

Phenology of *Avicennia marina* (Forsk.) Vierh. in a Disjunctly-zoned Mangrove Stand in Kenya

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Abstract—*Avicennia marina* in Gazi Bay, Kenya, displays a disjunct zonation pattern across the intertidal zone with a seaward and a landward *A. marina* fringe. Earlier studies revealed significant differences in its vegetation structure, physiognomy, root system and leaf morphology, which can be attributed to salinity and tidal inundation differences that characterise the forest zones. The main objective of this study was to investigate the phenology of *A. marina* in the disjunctly zoned stands by direct shoot observation. Vegetative and reproductive phenology of *A. marina* was studied from January 2005 to December 2006. Four natural and one reforested sites were used for the study in the landward and the seaward intertidal zone. Randomly selected shoots (54 per site) were carefully tagged for direct shoot observation and sampling done every fortnight for leaf emergence and fall, and bud, flower and fruit production. Vegetative and reproductive attributes of the species were clearly seasonal in both zones with distinct patterns. However, shifts in peaks in leaf fall and emergence were observed in 2006. Unimodal and bimodal leaf fall patterns were respectively observed at the landward and seaward sites. Monthly leaf emergence and fall was significantly different ($p < 0.05$) within sites, but not significantly different ($p > 0.05$) between sites. Mean leaf longevity was 11 months with a significant difference ($p < 0.05$) between the seaward reforested site and the landward site. Bud initiation occurred in November in both zones. However, flowering occurred earlier and the fruiting period was shorter in the landward zone compared to late flowering and prolonged fruiting in the seaward zone. Fruit fall peaked in April and May during the wet season. Differences in the vegetative and reproductive phenology of *A. marina* across the intertidal zone are discussed.

INTRODUCTION

Avicennia marina is a mangrove tree species that is extraordinarily adaptable with a wide latitudinal range closely associated with its flexible growth pattern. It is common throughout the Indo-Pacific region within a latitudinal range of 30° N to 38° S (Duke, 1990). In Kenya, *A. marina* is the third most dominant mangrove species after *Rhizophora mucronata* Lamk. and *Ceriops tagal* (Perr) C. B. Robinson (Kairo *et al.*, 2002). The species displays a disjunct zonation pattern across the intertidal complex (Dahdouh-Guebas *et al.*, 2002). A comparison of landward and seaward *A. marina* zones revealed significant differences in physiognomy (Dahdouh-Guebas *et al.*, 2004, 2007). *Avicennia marina* trees in the seaward zone are also structurally complex in terms of plant height and stem diameter, while those in the landward zone are dwarfed.

Extensive phenological studies of *A. marina* have been undertaken (Wium-Andersen & Christensen, 1978; Duke, 1990; Hegazy, 1998; Coupland *et al.*, 2005). Wium-Andersen and Christensen (1978) observed that species growing in the landward part of a mangrove forest with large seasonal variations in groundwater salinity had a unimodal growth pattern, while species in more frequently flooded areas had a bimodal pattern. Coupland *et al.*, (2005) observed a unimodal leaf growth pattern in *A. marina* trees growing in the highest intertidal area. Apart from studies by Steinke and Charles (1984) in South Africa and Ochieng and Erftemeijer (2002) in Kenya, there is little documentation on the phenology of mangroves in the Western Indian Ocean region, making a comparative study with other regions difficult. However, these were carried out by litter fall studies and not through direct shoot observation. In Australia, the phenology of at least 35 mangrove species has been documented (Duke *et al.*, 1984; Duke, 2006). Documentation of the phenology of mangroves is important if the effects of climate change on these forests are to be well-understood, especially since mangrove forests are faced with the problem of sea level rise due to climate change. Previous phenological

studies conducted at Gazi Bay in Kenya from 1993 to 1994 concentrated on the landward stands of *A. marina* (Ochieng & Erftemeijer, 2002). However, data from this study can be used to compare past and present phenological characteristics of the species. The present study thus set out to investigate the phenology of *A. marina* in landward and seaward mangrove stands. The aim was to establish the existence of similarities or differences in the phenological attributes of *A. marina* in the two zones.

MATERIALS AND METHODS

Study area

The study was conducted at Gazi Bay (4°25'S, 39°30'E) located 50 km south of Mombasa, in the Kwale district (Fig.1). The total area of Gazi embayment is 18 km², with mangrove forests occupying 6.6 km² (Slim *et al.*, 1996).

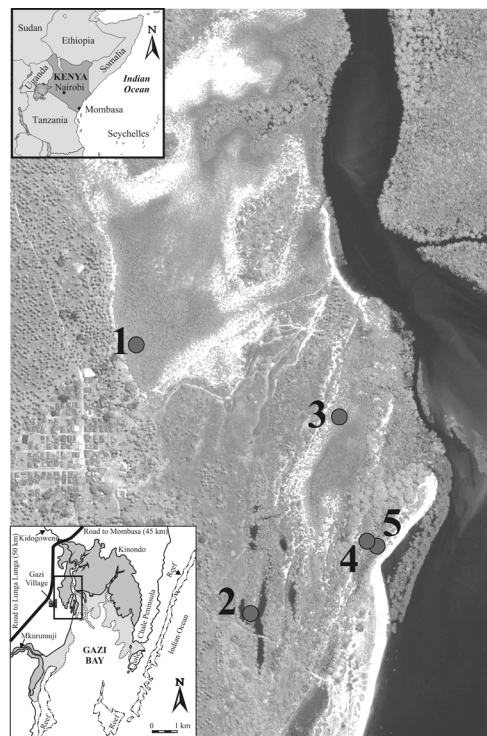


Fig. 1: Map of the Kenyan Coast (top and bottom) showing study sites 1-3 at Gazi Bay, representing the landward *A. marina* sites, while sites 4 and 5 represent the seaward natural and reforested sites respectively. (Modified from Dahdouh-Guebas *et al.*, 2000; Dahdouh-Guebas *et al.*, 2002; Neukermans *et al.*, 2008.)

The climate is influenced by the South-East Monsoon (April–October) and the North-East monsoon (November–March) winds, during which the long rains (April–July) and short rains (October–December) occur respectively. The ten mangrove species found in Kenya occur at Gazi Bay, the dominant species being *A. marina*, *C. tagal* and *R. mucronata* (Dahdouh-Guebas *et al.*, 2002). Mangroves of Gazi are heavily harvested for firewood and building poles leading to their degradation. A programme to rehabilitate degraded mangroves sites in Gazi was initiated in 1990 (Kairo, 1995; Kairo *et al.*, 2001).

Study design

Four natural sites and one reforested monospecific *A. marina* stand were used for the study. Three natural sites were located in the landward zone, whereas two sites (natural and reforested) were located in the seaward zone. The only reforested site used for the study was established in 1993 (Kairo, 1995). A randomly selected 10 m × 10 m plot was established in each of the five mangrove sites. The D_{130} and height of the trees in the plot was measured to establish the stand characteristics of trees with a D_{130} of ≥ 2.5 cm. Basal area and stand densities were derived from these data. Canopy cover was also estimated. Problematic tree architectures were dealt with as suggested by Dahdouh-Guebas and Koedam (2006).

Phenological observations

At each site, fifty four shoots from nine randomly selected trees were marked for easy identification. The shoots were tagged at an accessible height in the crown canopy for phenological shoot observations. Leaves present at the beginning of the study were numbered consecutively on the adaxial surface with a xylene-free permanent marker. Care was taken not to damage the leaves. In subsequent sampling, unnumbered leaves were treated as newly-emerged and were numbered with further consecutive numbers. Numbered leaves that were lost were recorded as leaf fall. Newly-emerged and lost leaves were recorded fortnightly from January 2005 to December 2006. The shoots were carefully monitored for reproductive structures (buds, flowers and fruits) until the mature propagules fell, providing a reproductive phenological record of the species in the respective sites. Data on litter fall were also collected but are not reported here. Climatic data (rainfall and air temperature) were obtained from the Mombasa Meteorological Station; the precipitation in 2005 and 2006 totalled 848 mm and 1581 mm respectively, with mean annual air temperatures respectively of 28.1°C and 30°C (Fig. 2).

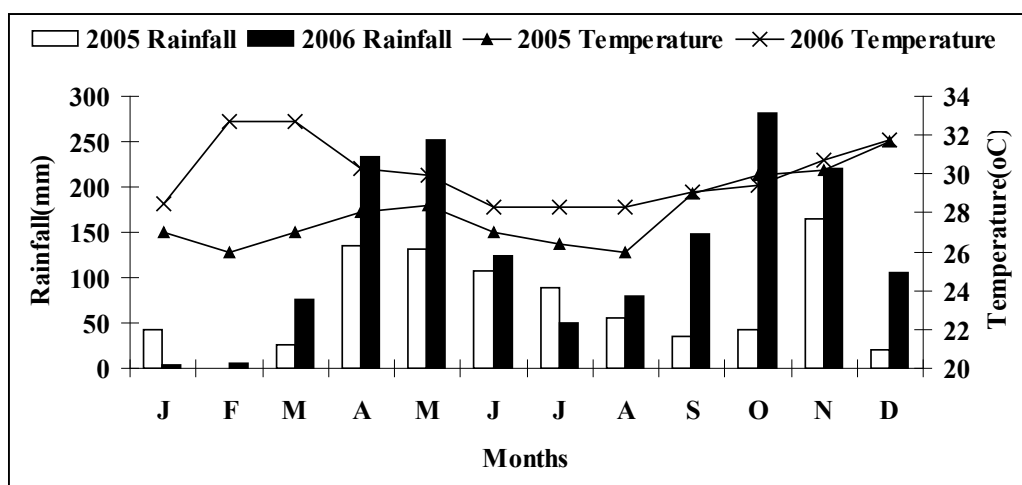


Fig. 2: Monthly rainfall (mm) and mean monthly temperatures (°C) at Mombasa in 2005–2006. April–June comprises the long rain season and October–November the short rain season. (Source: Mombasa Meteorological Station.)

Statistical analysis

All data were analysed using STATISTICA 6.0 software. Monthly, annual and site means were compared using One-way ANOVA and the Kruskal Wallis non-parametric test when the data did not meet parametric assumptions, even after log transformations. Tukey's Honestly Significant Difference (HSD) test and *post hoc* multiple comparisons of means were carried out to establish differences between means.

RESULTS

Stand characteristics

Structural and stand characteristics of *A. marina* in the two zones are presented in Table 1. Landward sites 1, 2 and 3 had shorter trees compared to seaward sites 4 and 5, with trees in site 1 bordering the Gazi village being taller than those at sites 2 and 3. The percentage canopy cover was also lower in the landward than in the seaward sites, with site 1 having a higher canopy cover than sites 2 and 3.

Vegetative phenology

Seasonality in leaf fall

Leaf fall in the landward *A. marina* zone was seasonal and characterised by a unimodal leaf fall pattern in the two years of study (Fig.3). In 2005, the major peak leaf fall occurred between the months of July to September at these sites, whereas in 2006 leaf fall peaks occurred in September to November. The seaward sites displayed a bimodal leaf fall pattern, with peaks in February and September

to December in both years (Fig. 4). Leaf fall was lower in 2006 than 2005 at all *A. marina* sites, especially during the months of March to August.

There was no significant difference in leaf fall between the five sites ($p > 0.05$) or in annual leaf loss within sites. However, significant differences in monthly leaf fall were observed in the year 2006 ($p < 0.05$) between the months of January to July and August to October. Leaf fall peaks generally coincided with the dry months of January-February and July-September. However, 2006 was a wetter year and leaf fall patterns at the seaward sites appeared to be disrupted.

Seasonality in leaf emergence

Leaf emergence in *A. marina* was also seasonal and displayed unimodal and bimodal patterns at the landward and seaward sites respectively. At the former, leaf emergence peaked from March to September in 2005 and September to November in 2006. The seaward sites manifested peaks in leaf flush in February and from July to September in 2005. Leaf emergence at these sites was reduced in 2006, but major peaks occurred from September to November. Little or no leaf emergence was observed during the months of January to May at all sites in 2006. There was a close relationship between leaf emergence and leaf fall, the latter occurring 1-2 months after peak leaf emergence. There was no significant difference in leaf emergence among the sites ($p > 0.05$). Monthly leaf emergence was, however, significantly different at all sites ($p < 0.001$).

Table 1: Structural characteristics (means \pm S.D) of *A. marina* at the five study sites in Gazi Bay. *n* = number of trees in each site with a D_{130} of ≥ 2.5 cm. ns = natural site; rs = reforested site

| Site | <i>n</i> | Mean height | D_{130} (m) | Density (stems/ha ⁻¹) | Basal area (m ² /ha ⁻¹) | Total cover (%) |
|-----------------|----------|-----------------|------------------|--------------------------------------|---|--------------------|
| 1 (Landward ns) | 50 | 4.94 \pm 0.51 | 7.81 \pm 2.81 | 5 000 | 0.28 | 70-80 |
| 2 (landward ns) | 71 | 3.71 \pm 0.68 | 4.4 \pm 1.47 | 7 100 | 0.13 | 40-50 |
| 3 (Landward ns) | 63 | 2.73 \pm 0.52 | 6.28 \pm 1.99 | 6 300 | 0.22 | 40-50 |
| 4 (Seaward ns) | 37 | 6.34 \pm 0.81 | 11.02 \pm 5.14 | 3 700 | 0.44 | 80-90 |
| 5 (Seaward rs) | 41 | 5.1 \pm 0.6 | 7.11 \pm 3.65 | 4 100 | 0.22 | 60-70 |

Table 2: Mean, minimum and maximum longevity (months) of *A. marina* leaves at sites in Gazi Bay. Ns = natural site; rs = reforested site; *n* = number leaves that emerged and fell during the study period.

| Site description | <i>n</i> | Mean±(S.E) | Minimum | Maximum |
|------------------|----------|--------------|---------|---------|
| 1 (Landward ns) | 278 | 11.22 (4.73) | 0.93 | 18.66 |
| 2 (Landward ns) | 292 | 10.56 (3.88) | 1.40 | 16.80 |
| 3 (Landward ns) | 320 | 10.95 (3.67) | 0.46 | 17.73 |
| 4 (Seaward ns) | 124 | 10.63 (4.07) | 1.86 | 18.66 |
| 5 (Seaward rs) | 233 | 9.24 (4.04) | 0.93 | 16.80 |

Trends in reproductive phenology

The timing of the reproduction cycle in *A. marina* was seasonal and its initiation coincided with the short rainy season. Bud initiation started in the month of November at all *A. marina* sites during the study period. Peaks in bud production were observed in December and January at all the sites (Fig. 3 and 4). However, no new buds were produced after February at the landward sites, whereas bud formation was prolonged at the seaward sites until April and March in 2005 and 2006 respectively (Fig.3). Bud production was much lower at all sites in 2005 than in 2006. Bud production also differed significantly among sites ($p<0.001$). Landward site 1 and seaward site 4 differed significantly from landward sites 2 and 3 ($p<0.01$) as they produced the least number of buds.

At the landward sites, flower production commenced in November to March in site 2 and December to March in sites 1 and 3 (Fig. 3). It started later at the seaward sites, from January to March in site 4, and January to May in site 5 (Fig. 4). Flower production was higher in 2006 than in 2005 but lower than bud production at all the sites. There was a significant difference ($p<0.001$) in flower production between sites, with site 4 producing the least flowers and having the shortest flowering period of three months.

Avicennia marina fruits were observed from the months of March to May at the landward sites with a peak in April. At the seaward sites, fruits were observed from March to May in site 5 and July in site 4. There were no significant differences ($p>0.05$) in

fruit production between the sites. Peak fruit production occurred in April and May which coincided with the wet season. It is notable that reproductive activity in 2005 was lower at all sites compared to 2006 and, though bud production was recorded at all the sites in 2005, fruits were only found at the reforested site.

Leaf longevity

Mean leaf longevity in *A. marina* was 11 months (Table 2). There was a significant difference in leaf longevity between the sites ($p<0.001$), with the seaward reforested site manifesting the shortest leaf longevity of 9.24 ± 4.04 months and site 1 the greatest leaf longevity of 11.22 ± 4.73 months

DISCUSSION

Vegetative phenology

Seasonality was observed in *A. marina* leaf production and fall at both the landward and seaward sites but the period of leaf production was longer at the former (January-April) in 2005. Thus the vegetative phenology of landward and seaward *A. marina* varied with respect to the timing and abundance of leaf emergence and fall.

Unimodal and bimodal peaks in mangrove leaf production are known to be associated with forests growing in higher and lower intertidal areas respectively due to fluctuations in ground water salinity (Wium-Andersen, 1981). High interstitial water salinity elevates stress in mangroves, resulting in increased leaf loss to reduce water loss from transpiration, especially during the dry season, thus reducing water

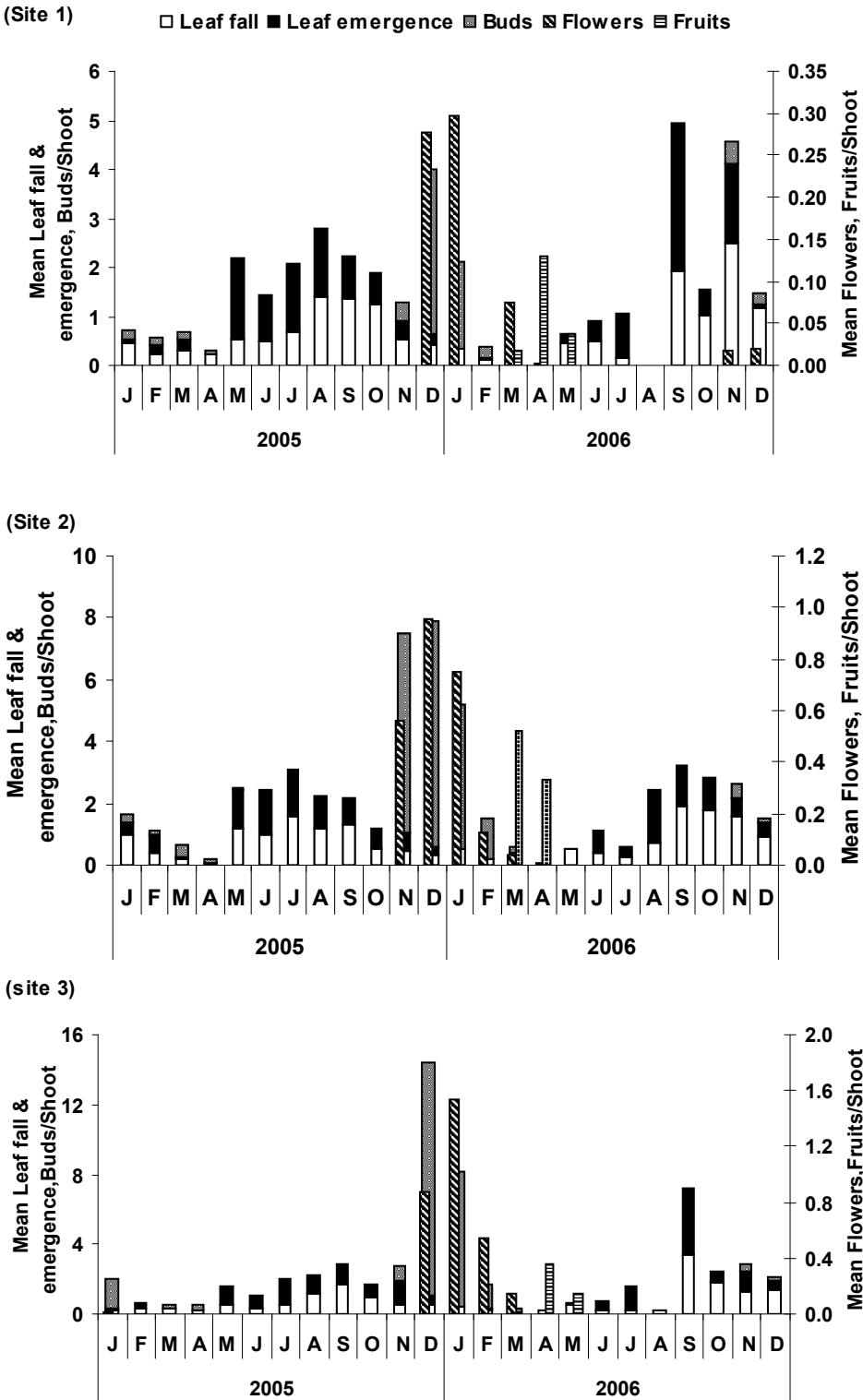
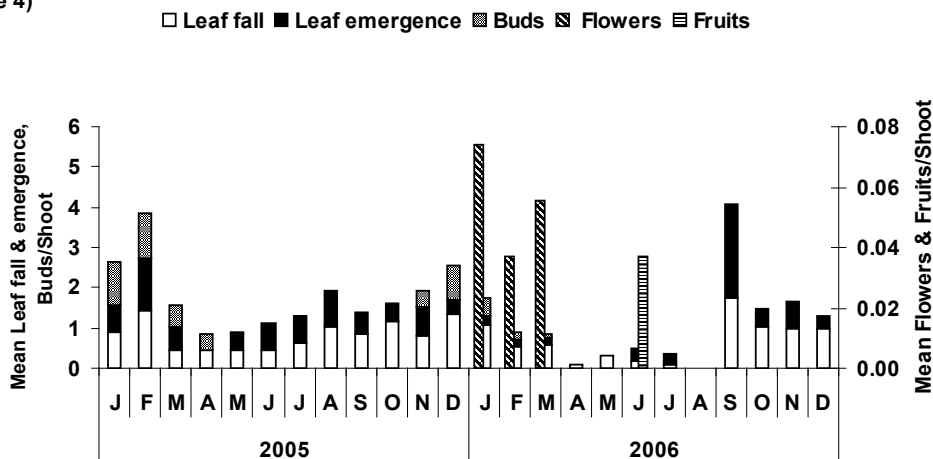


Fig 3: Leaf fall and emergence, production of buds, flowers and fruits in *A. marina* at the landward Sites 1, 2 and 3 in Gazi Bay.

(site 4)



(site 5)

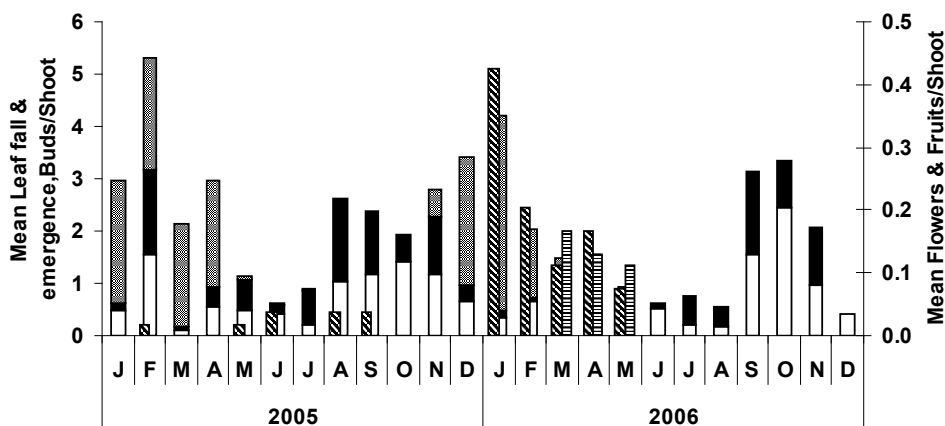


Fig 4: Leaf fall and emergence, production of buds, flowers and fruits in *A. marina* at the seaward Sites 4 and 5 in Gazi Bay.

stress. Increased leaf loss by the landward *A. marina* trees during the dry season is indicative of their adaptive measures to reduce water loss. The lack of clear unimodal and bimodal leaf fall and emergence patterns at both the landward and seaward sites in 2006 compared to 2005 may be attributable to the high and continuous rainfall experienced in that year. This may have lowered the salinity levels of the interstitial water, thus reducing salt stress and changing the leaf fall and emergence patterns.

The lower leaf fall and emergence in 2006 may also be related to the reproductive status of the trees at that time. There possibly was a link between vegetative production and the reproductive cycle in that there was very

little vegetative activity while the trees were flowering and fruiting, and leaf production and fall only resumed in June after completion of fruit fall. In 2005 there was little or no reproductive activity and it was associated with higher leaf fall and emergence. These results are corroborated by other studies (Duke *et al.*, 1984; Wium-Andersen and Christensen, 1978; Coupland *et al.*, 2005).

Increased leaf production by *A. marina* has been reported during the wet season in Darwin Harbour in Australia (Coupland *et al.*, 2005). Ochieng and Erftemeijer (2002) reported unimodal leaf flush patterns in landward *A. marina* at Gazi in June to July (wet season) in 1993-1994. In the present study,

similar observations were made between July and September, which is normally a dry season, indicating the likelihood of a shift in phenological trends in species with respect to the prevailing climatic conditions. Peak leaf fall occurred one to two months after peak leaf emergence at all the sites, corresponding with findings on *A. marina* in Australia (Duke, 1988). Shifting of leaf fall and emergence peaks to later months, especially in 2006, indicates that the phenological patterns are not static and may be influenced by changing climatic factors; this is evidenced by the different rainfall and air temperatures during the two years of study. However, long-term phenological studies are necessary to draw conclusions regarding the effects of climate change on mangrove phenology.

The leaf longevity in *A. marina* observed in this study corresponded with that reported for the same species at Gazi Bay (Ochieng & Erftemeijer, 2002). It is close to the 14 months reported for the same species in Australia (Coupland *et al.*, 2005). Significant differences in leaf longevities at the landward and seaward sites may be indicative of a response to stress brought about by differences in ground water salinity resulting from differences in inundation. The seaward reforested and natural sites in this study manifested reduced leaf lifespan. Frequent inundation of the seaward sites results in less stress, hence possibly a higher leaf turnover. The seaward reforested site 4 comprised a young stand (12 yrs old) that may have been actively growing, causing a similar reduction in leaf longevity.

Reproductive phenology

The synchronised initiation of budding at all sites may be indicative of the adaptability *A. marina* in the two zones. However, earlier flowering of trees in the landward zone than those in the seaward zones was indicative of a lack of uniformity in phenological trends in this species, even within the same locality. Prolonged flowering at the seaward sites may have resulted from more favourable environmental factors compared to the landward sites. Flowering peaked during the

dry months which corroborates the results of other studies (Duke *et al.*, 1984; Fernandes 1999; Ochieng & Erftemeijer, 2002). *Avicennia marina* in Gazi Bay (4° 25'S, 39° 3' E) was nevertheless observed to flower later than in Darwin Harbour (12° 26'S, 130° 51' E) (Coupland *et al.*, 2005).

Significant differences in bud and flower production between the sites can be related to stand structure and tree height. *Avicennia marina* trees at sites 2 and 3 were short and stunted and had a lower canopy cover, thus allowing more light penetration due to less shading. Sites 1, 4 and 5 conversely had taller trees and higher canopy cover. This may explain why a greater production of buds and flowers was recorded at sites 2 and 3.

Timing of fruit production in the two zones was uniform; however, fruits at the seaward site 4 persisted up to June. Fruit fall in the two zones coincided with the wet season, consistent with findings in other studies (Duke *et al.*, 1984; Fernandes, 1999; Ochieng & Erftemeijer, 2002; Coupland *et al.*, 2005). The reproductive cycle of *A. marina* from bud initiation to fruit fall was observed to last 6-7 months in the landward zone and 7-8 months in the seaward zone. Other studies have reported varying reproductive cycles at different latitudes, e.g. five months in Darwin Harbour (Coupland *et al.*, 2005), six months in southern Thailand (Wium-Andersen & Christensen, 1978) and one year in south-eastern Australia (Clarke & Myerscough, 1991). Zonation may have had an influence in fruiting of *A. marina* since sites that were frequently inundated (seaward) supported prolonged budding and fruiting relative to those that were less inundated (landward sites).

The relationship between vegetative and reproductive cycles cannot be ignored in this study as reproductive months were associated with very little vegetative activity, both in terms of leaf production and fall. Leaf production peaked prior to bud initiation and again later after fruit fall in May. This corroborates the work of Duke (1990) who found a link in the timing of leaf appearance and leaf fall with inflorescence development. This has been attributed to resource partitioning within plants

(Duke *et al.*, 1984), as evident in *S. alba* and *A. marina* (Coupland *et al.*, 2005) as well as *C. tagal*, *Lumnitzera littorea* and *A. marina* (Wium-Andersen & Christensen, 1978).

This study has thus shown that the vegetative and reproductive phenology of *A. marina* at Gazi Bay is clearly seasonal, evidenced by peaks in the various phenophases. However, vegetative peaks appeared not to be restricted to certain months since there were some shifts in peaks in separate years, suggesting a response triggered by environmental factors.

Earlier studies indicated significant differences in vegetation structure, physiognomy, root development and leaf morphology in trees in different zones which could be attributed to differences in salinity and the frequency of tidal inundation (Dahdouh-Guebas *et al.*, 2004, 2007). This study revealed differences in *A. marina* leaf growth patterns between the landward and seaward zones studied. The timing and duration of the reproductive phenology of *A. marina* also varied in the two zones. This may be indicative of variations and adaptive responses in this species to prevailing environmental conditions in these zones.

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