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## Vegetative and reproductive phenological traits of *Rhizophora mucronata* Lamk. and *Sonneratia alba* Sm.



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### ABSTRACT

Mangrove phenology is important in understanding the past, present and future response of mangrove species to impacts of climate change. Our study is the first long term direct observation of the phenology of *Rhizophora mucronata* and *Sonneratia alba* in Kenya. Objective of the study was to determine, interpret and document the timing of the various phenoevents and phenophases, and to establish relationships between phenology and the climatic variables. Phenological traits were investigated in six monospecific mangrove stands in Gazi Bay, south of Mombasa, for 2 years. Leaf emergence, leaf fall, flower bud, flower and fruit initiation data were recorded every fortnight in 54 shoots of 9 trees at each site. Continuous leaf emergence and loss characterized by multimodal peaks was observed for the two species. Leaf emergence and leaf fall peaked in the wet months and was reduced in the dry months. There was a relationship between the leaf emergence and drop with the reproductive phenology in the two species. Mean leaf longevity for *R. mucronata* and *S. alba* was  $12.8 \pm 1.2$  and  $4.9 \pm 0.5$  months respectively. The reproductive cycle took approximately 16–20 months in *R. mucronata* and 4–5 months in *S. alba*. Bud initiation in *R. mucronata* was seasonal and occurred in October and September. Buds were observed for 8–11 months developing slowly on the shoots. Shifts were observed in the timing of flower initiation, and the flowering period lasted in total for 4–5 months. The time period from flower appearance to the developmental start of immature propagules lasted about 1 month at reforested sites and up to 5 months in stands of natural vegetation. In *R. mucronata* initiation of immature propagules was not seasonal and varied among the sites. Fruiting in *S. alba* was short and seasonal without overlap, and shifts were observed in the timing of flowering, flowering and fruiting peaks. Abscission of reproductive parts started in July and in June, respectively, in the years 2005 and 2006. Fruiting was observed starting in August in both years, and fruiting peak was reached in October in 2005 and one month earlier in 2006. In *R. mucronata* vegetative and reproductive phenophases significantly correlated with climatic variables, whereas in *S. alba* only leaf emergence and leaf fall correlated with temperature. The flowering plasticity in the reproductive phenology of the two species indicates possible sensitivity to certain climatic and environmental triggers. Our results also indicate that *R. mucronata* trees have a distinctly higher investment in the reproductive cycle than *S. alba*.

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### Introduction

Mangrove forests belong to the most productive ecosystems and are a source of energy in the marine detritus food chain (Donato et al., 2011; Field, 1995; Snedaker, 1978). They provide habitats for the marine and terrestrial fauna (Nagelkerken et al., 2008), play a role in the mangrove food web and influence positively near-shore fisheries (Lee, 1998; Nagelkerken et al., 2008). Phenology is the study of seasonal timing of life cycle events (Rathcke and Lacey, 1985) of plants and animals. In mangroves such life cycles refer

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to periods of intense leaf emergence and fall, of flowering and fruiting (Duke, 1990). Phenology is often an overlooked aspect of plant ecology, from the scale of individual species to whole ecosystems (Cleland et al., 2007). Phenological studies involve observation, recording and interpretation of the timing of life history events of plants (Fenner, 1998). They are important in the understanding of mangrove ecology, productivity and contribution to near shore environment (Duke, 1990). Phenological patterns are closely related to climate, and anticipated global climate change is expected to affect phenological growth patterns and timing of flowering and fruiting of plants, also of mangrove taxa (Ellison, 2000; Field, 1995).

Data of the present study shall contribute to quantification and understanding of the extent of phenological changes and effects of mangroves in case of climate changes. Respective knowledge across latitudes is necessary for comparative purposes across extended distribution areas, as it is the case with pan-tropically distributed mangrove species (Duke et al., 1984).

In the Western Indian Ocean region numerous studies have been carried out on other aspects of mangroves, but detailed phenological data are scarce (Steinke and Charles, 1984; Steinke and Rajh, 1995; Steinke, 1988). Also in Gazi Bay, Kenya, mangroves were studied, e.g. about structural developments and productivity (Kairo et al., 2008), mangrove wood anatomy (Schmitz et al., 2007), and secondary succession and nutrient dynamics (Bosire et al., 2004, 2005). Studies exist also about the phenology of *Avicennia marina* (Forssk.) Vierh. at Gazi Bay (Ochieng and Erfertemeijer, 2002; Wang'ondu et al., 2010). However, no study has focused in detail on the vegetative and reproductive phenological patterns of the other two important mangrove taxa there, *Rhizophora mucronata* Lam. and *Sonneratia alba* Griff.

*Rhizophora mucronata* is very important locally as a source of wood and non-wood products to the local community (Dahdouh-Guebas et al., 2000; Kairo et al., 2009). *Rhizophora mucronata* and *Sonneratia alba* are seaward growing species at the coasts and must be expected to be on the first line of experiencing the effects of global climate change, especially due to sea level rise (Di Nitto et al., 2008). The latter species is also experiencing insect infestation by two species, a beetle (*Bottergia rubra* Aurivillius 1922) and a moth (*Salagena obsolescens* Hampson 1910) which have been associated with damage to the trees affecting their growth, and may even cause death to the entire *S. alba* forest. Their unique socio-economic and ecological significance made the two species to be of choice for this study. It is the first to report on the phenology of the two species through direct long-term observations of tagged shoots. Leaf growth and senescence can also be characterized by litter fall studies (Duke, 1988, 1990). However, litter fall studies do not indicate the actual timing of the various phenoevents due to the time lag between initiation and the time the leaves, buds, flowers and propagules falls into the traps. The phenological data on these mangroves will contribute to the understanding on their response to climate and will have relevance for mangrove forest management.

The objectives of this study were to (1) investigate, interpret and document the phenology of the two principal mangrove species in Gazi Bay, Kenya; (2) determine the timing of the phenoevents and phenophases; (3) establish the relationship between the phenology of the two species with climatic variables.

## Materials and methods

### Study area and study sites

The study was conducted in Gazi Bay, Kenya (4°25' S, 39°30' E), located 50 km from Mombasa in the Kenyan Southern coast (Fig. 1). Total embayment of the area is 18 km<sup>2</sup>, with a mangrove

area of 6.6 km<sup>2</sup> (Slim et al., 1996). The climate is influenced by two monsoon winds, the South-East Monsoon (April–October) and the North-East monsoon (November–March) which brings about a bimodal pattern of rainfall with a long (April–July) and a short period of rains (October–December). All 9 East African mangrove species are present in Gazi Bay, of which *R. mucronata* is the dominant species followed by *Ceriops tagal* C.B. Robinson and *A. marina*, respectively. Mangroves of Gazi are threatened by over-harvesting of wood products for firewood and building poles (Abuodha and Kairo, 2001). Efforts to rehabilitate the degraded mangrove areas were initiated in 1991 (Kairo, 1995).

The study was carried out in six monospecific *R. mucronata* and *S. alba* stands of which two were reforested stands of each species, while the rest were natural. The *R. mucronata* reforested stands were 5 years (yrs) and 12 yrs old at the start of this study whereas the *S. alba* stands were 11 yrs and 13 yrs. Observations on the 11 yrs old *S. alba* site was discontinued in May of 2006 as the trees in the site were dying due to sedimentation and silting up, a process which had not started at the time the study was initiated. Total annual rainfall and mean annual air temperature data for Mombasa from 1990 to 2006 are shown in Fig. 2a. Total annual rainfall at the time of the study was 848 mm and 1580 mm in 2005 and 2006 respectively. The year 2006 received more rainfall than normal. The mean annual temperature was 28.1 °C and 30 °C for 2005 and 2006, respectively. Mean annual humidity for the period was 62.4% and 63.4%, respectively (Fig. 2b).

### Phenological shoot observations

In each stand a 10 m × 10 m study plot was established. The diameter at breast height ( $D_{130}$ ) of the trees was measured. Trees with a  $D_{130}$  of  $\geq 2.5$  cm were used for the phenological shoot observations. Six shoots in nine randomly sampled trees ( $n=54$  shoots) distributed in the crown canopy but within reach were marked for easy identification in each plot. The shoots were tagged and leaves numbered consecutively on the adaxial surface with a xylene free permanent marker. Data were recorded fortnightly from January 2005 to December 2006. Any unnumbered young leaves on these shoots were treated as newly emerged and were numbered with the numbering pattern of the shoot. Loss of a numbered leaf was considered as leaf fall. The data were used to quantify leaf emergence and leaf fall and to determine the timing and seasonality of the two phenoevents. The same shoots were carefully followed for emergence of reproductive structures (flower buds, flowers and fruits) until mature propagules fell. This data gave the timing, the seasonality of the reproductive phenoevents, and the duration of the phenophases of the two species. In this study mature fruiting structures of *R. mucronata* and *S. alba* are referred to as propagules and fruits, respectively. There were no reproductive structures observed on the studied shoots of *S. alba*. Reports on the reproductive phenology of this species are from litter fall studies we carried out concurrently with this study.

### Statistical analysis

All data were analyzed using STATISTICA (Statsoft, Tulsa, USA) package. ANOVA and Kruskal–Wallis ANOVA were used to determine annual and site differences between means of phenological components. Spearman Rank Order Correlation was used to establish any correlation between phenological traits with total monthly rainfall, mean air temperature and mean relative humidity.

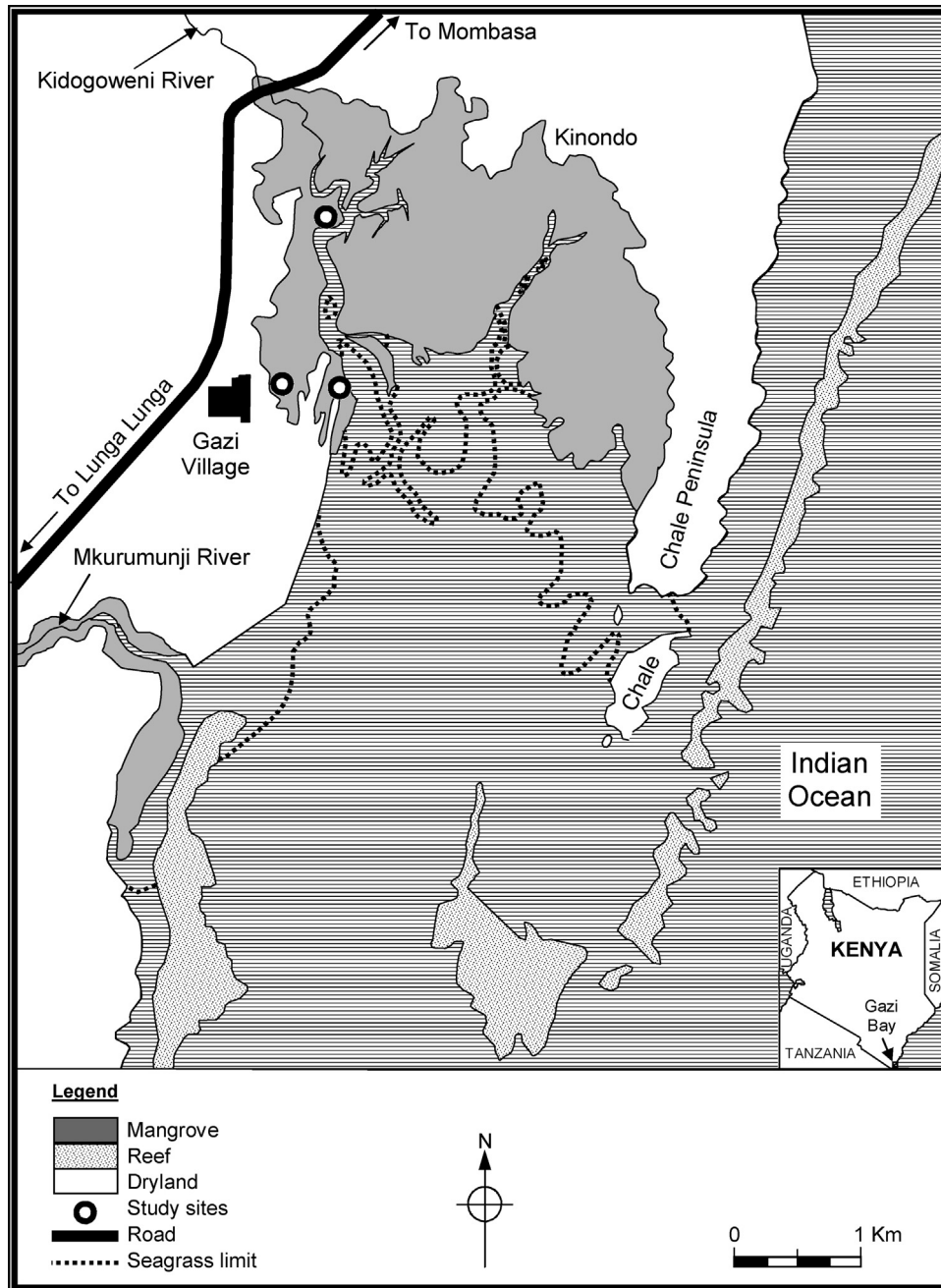


Fig. 1. Map of the Kenyan Coast showing the study area of Gazi Bay. The study sites are indicated in black circles. (Modified from Dahdouh-Guebas et al., 2002; Bosire et al., 2004).

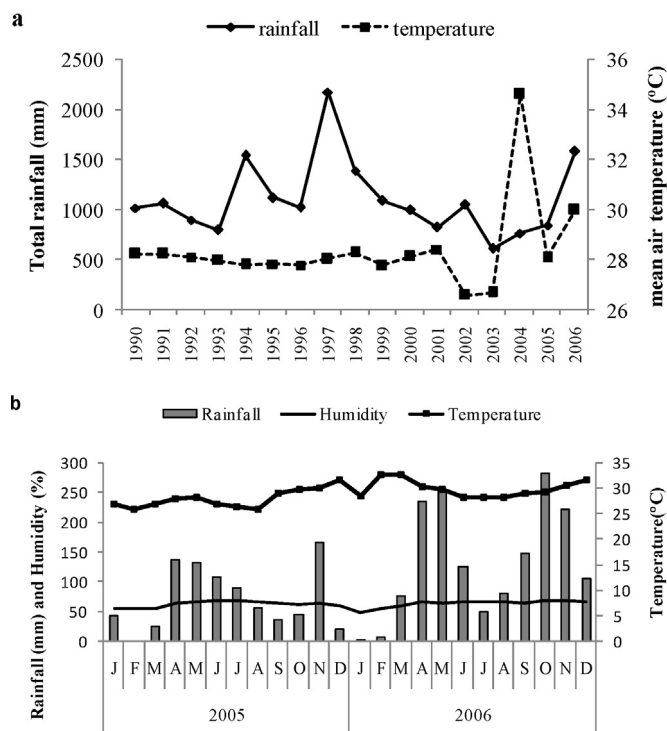
## Results

### Vegetative phenology

Leaf emergence and leaf fall in *R. mucronata* were observed to be continuous, occurring throughout the year, and are characterized by multimodal peaks (Fig. 3). Peaks in leaf emergence and leaf fall in *R. mucronata* were not consistent among sites and year. The highest peak in leaf emergence in the youngest site was observed in May of 2005 and 2006 and that of leaf fall in October. In the 12 yr old site, peak leaf emergence was observed February, May and December in 2005 and January, May and October in 2006. Leaf fall peaked there in April and November in 2005 and January and October in 2006. In the natural site leaf emergence occurred in February, April and November in 2005 and in January, May and

December in 2006. Leaf fall was observed in May and December in 2005 and in May and November in 2006. Despite the multimodal and staggered peaks, leaf emergence and leaf fall were observed to peak during the wet season and at a reduced rate in the dry season in *R. mucronata*. A relationship between leaf emergence, leaf fall and reproductive phenology could be observed in this species. Leaf emergence increased during the budding and flowering period in all the sites, whereas leaf fall increased prior to the budding period. Leaf emergence and fall was significantly higher in the youngest *R. mucronata* site (Table 1). Annual leaf emergence and leaf fall was not significantly different between the sites. There was no significant correlation between leaf emergence and leaf fall in *R. mucronata*.

In *Sonneratia alba* leaf emergence and fall were also observed to be continuous, with leaf growth and leaf death occurring throughout the year (Fig. 4) in all the sites. Though multimodal peaks were



**Fig. 2.** (a) Rainfall and temperature for Mombasa from the year 1990 to 2006; (b) rainfall, temperature and relative humidity for Mombasa during the study period. (Source, Kenya Meteorological Department, Mombasa).

observed in leaf emergence and leaf fall in the sites, peaks could be observed in both the dry and wet seasons. In the 11 yr old site peaks in leaf emergence occurred in February, May and December in 2005 and in May and November in 2006. Peaks in leaf fall were registered in January, May and December in the two years. In the 13 yr old site leaf emergence peaked in February and November in 2005 and February in 2006. Peak leaf fall occurred in January, July and December in 2005 and March in 2006. In the natural site peak leaf emergence was observed in May and December in 2005 and in May and November in 2006. Leaf fall peaked there in May and December in 2005 and May and October in 2006. No significant difference among sites was found for *R. mucronata* (Table 2). However, there was a significant difference in annual leaf emergence

( $H_{1,65} = 5.24$ ;  $p < 0.05$ ) and leaf fall ( $H_{1,65} = 10.37$ ;  $p < 0.01$ ) and both were higher in 2006 than in 2005. A relationship between leaf traits and the reproductive phenology was also observed in *S. alba* with leaf growth and death increasing in intensity during the initiation of the reproductive period and decreasing towards the end of mature fruit production. There was a significant correlation between leaf emergence and leaf fall in all the *S. alba* sites.

Leaf longevity estimates for the two species varied, with *R. mucronata* leaves having a longer life span than *S. alba* (Table 3). The overall mean leaf longevity was  $12.8 \pm 1.2$  months for *R. mucronata* and  $4.9 \pm 0.6$  months for *S. alba*. The 13 yr old *S. alba* site which was experiencing siltation had the shortest leaf longevity of  $4.4 \pm 1.5$  months, based on the data sampled during the observation period. The minimum and maximum leaf longevity was more extreme in *R. mucronata*, with 1.9 months and 20.5 months, respectively.

**Reproductive phenology**

Timing of the initiation of flower buds and flowers in *R. mucronata* was observed to be clearly seasonal (Fig. 3) with the timing of the phenoevents repeated in the following year. Flowering was also seasonal but timing of the initiation shifted to earlier months in 2006. Flower bud initiation in the two years was observed to start in September in the youngest site, where flower initiation started in April of 2005 and in March of 2006. In this site buds were observed on the shoots for 11 months and flowers for 3 months in 2005 and 4 months in 2006. During the two years of study in the 12 yr old site, bud initiation started in October whereas flowering was observed to start in April and March in 2005 and 2006, respectively. Presence of buds on the shoots was observed for 8 months and flowering for 3 and 4 months in 2005 and 2006, respectively. At the natural site, buds were initiated in September and flowers in April and March in 2005 and 2006, respectively. Buds were observed on the shoots for 11 months and flowers for 5 months in the two years. The flowering period was observed to vary in the two years in the reforested sites occurring for 3 months in 2005 and 4 months in 2006. It had a constant duration in the natural site, lasting for 5 months. There was no distinct peak in flowering of *R. mucronata* although the intensity increased somewhat in April and May. Flowers lasted on the shoots for only one month after initiation. The percentage of flowering shoots varied among sites and was highest in the youngest site, followed by the 12 yr old and natural site respectively (Table 4). Flower initiation in

**Table 1**  
Mean counts/shoot of leaf emergence, leaf fall, buds, flowers and propagules for *Rhizophora mucronata* ( $\pm$ sd).

Species/site	Leaf emergence	Leaf fall	Buds	Flowers	Propagules
<i>R. mucronata</i>					
5 yrs	1.16 (0.57) <sup>a</sup>	1.05 (0.72) <sup>a</sup>	1.55 (1.56) <sup>a</sup>	0.08 (0.12) <sup>a</sup>	0.02 (0.02) <sup>a</sup>
12 yrs	0.56 (0.28) <sup>b</sup>	0.60 (0.44) <sup>b</sup>	0.42 (0.34) <sup>a</sup>	0.03 (0.06) <sup>a</sup>	0.01 (0.01) <sup>a</sup>
Natural	0.50 (0.25) <sup>b</sup>	0.62 (0.42) <sup>a</sup>	0.33 (0.33) <sup>b</sup>	0.03 (0.05) <sup>a</sup>	0.00 (0.01) <sup>a</sup>
H	24.28 <sup>***</sup>	7.15 <sup>*</sup>	8.21 <sup>**</sup>	1.04 <sup>ns</sup>	5.11 <sup>ns</sup>

Means with identical letters are not significantly different from each other within the components. Kruskal–Wallis ANOVA (df = 2, N = 72). ns; not significant ( $p > 0.05$ ).

<sup>\*</sup>  $p < 0.05$ .  
<sup>\*\*</sup>  $p < 0.01$ .  
<sup>\*\*\*</sup>  $p < 0.001$

**Table 2**  
Mean counts/shoot of leaf emergence and leaf fall for *Sonneratia alba* sites ( $\pm$ sd).

Site	Leaf emergence	Leaf fall	Correlation (r)
11 yrs	0.73 (0.68) <sup>a</sup>	1.05 (0.59) <sup>a</sup>	0.79
13 yrs	0.84 (0.76) <sup>a</sup>	1.19 (0.73) <sup>a</sup>	0.83
Natural	0.73 (0.51) <sup>a</sup>	1.04 (0.39) <sup>a</sup>	0.68

Means with identical letters are not significantly different from each other within component. Kruskal–Wallis ANOVA; leaf emergence ( $H_{2,65} = 0.3$ ;  $p > 0.05$ ); leaf fall ( $H_{2,65} = 0.13$ ;  $p > 0.05$ ); Correlation between leaf emergence and leaf fall; r is significant at  $p < 0.05$ .

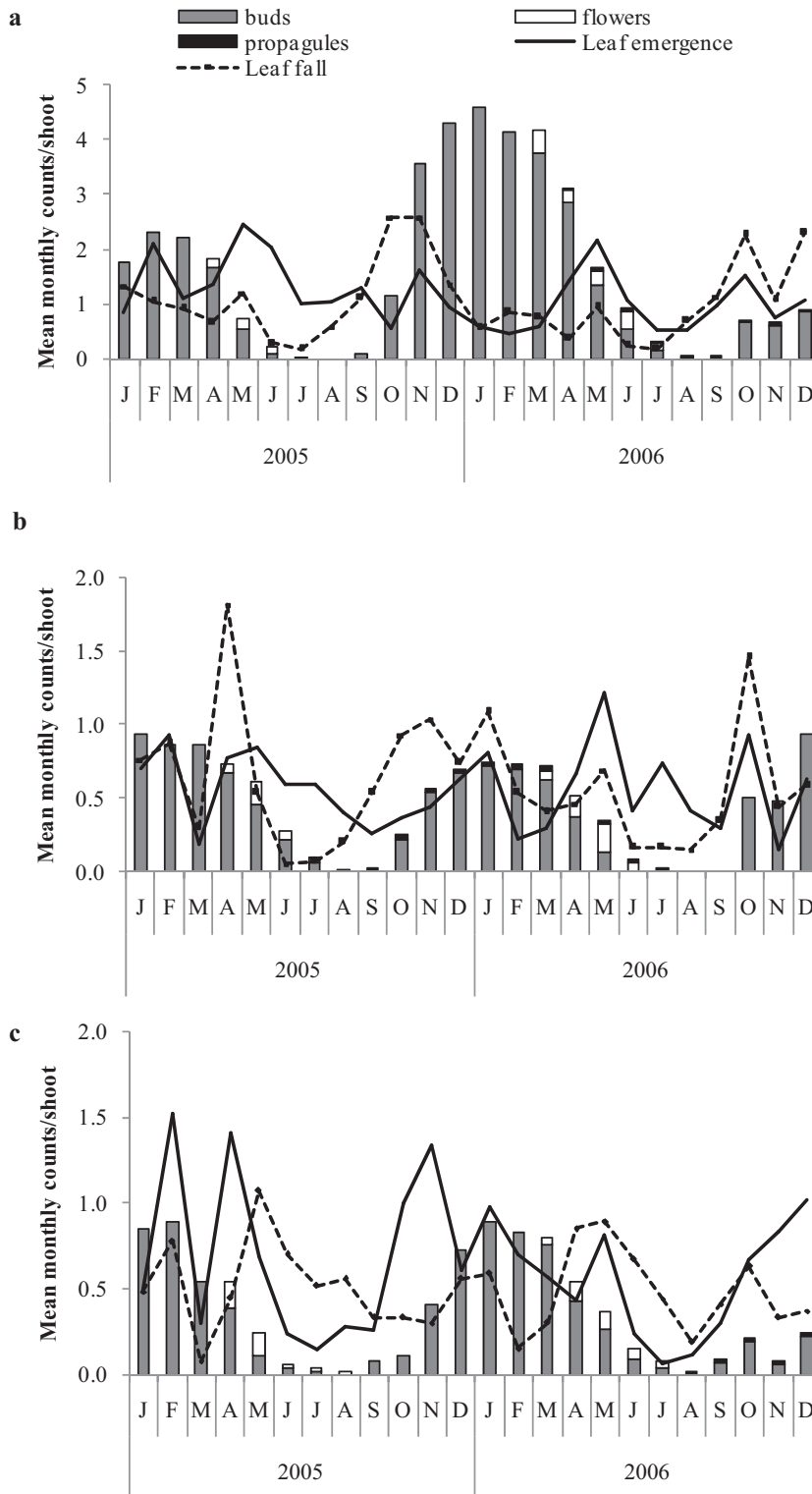
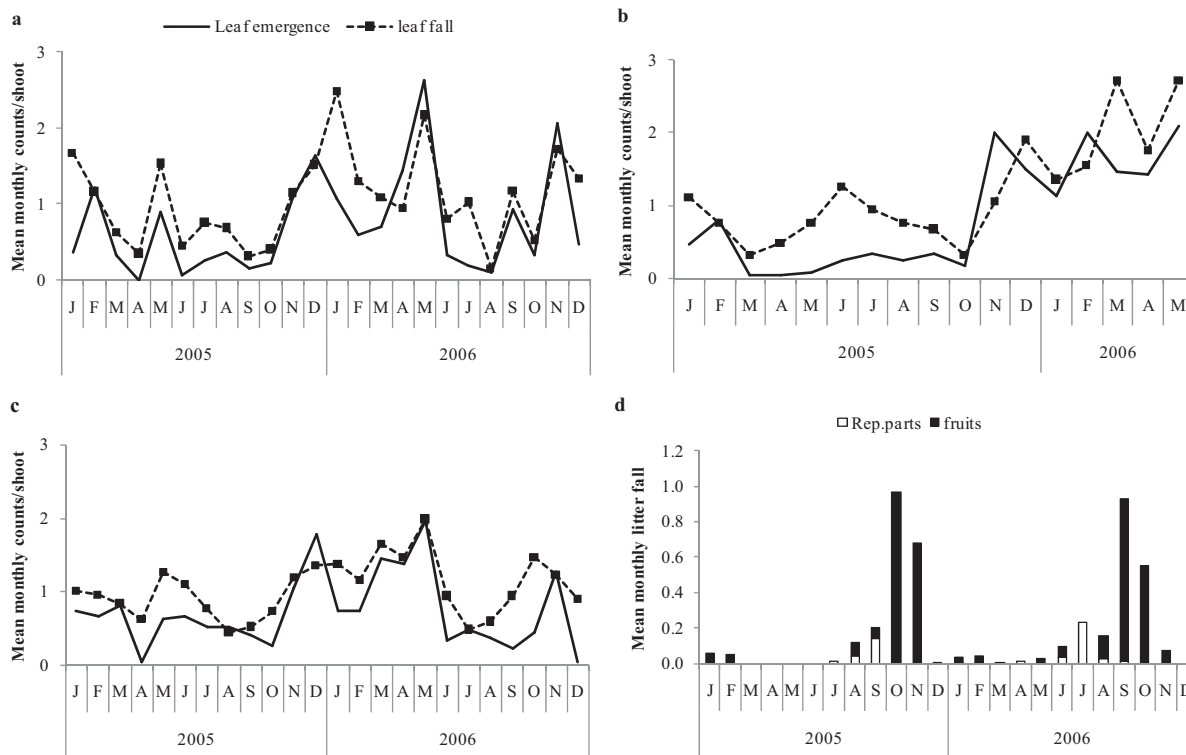


Fig. 3. Mean monthly counts/shoot of leaf emergence and fall, buds, flowers and propagules for *Rhizophora mucronata* sites (a) 5 yrs, (b) 12 yrs and (c) natural.

the shoots decreased or increased in the following year depending on the flowering intensity in the previous year.

Development of immature propagules was reduced in comparison with bud development in all the *R. mucronata* sites. Initiation of immature propagules was observed to vary among sites and was not clearly seasonal. In the youngest site immature propagule initiation did not take place in 2005 in the studied shoots and in 2006

occurred in April, one month after flower initiation. In the 12 yr old site it was observed in September and March in 2005 and 2006, respectively, one month after flower initiation. In the natural site it was observed only in August of 2006 and occurred 5 months after flower initiation. Two propagules, measuring 44.8 cm and 41.4 cm, in the 5 yr old site had not yet abscised by end of the study, having lasted 9 months on the shoots. Overlap of reproductive cycles



**Fig. 4.** Mean monthly counts per shoot of leaf emergence and fall for *Sonneratia alba* sites (a) 11 yrs, (b) 13 yrs, (c) natural forest and (d) mean monthly litter fall ( $\text{g m}^{-2} \text{day}^{-1}$ ) of reproductive parts (buds and flowers) and fruits in the natural site.

**Table 3**  
Mean leaf longevity in months for *Rhizophora mucronata* and *Sonneratia alba* ( $\pm$ sd).

Species	Site	n	Mean	Minimum	Maximum
<i>Sonneratia alba</i>	11 yr	306	4.7 (1.3)	1.40	11.67
	13 yr	119	4.4 (1.5)	1.40	9.80
	Natural	558	5.6 (1.4)	1.87	14.00
<i>Rhizophora mucronata</i>	5 yr	205	11.8 (3.8)	4.20	20.07
	12 yr	127	14.2 (4.2)	2.80	20.06
	Natural	139	12.5 (7.1)	1.87	20.5

was observed and new flower buds were initiated in the same shoots before propagule fall. Though the mature propagules had not fallen by the end of the study, the whole reproduction cycle for *R. mucronata* was estimated to take 16–20 months from bud initiation to mature propagule fall.

The flowering and fruiting phenology of *S. alba* was observed to be short and clearly seasonal, with no overlap (Fig. 4). Similar to *R. mucronata*, also in *S. alba* shifts were observed in the timing of the start of flower fall and in peaks in flowering and fruiting. A start in the fall of reproductive parts (buds and flowers) was observed in July of 2005 and shifted to June in 2006. Fall of fruits started in August in the two years. Peaks in flowering occurred in September and July and fruiting in October and September in 2005 and 2006, respectively. The reproductive period in *S. alba* was estimated to take 5–6 months. However, smaller amounts of mature fruits were observed in January and February in the two years of study.

**Table 4**  
Shoot flowering percentage (%) in year 2005 and 2006 ( $\pm$ sd).

Site	n	2005	2006	Mean
5 yr	54	25 (46.3)	13 (24.1)	19 (35.2)
12 yr	54	9 (16.6)	18 (33.3)	13.5 (24.95)
Natural	54	10 (18.51)	5 (9.26)	7.5 (13.86)

### Correlation with climatic variables

In the reforested stands leaf emergence and fall in *R. mucronata* significantly correlated with mean monthly air temperature, total monthly rainfall and mean monthly relative humidity (Table 5). However, there was no significant correlation of leaf emergence and leaf fall with the climatic variables in the natural stand. Reproductive structures of *R. mucronata* significantly correlated with the climatic variables; flower buds with temperature and humidity, open flowers with rainfall, and propagules with all the variables. In *S. alba* leaf emergence and fall significantly correlated with temperature (Table 6). There was no significant correlation between the phenology of reproductive structures of *S. alba* with climatic variables.

### Discussion

#### Vegetative phenology

We observed continuous leaf growth throughout the year for *R. mucronata* and *S.alba*. This has been reported for *R. mucronata* also in southern Thailand (Wium-Andersen, 1981), for *R. mangle* in Brazil (Mehlig, 2006), for Rhizophoraceae in general (Sharma and Kamruzzaman, 2012; Wium-Andersen and Christensen, 1978)

**Table 5**  
Correlation of vegetative and reproductive components of *Rhizophora mucronata* sites with climatic variables. Spearman Rank Order Correlations; (*r* values are significant at  $p < 0.05$ . (–) not significant.

Site	Climatic variable	Leaf emergence	Leaf fall	Buds	Flowers	Propagules
5 yrs	Rainfall	0.44	–	–	0.41	0.58
	Temperature	–	0.44	0.48	–	–
	Humidity	–	–	–0.64	–	0.50
12 yrs	Rainfall	–	–	–	0.49	–
	Temperature	–	–	–	–	0.45
	Humidity	–	–0.41	–0.43	–	0.46
Natural	Rainfall	–	–	–	0.42	0.41
	Temperature	–	–	–	–	–
	Humidity	–	–	–0.75	–	0.48

and other tropical coastal woody species (Wanderley de Medeiros et al., 2007). The continuous leaf emergence and fall of *R. mucronata* was characterized by multimodal peaks in all the sites. However, peaks of leaf growth and drop were obvious during the wet season and were reduced in the dry season. Leaf growth and death rates in both seasons corroborate other findings for *Rhizophora* spp. (Christensen and Wium-Andersen, 1977; Coupland et al., 2005; Wium-Andersen, 1981) and coastal woody vegetation (Wanderley de Medeiros et al., 2007). Duke et al. (1984) reported leaf growth for *R. apiculata* Blume., *R. stylosa* Griff., *C. tagal* and *Brughiera gymnorhiza* (L.) during and after the wet months. Unimodal leaf flush has been reported for *S. alba* in northern Australia (Coupland et al., 2005). Unimodal and bimodal leaf growth peaks have been suggested for species growing in irregularly and regularly inundated areas respectively (Wium-Andersen and Christensen, 1978). Duke (1990) suggested multimodal peaks to occur in many species particularly in the tropics.

Leaf longevity was different among the two species, with *R. mucronata* leaves having the longest lifespan. Varying leaf longevities have been reported for *R. mucronata* – 10 months (Wium-Andersen, 1981); 18 months (Christensen and Wium-Andersen, 1977); 1 year for *R. mangle* (Mehlig, 2006); 11 months and 13.9 months for *R. stylosa* (Coupland et al., 2005; Sharma and Kamruzzaman, 2012). Leaf longevities of 17.2 and 12.1 months were reported for *B. gymnorhiza* and *Kandelia obovata* (S. L.) Yong, respectively (Sharma and Kamruzzaman, 2012). Our observation on leaf longevity for *S. alba* is close to that observed for the species of  $4.6 \pm 0.1$  months in northern Australia (Coupland et al., 2005). Leaf longevity is thought to be a compromise between leaf retention and leaf abscission where the former aims at maximizing investment on biomass that goes into the construction of the appendage (Tomlinson, 1986). There is a likelihood that this tree species heavily invests into the biomass of shoot axes, so that longer leaf longevities will be favourable for adequate synthesis of photosynthates to be invested into such structures. The mangrove species *R. mucronata*, *Heritiera littoralis* Dryand, *B. gymnorhiza* and *C. tagal* are reported to have strong, attractive and durable wood, used for firewood, charcoal, poles for boats and housing (Abuodha and Kairo, 2001), which quality conforms with such an allocation pattern of *R. mucronata*. This is not as drastically the case with *S. alba*,

where mean leaf longevity does not exceed 4–5 months. In addition, longer leaf longevities of *R. mucronata* can be related to the need by this species to support a large number of reproductive structures, in addition to prolonged and overlapping reproductive cycles. A shorter and non-overlapping reproductive cycle was observed for *S. alba*. Leaf lifespan of 2–3 yrs and even 3–4 yrs have been reported for *B. gymnorhiza* and *C. tagal*, respectively, in north-eastern Australia (Duke et al., 1984).

### Reproductive phenology

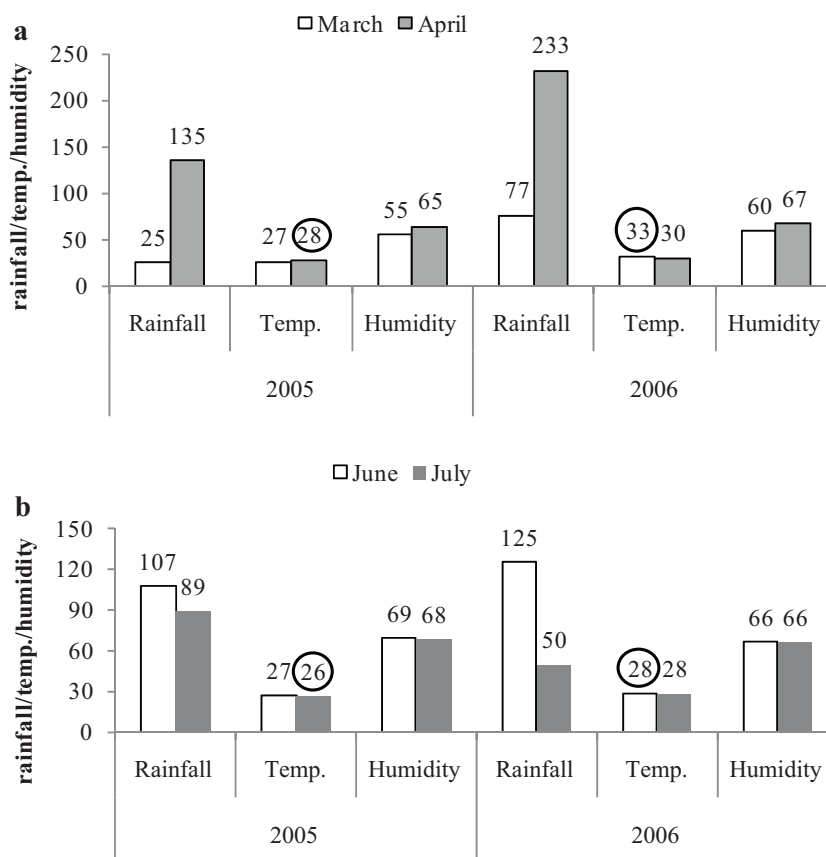
Seasonality was observed in the initiation of reproductive phenoevents of both *R. mucronata* and *S. alba*. Reproductive organs were observed in *R. mucronata* and lasted during most part of the year; however, the different reproductive phenophases were characterized by seasonality. This corroborates similar findings on *R. mucronata* and other *Rhizophora* species (Coupland et al., 2005; Mehlig, 2006; Nadia et al., 2012; Sharma and Kamruzzaman, 2012; Wium-Andersen and Christensen, 1978; Wium-Andersen, 1981). Initiation of flower buds in *R. mucronata* occurred towards the end of the dry period and in the wet season, and this seasonality was found in both years of the study in all sites. *Rhizophora mucronata* flowers were produced still in the wet months. Migeot and Imbert (2012) reported similarly massive blooming and fruiting during the rainy season for *Pterocarpus officinalis* (Jacq.) at seashore sites.

An overlap of reproductive cycles was observed for *R. mucronata*, where new buds were produced on shoots that already bore maturing propagules. Duke (1990) observed that most mangrove trees at equatorial sites in less than 9° in latitude do not have overlapping reproductive cycles, which is contrary to our observations for *R. mucronata*. The small number of flowers recorded in comparison with buds, reflects the short presence of the flowers on the shoots. Wium-Andersen (1981) reported flower presence on the shoots of *R. mucronata* for only 1–2 days. In our study the number of shoots flowering in the following year increased or decreased depending on the shoot flowering percentage in the previous year. Highest mean shoot flowering percentage was 19% in the youngest *R. mucronata* site. Development of immature propagules was also low considering the high number of buds formed. Decrease in the number of reproductive structures from the initiation of

**Table 6**  
Correlation of vegetative components of *Sonneratia alba* sites with climatic variables. Spearman Rank Order Correlations; (*r* values are significant at  $p < 0.05$ . (–) not significant.

Site	11 yrs		13 yrs		Natural	
	Leaf emergence	Leaf fall	Leaf emergence	Leaf fall	Leaf emergence	Leaf fall
Rainfall	–	–	–	–	–	–
Temperature	0.48	–	0.63	0.55	0.63	0.55
Humidity	–	–	–	–	–	–





**Fig. 5.** Mean monthly air temperature (°C) total monthly rainfall (mm) and relative monthly humidity (%) during the flower initiation shifts in (a) *R. mucronata* and (b) *S. alba*. Temperature differences in the two years are encircled.

flower bud primordia to mature propagules has been reported for *R. mucronata* (Wium-Andersen, 1981) and *Rhizophora* spp. (Christensen and Wium-Andersen, 1977; Coupland et al., 2006; Sharma and Kamruzzaman, 2012). The period from flower bud initiation to propagule maturity (propagule length above 40 cm) was observed to take approximately 16–20 months in this study. Christensen and Wium-Andersen (1977) reported an even longer duration of 3 yrs for *R. apiculata*. There was no synchrony in the initiation of *R. mucronata* immature propagules in the three study sites in East Africa, which could have been dependent on the time the flower buds were initiated. In our study the period from immature propagule initiation to propagule maturity was approximately 9 months – which is close to the 6–8 months reported for *R. mucronata* (Wium-Andersen, 1981). Gill and Tomlinson (1971) reported a period of 8–13 months for *R. mangle* propagules in Florida, timings which may be associated with site specific climatic conditions.

Reproductive phenology of *S. alba* was seasonally characterized by distinct patterns. Duration of the reproductive phase was much shorter than in *R. mucronata* and without overlap of reproduction cycles. Flowering and fruit fall occurred during the dry period and short rainy season respectively. Similar timing in flowering period with reference to rainfall was reported for this species in northern Australia (Coupland et al., 2005). However, flowering for *S. alba* in northern Australia was observed in May–June and fruiting in July–August which is earlier than that observed in our study. Fall of mature propagules and fruits during the wet season for both species provide favourable environmental conditions for propagule establishment.

A close relationship between the leafing and fruiting phenologies was observed for *R. mucronata* and *S. alba* in this study. In *R. mucronata* leaf growth increased towards the start of the budding period and decreased after peak bud formation. In *S. alba* leaf growth also increased during the flowering season and decreased after mature fruit fall. Such patterns have also been observed for *A. marina* in Gazi Bay (Wang'ondou et al., 2010). This is likely to ensure increased photosynthate synthesis for the prolonged budding in *R. mucronata* and during the whole reproductive season in *S. alba*. Relationships between leafing and fruiting phenologies have been reported elsewhere for other mangrove species (Coupland et al., 2005; Duke, 1990; Mehlig, 2006; Wium-Andersen and Christensen, 1978).

#### Correlation with climatic variables

We observed significant correlation between leaf emergence and rainfall, and between leaf loss on the one hand and temperature and humidity on the other hand in the reforested sites of *R. mucronata*. In *S. alba* leaf emergence and leaf fall significantly correlated with temperature. Sharma and Kamruzzaman (2012) reported strong correlation of leaf growth with monthly mean air temperature and hours of sunshine, and between leaf death and temperature, sunshine, vapour pressure deficit and rainfall in *K. obovata* and *R. stylosa*. In our study, presence of the reproductive structures of *R. mucronata* significantly correlated with climatic variables. Budding strongly correlated with humidity and temperature, flowering with rainfall, and development of propagules with rainfall, temperature and humidity. Nadia et al.

(2012) observed a strong correlation between rainfall and reproduction and suggested that day length, rainfall and temperature determined the flowering and fruiting patterns of the mangroves. However, Wanderley de Medeiros et al. (2007) found no relationship between reproductive phenological patterns of coastal vegetation and rainfall. In our study it was *S. alba* that did not show a significant correlation of reproductive structures with climatic variables.

*Rhizophora mucronata* and *Sonneratia alba* displayed distinct reproductive phenologies in the natural and reforested stands. The phenoevents were repeated in the two years of study. However, shifts in timing of flowering to earlier months were observed. Although correlations of flowering with temperature were not significant, a slight increase in mean monthly air temperature may lead to earlier flowering. Mean air temperature for the two months was 28 °C and 33 °C, respectively, indicating a difference of 5 °C (Fig. 5). Likewise fall of *S. alba* flowers occurred in July in 2005 and shifted to June in 2006. Mean monthly air temperature for the two months was 26 °C and 28 °C, respectively, indicating an average difference in temperature of 2 °C. Peaks in *S. alba* flowering and fruiting were also observed to advance to earlier months in 2006. We cannot conclusively implicate temperature as the causative agent in the shifts, but higher temperature could be a driving force behind the observed shifts in the timing of flowering and peaks in flowering and fruiting in *R. mucronata* and *S. alba* respectively. Global climate change through temperature rise is projected to impact phenological patterns especially timing of flowering and fruiting. Change in species composition may be a consequence (Alongi, 2008) and result in mangrove expansion to higher latitudes, where it presently is limited by temperature (Ellison, 2000; Field, 1995; Fitter and Fitter, 2002; Gilman et al., 2008; Soares et al., 2012).

Advancement in the flowering phenology of other plant species in relation to warmer temperatures has been reported for *Boechera stricta*/Brassicaceae (Anderson et al., 2012); whole herbaceous semi-arid plant communities (Lesica and Kittelson, 2010), but also for tree species (Lu et al., 2006). There is a likelihood that advanced flowering could uncouple the timing in flowering with pollinator resources (Willmer, 2012), so that plants could lose their pollinator service. *Rhizophora mucronata* is wind pollinated, whereas *S. alba* is pollinated by bats (Tomlinson, 1986) and relies also on self pollination (Coupland et al., 2006). Competition for pollination services is likely to occur in the larger mangrove community, as far as species depend on the same pollinator resource. However, some species have developed non-synchronized timing in their flowering (Tomlinson, 1986). With global climate change such non-synchronized events could interfere with the flowering and fruiting of plant species that follow staggered phenophases. Though we do not yet know in detail the mechanisms which trigger the shifts in flowering of the two species studied, our findings could possibly be an indication that mangrove species are likely to be affected by slight changes in climatic variables. Though our data were collected over a short period of time, the findings tentatively point that climate change is likely to impact differently the two species. Interspecific differences in phenological timings at similar latitudes point to the need for documentation of the regional phenology of mangrove species the occurrences of which span a rather wide range of latitudes at tropical and subtropical coasts. This will help to monitor routinely the phenological trends with changing climate and to predict future impact of climate change on the mangrove trees and other plant species. This, again, will be important for restoration of their stands, as proper timing will make restoration programmes more cost effective and with a greater probability of success. Planting continuously fruiting species, such as *R. mucronata*, may enhance mangrove restoration, as they ensure availability of propagules for most parts of the year.

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