni Estuary (SA)	A & B	7.5	Steinke & Charles (1984)
Gazi bay (EA)	R	9.6	Slim *et al.* (1996)
Gazi bay (EA)	C	4.0	Slim *et al.* (1996)
Village undisturbed	C & R	4.2	*This study*
Village disturbed	C, R & A	2.6	*This study*
Swere disturbed	C & R	6.4	*This study*
Swere disturbed	C & R	4.5	*This study*

Mangrove species A - *Avicennia*, B - *Bruguiera*, C - *Ceriops*, and R - *Rhizophora* in litterfall composition have also been reported for riparian and terrestrial forests (Gairola *et al.* 2009). Evidence of human disturbance corresponded to lower productivity and contribution of *R. mucronata* and increased yield of other species, especially *A. marina* and *C. tagal.*

Human disturbance also corresponded to reduced yield of reproductive components such as flowers and fruits. This was attributed to selective harvesting of relatively older trees. This may indicate that, apart from influencing litter yield, human disturbance also affects the reproductive regime of the forest. Hence human disturbance gives a competitive advantage to species with coppicing ability at the expense of sexual reproduction through fruits and flowers and may explain the observed predominance of *A. marina* at disturbed sites. *Avicennia* species have been reported to reproduce by both sprouting from stumps and sexually (Robertson 1991). In addition, Duke (2001) reported a prevalence of *A. marina* species in forest gaps created by natural disturbances such as wind, storms, and hurricanes. This may explain the increased predominance of *A. marina* in highly disturbed sites where gaps are created by active deforestation. The lower litter yield in overexploited forest may be attributed to increased substrate exposure by removal of tree cover and creation of gaps within the forest, causing increased fluctuations in substrate salinity, aeration, pH, and redox potential and subsequent immobilization of limiting nutrients essential to sustaining productivity. Exposure of mangrove forest soils as a result of clearing for construction of aquaculture ponds is reported to cause acidification of the substrate and to limit productivity (Valiela *et al.* 2001, Bandeira *et al.* 2009).

Lower contribution by *R. mucronata* to litterfall at disturbed sites may also be attributed to selectivity of the forest product harvesters. Dahdouh-Guebas *et al.* (2000) showed that among the exploited mangrove species *R. mucronata* and *B. gymnorhiza* were preferred by harvesters and consumers at Mida, Kenya, due to the superior timber, poles, and charcoal obtained from the species.

Lower litterfall at disturbed sites of Gazi forest may also be attributed to change in the age structure of the forest due to selective harvesting of the preferred 2- to 40-cm range of stem diameter. This implies that overexploited forests are left with only old and very young trees, as has been demonstrated by Allen *et al.* (2001) and also Bandeira *et al.* (2009). Clough *et al.* (2000) showed that old (> 20 years) and young mangrove trees have lower productivity and hence lower litter yield than forest stands of intermediate ages (10-12 years). The age of the trees at Gazi may also have contributed to variation in the production of reproductive components such as flowers and propagules, which was highest at undisturbed sites, especially in Swere forest. Clough *et al.* (2000) also showed that propagules and flower production in *Rhizophora apiculata* forest was 5 to 10 g m^{-2} yr^{-1} in trees less than 12 years old, but above 100 g m^{-2} yr^{-1} in a 35- year-old forest stand. The average flower and propagule yield recorded from Gazi forest in this study (43.5 and 36.5 g m^{-2} yr^{-1} for flower and propagules respectively) are intermediate to those obtained by Clough *et al.* (2000) on 12-year-old (10.0 and 14.6 g m^{-2} yr^{-1} for flower and propagules respectively) and 21-year-old forest stands (71.0 and 312.1 g m^{-2} yr^{-1}).

Conclusion. Lower litterfall biomass input occurs in mangrove forests with evidence of human disturbance. Litterfall biomass at disturbed sites showed an increase in the relative contribution of *Avicennae marina* but lower flower and fruit yield. Changes in litter biomass and composistion are attributed to changes in predominant mangrove species as a result of size, site, and species selectivity by harvesters, and also to the competitive ability of species left uncut.

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