Growth and population dynamics during early stages of the mangrove *Kandelia candel* in Halong Bay, North Viet Nam

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Received 17 May 2002; accepted 31 March 2003

**Abstract**

Quantifying the dynamics of the early stages in the life cycle of mangroves is essential to predict the distribution, species composition and structure of mangrove forests, and their maintenance and recovery from perturbations. The growth and population dynamics of two stands of the mangrove *Kandelia candel* in Halong Bay (Viet Nam) were examined for 1 year. Growth was highly seasonal, with high growth rates and fast internode formation in the summer, dropping to extremely low growth during January–February, the coldest and driest months in the year. In addition, growth and internode formation rates showed important inter-annual variability during the last decade. The complete reproductive period required 7–8 months. Flower initiation was maximal in June and peak propagule maturity occurred in December–January. Only one mature propagule developed for every 67 and 127 inflorescence buds formed at Site 1 and Site 2, respectively. *Kandelia candel* propagules began to sink 10 days after being released, and after 18 days all propagules had negative buoyancy. The propagules developed roots within 19–68 days, depending on whether they were held on the water or sediment, and were capable of long range dispersal, for 15–20% of them dispersed more than 100 m within 1 day. The median age of *K. candel* plants ranged between 8.7 and 5.6 years, with a density of 1900 and 470 plants ha⁻¹ in Sites 1 and 2, respectively. Plant mortality was high, with 64 and 74% of the plants surviving after a year at Sites 1 and 2. Life expectancy (i.e. median age-at-death) of only 2.2 and 2.7 years at Sites 1 and 2, respectively, indicates that mortality of young *K. candel* plants was specially high. Recruitment occurred in early spring, and did not suffice to balance the mortality within the annual period examined. These results suggest that the *K. candel* stands in Halong Bay might be maintained by a few years of high recruitment which would compensate for generally high mortality rates.

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**Keywords:** growth; recruitment; mortality; mangrove; *Kandelia candel*

1. Introduction

Mangrove forests are important components of shallow, tropical coastal areas, which have experienced an important decline, largely due to logging and other human-derived transformations, over the last 50 years (Aksornkhoe, 1993; Arrhenins, 1992; Gómez, 1988). The loss of mangroves has been particularly large in Southeast Asia, to the extent that many countries have lost most of their original mangrove cover (Adeel & Pomeroy, 2002). Realization of the detrimental ecological consequences of mangrove loss has led to the development of large-scale afforestation projects in many Southeast Asian countries, as well as measures to conserve the natural forests still existing and promote the recovery of perturbed mangrove systems (Field, 1998; Ong, 1995).

Knowledge of the population dynamics of mangroves is essential to forecast their dynamics and eventual
recovery from perturbation. While much research has been done on the primary productivity of mangroves (Ball, 2002; Bunt, 1995; Christensen, 1978; Christensen & Wium-Andersen, 1977; Clarke, 1994; Clough, Ong, & Gong, 1997; Clough, Tan, Phuong, & Buu, 2000; Coulter et al., 2001; Duarte et al., 1998; Feller, 1995; O’Grady, McGuinness, & Eamus, 1996; Onuf, Teal, & Valiela, 1977; Saenger & Snedaker, 1993; Twilley, Lugo, & Patterson-Zucca, 1986), their population dynamics remain, in contrast, relatively poorly known. In particular, quantifying the dynamics of the early stages in the life cycle of mangroves is essential to predict the distribution, species composition and structure of mangrove forests. Mangroves propagate by sexual reproduction mainly, and both the maintenance and recovery of mangrove forests depend on propagule production, dispersal and establishment, and the successful recruitment of mangrove seedlings into the reproductive tree status (Tomlinson, 1994).

The phenology and rates of propagule production are known for a few species only (Avicennia marina: Clarke, 1994; Clarke & Myerscough, 1991a; Duke, 1990; Aegiceras corniculatum: Clarke, 1994; Rhizophora apiculata: Christensen & Wium-Andersen, 1977). The dispersal and establishment capacity of mangrove propagules have been characterized, and their power to explain adult tree distribution has been discussed for a larger number of species (Clarke, 1993; Clarke, Kerrigan, & Westphal, 2001; Clarke & Myerscough, 1991b, 1993; Maxwell, 1996; McGuinness, 1997a; McKee, 1995a; Minchinton, 2001; Rabinowitz, 1978). Overall, these studies suggest that the maintenance of mangrove populations depends less on their dispersal properties and their rate of supply to a given mangrove stand, and more on the factors that influence the establishment of propagules and their early survival and growth.

The growth and survival of mangrove seedlings depends on several factors such as tidal position and desiccation (Ellison & Farnsworth, 1993, 1996; McKee, 1995a), salinity (Ball, 2002; Ball & Pidsley, 1995; Clarke & Allaway, 1993; McGuinness, 1997a), redox potential and sulfide concentration in pore water of the sediment (McKee, 1993, 1995a; Youssif & Saenger, 1998), nutrient availability (Clarke & Allaway, 1993; Duarte et al., 1998; Feller, 1995; McKee, 1995b; Onuf et al., 1977), light availability (Ball, 2002; Ellison & Farnsworth, 1993; McKee, 1995b; Minchinton, 2001; Smith, 1987a; Tamai & Iampa, 1988), wave exposure (Clarke & Myerscough, 1993; Tamai & Iampa, 1988; Thampanya, Vermaat, & Terrados, 2002), decreased sedimentation (Ellison & Farnsworth, 1996), burial by sediment (Terrados et al., 1997; Thampanya, Vermaat, & Duarte, 2002), sediment disturbance (McKee, 1995a; Minchinton, 2001) or fouling (Clarke & Myerscough, 1993).

Herbivory, in particular the predation of mangrove propagules by crabs, larval insects and snails is a source of mortality in the early stages of mangrove life cycle that has received close attention. First, there are species-specific differences in the frequency of predation for the propagules of Avicennia species are always more preyed on than those of other species while those of Rhizophora species are usually less preyed on (McGuinness, 1997b; McKee, 1995c; Smith, 1987b; Sousa & Mitchell, 1999). Second, intensity of herbivory can vary widely between different locations depending on several factors, such as nutrient content (Feller, 1995), availability of propagules of different, more preferred species (McGuinness, 1997b), tidal position and predator abundance (Dahdouh-Guebas, Vermeir, Taek, Van Speybroeck, & Koedam, 1998; Osborne & Smith, 1990; Robertson, Giddins, & Smith, 1990; Siddiqi, 1995; Smith, 1987a), or the local predator guild (Sousa & Mitchell, 1999). Then, herbivory can reduce seedling growth and survival (Ellison & Farnsworth, 1996; McGuinness, 1997b; McKee, 1995c; Minchinton & Dalby-Ball, 2001; Osborne & Smith, 1990). Furthermore, it was suggested that herbivory on mangrove propagules and seedlings could determine the spatial distribution of adult trees (Smith, 1987b), a contention which seems to hold for Avicennia species only (McGuinness, 1997b; McKee, 1995c; Sousa & Mitchell, 1999).

In spite of this wide knowledge of the environmental conditions and ecological processes that can potentially influence the growth and survival of mangrove seedlings, the dynamics of mangrove seedling populations under natural conditions remains to a large extent unknown (Clarke, 1995). Certainly, naturally occurring mangrove propagules or seedlings chosen according to particular objectives have been selected, tagged, and the percentage of them surviving after a given time and/or their size has been quantified on several occasions (Clarke & Myerscough, 1993; McGuinness, 1997a; McKee, 1995c; Minchinton & Dalby-Ball, 2001; Osborne & Smith, 1990, to cite only a few), but these studies hardly ever chose a naturally occurring population of mangrove seedlings, or a randomly chosen part of it, as the subject of study (but see Clarke, 1995 and Osunkoya & Creese, 1997) to evaluate recruitment and mortality, which are the basic demographic variables needed to characterize the dynamics of any population. As a result, even if previous studies suggest that mortality of early stages (e.g. seedlings) might be very high, it is not clear altogether its relevance to the actual dynamics of the population. Additionally, few estimates of recruitment are available (Clarke, 1995).

Kandelia candel is a common mangrove species in the central and north coasts of Viet Nam, where it is widely used for shoreline protection (Hong & Hoang, 1993). This species forms small pockets of vegetation in the bays of Halong Bay (North Viet Nam), which differ in
exposure and sediment characteristics, and may thus affect the dispersal of propagules, and their subsequent survival and growth. Here, an examination of the growth and population dynamics, with an emphasis on early stages, of *K. candel* in Halong Bay (North Viet Nam) is provided. Using reconstruction techniques (Duarte, Thampanya, Terrados, Geertz-Hansen, & Fortes, 1999; Duke & Pinzón, 1992), the growth dynamics of the plants over the past decade is examined, and then the seasonality of seedling growth using marking techniques is reported. Finally, the age distribution of the stands and the dynamics of sexual reproduction and early survival of the plants are examined.

### 2. Methods

Gia Luan is a bay on the northern coast of Cat Ba Island in Halong Bay (Quang Ninh Province, North Viet Nam). Bay waters are calm, with high levels of suspended sediment, and seasonally changing temperature, which drops to as low as 15°C in winter. The maximum depth of the bay at high tide is less than 2 m, the maximum tidal amplitude is 4.6 m, and the salinity ranges from 22.3 to 32. Two adjacent mangrove stands where *Kandelia candel* was abundant were selected (other species present were *Rhizophora stylosa*, *Bruguiera gymnorrhiza*, *Aegiceras corniculatum* and *Avicennia marina*): Site 1 (20°51.44’N, 106°59.11’E) was located inside the bay and the sediment was muddy (silt and clay particles: 75% of dry weight; coarse (>2 mm) particles: 3% of dry weight), while Site 2 (20°51.42’N, 106°59.22’E), with coarser sediments (silt and clay particles: 22% of dry weight; coarse (>2 mm) particles: 62% of dry weight), were located at the mouth of the bay. These stands were dominated by seedlings (plants less than 0.5 m in height) and saplings (plants less than 1 m in height), and none of the adult trees present exceeded 2.5 m in height.

In April 1999, a plot of 819 m² was established at Site 1 and all *Kandelia candel* seedlings, saplings and adult trees present inside the plot (*n* = 165) were tagged to allow individual identification. The plot extended from the seaward side to the center of the mangrove stand. One month later (May 1999), a plot of 1998 m² was delimited at Site 2 (the plot included the whole mangrove stand) and all of the *K. candel* individuals present inside were tagged (*n* = 94 plants). The height of the tagged plants was measured and the number of internodes of the main stem counted to estimate their age (Coulter et al., 2001; Duarte et al., 1999). The study sites were visited monthly until June 2000 and which of the tagged plants had died since the previous sampling date was assessed as well as, many new plants, which were also tagged, had recruited into the plots, allowing estimation of mortality and recruitment. A subset of 10 tagged *K. candel* plants randomly selected from those present in the plots at the beginning of the study at each site were used to estimate growth by recording the height of the main stem and the number of internodes on them at each sampling event.

To estimate the growth and internode production rates using reconstruction techniques (Coulter et al., 2001; Duarte et al., 1999) 10 of the oldest *Kandelia candel* trees present (>30 internodes) at each site were also selected at the beginning of the study and the length of all the internodes along the main stem of the plants measured from the apical meristem of the main stem down to the point where node rings were unclear. The series of internodal lengths were filtered through a long-term running average (150% of the number of internodes produced during 1 year, 12 internodes) and a short-term one (30% of the number of internodes produced during 1 year, three internodes) to remove inter-annual and sub-seasonal variations, respectively, from the series, and the cycles present in the filtered series were used to infer the internode production and elongation over the past decade, as described in Duarte et al. (1999) and Coulter et al. (2001). In brief, the average number of data points (i.e. internodes) between two consecutive maxima or minima in the filtered series of internodal lengths is an estimate of the average number of internodes produced per year if the cycles in the series are of an annual nature. The correctness of this assumption is tested using the data provided by the plants tagged and monitored for 1 year. Once the annual nature of the cycles is established, the correspondence between any individual cycle in a given series and year is straightforward, as it is the estimation of the number of internodes produced and the elongation of the main stem in that year (Duarte et al., 1999).

To quantify the seasonality of reproductive effort and seedling production of *Kandelia candel* in Halong Bay, 30 branches on at least 10 different reproductive trees at each site were selected, tagged and the number of inflorescence buds, flowers and stages of fruits and propagules counted monthly during the reproductive season (from May 1999 to March 2000). The length of the hypocotyl was measured to quantify propagule development. Rainfall, air temperature and insolation data were derived from a nearby meteorological station.

Fifty-six mature propagules were collected in Site 1 in May 2000 and transported to the laboratory to estimate how long the propagules maintained positive buoyancy, and the time needed to develop roots. The propagules were maintained in three different regimes: (1) 20 propagules were placed in a tank which contained sediment collected at the same site as the propagules and which was maintained wet during the experiment by adding small amounts of seawater (salinity of 26) when needed; (2) 18 propagules were placed in a tank containing only seawater; and (3) 18 propagules were transferred between the sediment tank to the seawater
tank to simulate the alternation of exposure to air (low tide) and seawater (high tide) that they would experience at the collection site in Gia Luan. The development of the propagules was monitored for 2 months at intervals increasing from 4 to 18 days in between observations (nine events) to record if they floated or not and the state of development of the roots, quantified as the number and length of the roots.

In May 2000, 30 propagules which seemed to have fallen to the sediment recently at each site were randomly selected, painted and their position marked on the sediment with a chopstick bearing the same number as that painted on the propagule. The short-term dispersal of these propagules was evaluated by measuring at low tide the distance the propagules moved during three consecutive days.

3. Results

3.1. Growth patterns: seasonal and decadal

There was a clear shift in weather conditions during the year, with very warm temperatures and abundant rainfall in the summer dropping to dry and cool temperatures in the winter (Fig. 1). Together with a pattern of decreasing insolation from summer to winter (Fig. 1), these data show strong seasonality in weather conditions at the study sites. The analysis of growth and internode formation of the marked seedlings revealed very clear seasonal patterns, with high growth rate and fast internode formation in the summer, dropping to an extremely low growth during January–February, the coldest and driest months in the year (Fig. 1). The formation of internodes by the main stem of K. candel was positively correlated ($ P < 0.05$, Fig. 1) with air temperature, rainfall and insolation in both sites; the elongation of the main stem, however, was positively correlated with air temperature only (Site 1: $ r = 0.83$, $ P < 0.01$; Site 2: $ r = 0.88$, $ P < 0.01$). Both the growth rate and the rate of internode formation tended to be somewhat higher at Site 1 than at Site 2 (Fig. 1).

The examination of the sequence of internodal lengths along the tree stems revealed clear cyclic patterns (Fig. 2), similar to those described already for this (Coulter et al., 2001) and other (Duarte et al., 1999; Duke and Pinzón, 1992) mangrove species. The presence of these clear signals reflected the strong seasonality of plant growth at the study site (Fig. 1), and allowed the reconstruction of the past growth history of the Kandelia candel stands.

The examination of the average growth of the trees revealed important inter-annual fluctuations (twofold) in plant growth (Fig. 3) about the long-term average values of 13.2 and 12.5 cm year$^{-1}$ at Sites 1 and 2, respectively. The patterns of inter-annual variation were also different between the two sites, with a tendency towards declining growth rates in the past 5 years at Site 2, while mean annual growth rates first decreased and then increased during the same period at Site 1 (Fig. 3). This variation was statistically independent (i.e. Pearson’s $r$, $ P > 0.05$) of climatic fluctuations, as represented by mean annual temperature, rainfall and the number of sun hours, further indicating the role of site-specific factors. The decadal-average (1990–1999) growth rates tended to be higher than the annual rates determined for the period 1999–2000 at Site 1 (9.4 cm year$^{-1}$) and Site 2 (5.5 cm year$^{-1}$) and the difference between these last two followed the recent trend observed in the years previous to the study, when differences between Sites 1 and 2 were greater than the average decadal values indicate (Fig. 3). In contrast, the variation of the internode formation rate was small and not statistically significant between years (Fig. 3), with a long-term average of 6.7 and 5.4
internodes year\(^{-1}\) at Sites 1 and 2, respectively, and annual rates for the period 1999–2000 of 8.4 internodes year\(^{-1}\) at Site 1 and 6.6 internodes year\(^{-1}\) at Site 2.

### 3.2. Sexual reproduction and propagule development

Flower development was at its maximum in June, and was followed by peak flowering in July, which led to peak fruit formation in August and maximum abundance of mature propagules in December–January (Fig. 4). It took, therefore, 7–8 months for mature propagules to form from flowers. The abundance of structures in the different stages of the sexual reproduction (inflorescence buds to mature propagules) declined drastically along their development (Fig. 4). The ratios of peak abundance of these structures were found to be 67 buds : 18 flowers : 4 fruits : 1 propagule at Site 1, and 127 buds : 34 flowers : 10 fruits : 1 propagule at Site 2. Provided that each inflorescence bud leads to four flowers, on average, these ratios indicate that only one mature propagule is formed for each 268 and 508 flowers at each site. The reproductive success, therefore, was greater at Site 1, where the number of propagules developed per flower bud initiated was twice as that at Site 2. The propagules elongated at a constant average rate of 0.098 \(\pm\) 0.027 (SE) cm day\(^{-1}\) during the period 1999–2000.

### 3.3. Stand age structure and seedling demography

The age structure of the *Kandelia candel* plants, established in April 1999, indicated a median age of 8.7 years at Site 1 and 5.6 years at Site 2 (Fig. 5). The maximum plant age, however, was similar at both sites (Site 1: 21.6 years; Site 2: 21.7 years; Fig. 5). The age distributions suggested—if stable in time—that mortality was higher at Site 2 than at Site 1 during the first 3–4 years of life, reversing afterwaters. Although the relative contribution of young plants to the population was greater at Site 2, their absolute abundance was greater at
Site 1, where plant density is much higher (1900 and 470 plants ha\(^{-1}\) in Sites 1 and 2, respectively).

The examination of plant survivorship indicated a comparable pattern of plant depletion in both sites (Fig. 6), with 64 and 74\% of the plants surviving within a year at Sites 1 and 2, respectively. Mortality occurred throughout the year but it seemed lowest during August and September (Fig. 6). The distribution of age-at-death indicated that most of the plants that died were young, with the life expectancy (i.e. median age-at-death) of 2.2 and 2.7 years for Sites 1 and 2, respectively (Fig. 5). Recruitment occurred in early spring, with a distinct period of recruitment about 3 months after the peak in propagule maturity (cf. Figs. 4 and 6). The number of new recruits was insufficient to balance the mortality within the annual period examined (Fig. 6), over which the number of new recruits was only 46 and 26\% of the number of plants lost, for Sites 1 and 2, respectively.

3.4. Propagule buoyancy, root development and dispersal

*Kandelia candel* propagules had positive buoyancy at the initiation of the experiment, but some began to sink after 10 days, and after 18 days all propagules had negative buoyancy, both when maintained constantly in seawater and when maintained alternatively in seawater and on the surface of wet sediment. Root initiation was dependent on the conditions the propagules experienced. Propagules maintained constantly over the surface of the sediment developed at least one root within 19 days. Propagules that were maintained alternately in seawater and on the sediment surface started to develop roots after 13 days, and after 28 days all of them had developed at least one root. Root initiation was slower in the propagules maintained constantly in seawater, which started to develop roots after 19 days and all propagules had developed at least one root only after 68 days. When propagules were maintained continuously in seawater, the roots elongated linearly with time reaching lengths greater than 10 cm during the first 45 days. Root elongation could only be reliably assessed for seedlings maintained in seawater, for those in sediments broke when pulled to measure the root length.
The monitoring of the distances moved by *Kandelia candel* propagules over three consecutive tidal cycles showed that 52.3 ± 3.6% of the propagules at Site 1 and 36.7 ± 4.7% of the propagules at Site 2 did not move; from those that dispersed, 56% at Site 1 and 77% at Site 2 moved less than 100 m, while the rest moved more than 100 m.

4. Discussion

The results obtained reveal a strong seasonality in the elongation and internode production of the main stem of *Kandelia candel* in Northern Viet Nam, with very low growth during the cold, dry months, and fast growth during the warm, rainy months. Strong, unimodal seasonality of the vegetative development of *K. candel* has also been found in other locations (Okinawa, Japan) where 70% of seasonal variation in leaf production could be explained by the seasonal change in air temperature, humidity and day-length (Gwada, Makoto, & Uezu, 2000). Other mangroves growing in subtropical locations show strong seasonality in their vegetative development (*Avicennia marina*: Clarke, 1994; Duke, 1990; Osunkoya & Cresse, 1997; *Aegiceras corniculatum*: Clarke, 1994). Mangroves growing in tropical locations, however, usually show weaker and/or multimodal seasonal signals in their vegetative development (Christensen & Wium-Andersen, 1977; Duke, 1990; Ellison & Farnsworth, 1996; Wium-Andersen, 1981; Wium-Andersen & Christensen, 1978). Air temperature/humidity, rainfall, and day-length/insolation have been consistently identified by these studies as the environmental factors driving the seasonality of mangrove growth and development.

The strong seasonality in the growth of *Kandelia candel* results in the presence of distinct, annual cycles of internodal length along the stems (Coulter et al., 2001; Duarte et al., 1999) which allows the elucidation of past growth patterns. This is an important feature for mangroves lack clear annual growth rings (Tomlinson, 1994). The evaluation of the past growth rates identified strong (twofold) inter-annual changes in *K. candel* growth over the past decade, but these variations were relatively independent at the two study sites and unrelated to changes in climate, suggesting that they relate to site-specific factors.

The reproductive success of *Kandelia candel* was low at the Cat Ba Island, with only one mature propagule formed for each 67 and 127 inflorescence buds initiated at Site 1 and Site 2, respectively. The low number of mature propagules recovered at the end of the study (Fig. 4) advises to consider these values as preliminary. However, low values of reproductive success have been estimated (*Avicennia marina*: only 3% of flower buds develop a viable fruit (Clarke & Myerscough, 1991a) and the amount of propagules formed is two orders of magnitude lower than that of ovules and zygotes, (Clarke, 1995); *Rhizophora apiculata*: only 1–3% of flower buds developed a fruit, (Wium-Andersen & Christensen, 1978)) or suspected (*Rhizophora mucronata*, Wium-Andersen, 1981) in other mangrove species, which suggests this might be a general feature of mangrove reproductive biology.

Similar to growth seasonality, the reproductive phenology of *Kandelia candel* was characterized by single annual peaks in the abundance of flower buds, flowers, fruits and mature propagules. Mangrove species growing in subtropical locations show unimodal patterns in the abundance of the reproductive organs as well (Clarke, 1994; Duke, 1990), while those growing in...
tropical locations may show single but broader peaks in the abundance of reproductive organs (Avicennia marina: Duke, 1990; Wium-Andersen & Christensen, 1978) or single peaks but with flowers present all year round (Rhizophora apiculata, Rhizophora mucronata, Bruguiera cylindrica, Ceriops tagal, Lumnitzera littorea, Sęphiphora hydrophyllacea: Christensen & Wium-Andersen, 1977; Wiium-Andersen, 1981; Wiium-Andersen & Christensen, 1978). The observation that the annual maximum of leaf production of A. marina and Aegiceras corniculatum in a subtropical location (Jervis Bay, New South Wales, Australia) occurred during the period of fruit maturity, and that leaf production was minimal at the time of flower development and during initial stages of fruit maturation led Clarke (1994) to suggest that there might be a trade-off between leaf growth and resource investment to sexual reproduction; this does not seem to be the case for K. candel in Gia Luan for the development of flowers and fruits occurred during summer months, when plant growth was also fastest; the fruits continue their development through fall in a context of decreasing plant growth rates, and propagules reached maturity in winter, when plant growth rate was lowest. The time needed by K. candel to produce mature propagules from flowers (7–8 months) was shorter than that required by subtropical A. marina (12 months: Clarke, 1994), although this last species can produce mature propagules in 3–4 months only in tropical locations (Wium-Andersen & Christensen, 1978). Other mangrove species living in tropical locations can produce mature propagules in 3–6 months (B. cylindrica, C. tagal, L. littorea: Wiium-Andersen & Christensen, 1978; S. hydrophyllacea: Wium-Andersen, 1981) or longer times (6–8 months in R. mucronata, Wium-Andersen, 1981; 3 years in R. apiculata, Christensen & Wium-Andersen, 1977).

The propagules of Kandelia candel are capable of long-range dispersal for between 33 and 46% of dispersing propagules in Gia Luan dispersed to distances larger than 100 m within 3 days. Similarly, 84% of fallen K. candel propagules did not settle near the parental trees in Ranong, Thailand (Maxwell, 1996). The distance traveled by K. candel propagules might be considerable, since they float for an average of 10 days at least. After this time, they sink and can rapidly develop roots (2–3 weeks) when in contact with suitable sediments. Avicennia marina propagules shed their pericarp and sink within 1–3 days when exposed to seawater, and it takes 7–10 more days to develop roots (Clarke, 1993). The period of obligate dispersal might be of about 2 weeks, and within it most propagules strand within 500 m of the release site, usually during the first tidal cycles (Clarke, 1993). The present results show that the period of obligate dispersal of K. candel propagules varies from 3 to 9 weeks depending on the particular conditions experienced by the propagules, which suggests that the dispersal capacity of K. candel might be higher than that of A. marina. The duration of the obligate dispersal period for propagules of other mangrove species varies from 4 to 40 days (Clarke et al., 2001; Rabinowitz, 1978). It must be realized that these are minimum estimates based on the fastest-developing propagules; the percentage of propagules which have not developed a root after the estimated period of obligate dispersal may be quite high in some species (Clarke et al., 2001). Kandelia candel propagules developed roots at the slowest rate when exposed to seawater only, a result consistent with previous observations in other mangrove species (Clarke et al., 2001; Rabinowitz, 1978). This response of mangrove propagules might increase their dispersal potential and has been considered as a possible reason why propagules of some species are not able to recruit in apparently suitable habitats near their release site, making those species infrequent (Clarke et al., 2001).

The uneven age distribution of Kandelia candel observed, specially in Site 1, is indicative of either age-specific mortality or the occurrence of important inter-annual differences in seeding recruitment or mortality. Mortality was high during the early stages of life (age <3 years) at both sites but decreased afterwards, which suggests that the uneventfulness of the age distribution of the population might be driven, then, by inter-annual differences in propagule production and/or seedling recruitment. Inter-annual differences in sexual reproduction output of mangroves have been described for Avicennia marina in southeastern Australia (Clarke & Myerscough, 1991a), a mangrove species which shows ‘uneven size distributions’ (Clarke, 1995). It seems, therefore, that events of high recruitment and/or mortality might be a general feature of the dynamics of mangrove populations.

The present results indicate that both populations of Kandelia candel were not in demographic steady-state at the annual scale, and that both were in regression (mortality was higher than recruitment) over the period studied. These observations of direct recruitment and mortality, together with the reconstructed age structure of the populations, suggest that the K. candel stands in Ha Long Bay are probably maintained by a few years of high recruitment, due to either unusually high sexual reproduction or currents that bring imported propagules to the sites, to compensate for generally high mortality rates. This hypothesis remains, however, speculative and requires sustained observations over long periods to be tested.
Acknowledgements

This is a contribution to the PREDICT (Prediction of the REcovery and Resilience of Disturbed Coastal Tropical) communities project, funded by the INCO programme of the European Commission (ERBIC18-CT98-0292). We thank Mr Nguyen Van Tang, Ms Tu Lan Huong, Ms Sarah Coulter and Ms Cecile Padilla for assistance in the field.

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