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# Retrospective estimates of net leaf production in *Kandelia candel* mangrove forests

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ABSTRACT: A new, inexpensive, and time-saving method for the estimation of the net production of leaves and reproductive structures of mangroves was applied to 2 Vietnamese stands of *Kandelia candel*. The method combines the allometric relationship between the number of meristems in trees and their diameter with knowledge of the number of leaf pairs and reproductive structures each meristem develops annually to calculate the net leaf and inflorescence production of each tree in the stand. Each apical meristem of *K. candel* produced about 6 leaf pairs and 1.3 to 1.9 inflorescences annually, with the number of meristems in each tree increasing to the square of their girth. The size distribution of *K. candel* was highly skewed at all sites, with an exponential decline in the number of plants as the size increased. The net leaf production (dry wt), calculated by scaling the production per meristem to that of individual trees and then to the entire stand, ranged from 176.5 to 1338.7 g $m^{-2}$ $yr^{-1}$ among stands, with an estimated total inflorescence production ranging from 0.91 to 101 g $m^{-2}$ $yr^{-1}$. The largest individuals, comprising 10% of the population, contributed the majority of the stand production. The approach demonstrated overcomes serious deficiencies in the traditional litter-fall method, particularly when applied to developing mangrove stands, and should be applicable to other mangrove species as long as they display clear nodes, leaf, flower and fruit scars, as do other members of the Rhizophoraceae family.

KEY WORDS: Mangrove · Primary production · Litterfall · *Kandelia candel* · Rhizophoraceae · Vietnam



## INTRODUCTION

Mangrove forests are key components of tropical coastal ecosystems, where they protect the land from erosion and saline intrusion, and provide resources, as raw materials and food, to coastal populations through their primary production (Tomlinson 1994). Mangrove ecosystems rank amongst the most productive communities in the world, with their net primary production estimated at $1.1 \times 10^{15}$ g $yr^{-1}$ worldwide (Duarte & Cebrián 1996). Most of the biomass produced by mangroves falls off the trees (90% on average), and is stored in the sediments (10% on average), decomposed (40% on average), or exported (30% on average) to adjacent ecosystems (Duarte & Cebrián 1996). Hence, mangrove biomass supports detritus-based food webs in both the immediate and adjacent coastal ecosystems.

Despite their ecological and economic value, they are disappearing at alarming rates throughout the world. Loss rates of mangroves are currently highest in South East Asia, where they have declined dramatically since World War II (Gómez 1988, Aksornkoae 1993). This has led to increased saline intrusion and

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coastal erosion, while marine productivity and the availability of harvestable resources have declined (Aksornkoae 1993). In an attempt to reverse this situation, many of the region's governments have implemented broad reforestation and protection campaigns involving large-scale plantations (Hong & San 1993). There is, therefore, an interest in assessing the effectiveness of these actions in recovering ecosystem production. This is, however, rendered difficult due to the high costs, both in time and man power, required to estimate net mangrove production.

There are no reliable methods of estimating net mangrove production directly, since physiological estimates of primary production obtained at the level of individual leaves cannot be readily scaled to entire trees or stands. Hence, most estimates of net mangrove production are derived indirectly through measurements of litterfall, an activity that receives a significant proportion of the effort devoted to the study of mangrove ecology worldwide (Lugo & Snedaker 1974). Litterfall analyses require continuous effort over annual time scales, so that estimates can only be derived, at best, for a few plots in selected areas, precluding the comprehensive examination of net production across environmental ranges in mangrove forests. Most importantly, the litterfall method assumes the areal biomass of the mangrove stands to be in steady state and is, therefore, unsuitable for estimating the net production of developing stands, such as recently planted areas.

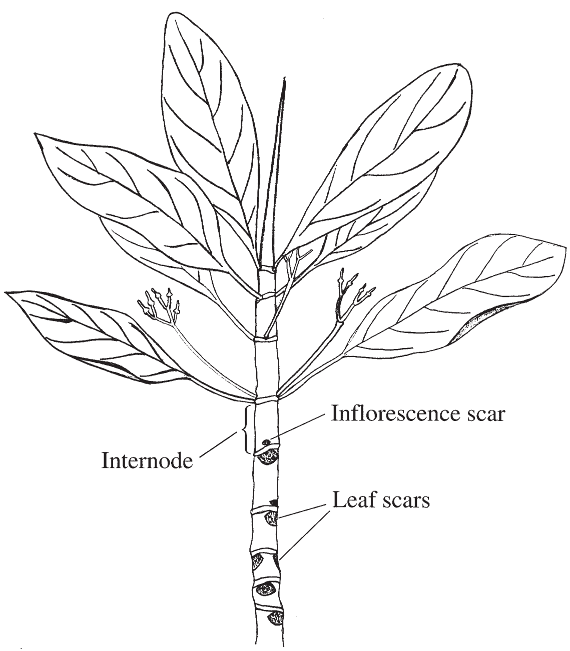


Fig. 1. *Kandelia candel.* Schematic representation of nodes on stems, showing the scars left by shedding of leaves and reproductive structures

Here we present a simple, inexpensive method of estimating the net leaf production of a mangrove stand based on the retrospective analysis of data collected in just 1 field visit. This method is based on a combination of estimates of the rate of production of mangrove nodes (Duarte et al. 1999) and allometric estimates of the number of node-producing meristems in a stand. We demonstrate this technique using 2 populations of *Kandelia candel* growing near its northern limit on the coast of Northern Vietnam. The first stand was a stunted, natural, mixed-forest of *K. candel*, which is abundant in the forest fringe, *Rhizophora stylosa*, A*egiceras corniculatum*, *Bruguiera gymnorrhiza* and *Sonneratia caseolaris* located in Gia Luan Bay (Ha Long Bay, Quang Ninh province). The second site was a monospecific *K. candel* plantation in the district of Thai Thuy (Thai Binh province, Red River Delta). The trees at both sites were short enough (<3 m) to allow an accurate account of the meristems present.

## METHODS

**Principle and assumptions.** Members of the Rhizophoraceae family, which includes *Kandelia candel*, bear fairly detailed records of their growth and development in the form of leaf and inflorescence scars along their stems (Fig. 1). As for most mangrove trees, Rhizophoraceae produce leaves in pairs at each of the nodes produced through the activity of apical meristems (Tomlinson 1994). A distinct scar is also left by the peduncle of the inflorescence at the point of its axillary insertion above the node (Fig. 1). The rate of node production has been shown to be very regular in some mangrove species (*Rhizophora mangle*: Duke & Pinzón 1992; *R. apiculata*, *Sonneratia caseolaris and Avicennia marina*: Duarte et al. 1999). The sequences of internodal lengths along the stems of these species have been shown to display a characteristic cyclical pattern which allows elucidation of the number of internodes each mertistem produced annually ($n_{nodes}$; Duke & Pinzón 1992; Duarte et al. 1999). Because of the 1:1 relationship between leaf pairs and nodes produced (Fig. 1), the number of leaves annually produced is twice the amount of nodes produced annually (i.e. $2 \times n_{nodes}$). Similarly, the frequency of inflorescences ($F_{inflor}$) production can be easily calculated as the fraction of the number of internodes in a large sample of stem material that bears inflorescence scars. The rate of production of inflorescences can, therefore, be calculated as $F_{inflor} \times n_{nodes}$ (i.e., the product of the frequency of inflorescence production and the number of nodes produced annually by each meristem).

The shoot meristems divide as the tree grows, producing branches. This process leads to a geometric increase in the number of meristems an individual plant bears with age. Hence, the number of meristems present on a tree ($M_{tree}$) can, in principle, be predicted from allometric relationships to mangrove girth:

$$M_{tree} = a \text{ girth}^b \quad (1)$$

where $a$ and $b$ are the allometric coefficients (Niklas 1994). Provided all meristems produce, on average, a similar number of nodes annually, the average number of leaves and inflorescences produced annually by any 1 tree can be estimated as $2 \times M_{tree} \times n_{nodes}$ and $M_{tree} \times F_{inflor} \times n_{nodes}$, respectively. Hence, the total number of meristems ($M_{total}$) present in a mangrove stand can be calculated from the distribution of girth in the stand using Eq. (1) as:

$$M_{total} = \sum a \text{ girth}^b \quad (1b)$$

allowing calculation of the total annual leaf and inflorescence production in the stand (i.e. $2 \times M_{total} \times n_{nodes}$ and $M_{total} \times F_{inflo} \times n_{nodes}$, respectively).

Knowledge of leaf and reproductive module production as number of units produced annually can be translated into dry weight production by multiplying the estimates by the average weight of fully-developed leaves and the weight of the modules. These steps should lead to an estimate of the net production of non-woody parts in a mangrove stand.

**Study sites.** Gia Luan is a bay on the northern coast of Cat Ba Island, and is characterized by high levels of suspended sediment, calm waters, and cool temperatures, dropping to as low as 15°C in the winter. *Kandelia candel*, *Ceriops tagal* and *Sonneratia caseolaris* are the dominant mangrove trees in Northern Vietnam, and are also the dominant species at Gia Luan. The Bay of Gia Luan is a mud flat extending more then 150 m from the edge of the mangrove towards the mouth of the bay. At high tide, the ocean water is less then 2 m in depth at the mouth of the bay. Maximum tidal amplitude is 4.6 m and salinity ranges from 18.54 to 27.60‰.

The Thai Thuy plantation was planted at a density of 1 tree/0.49 $m^2$ in various stages from 1986 to 1992 and now covers an area of more than 3293 ha. The section studied here was 7 yr old at the time it was sampled and had a density of between 22 and 262 plants $m^{-2}$, with an average of 57 plants $m^{-2}$. It was dominated by seedlings of <1 cm in girth, although the average height of the originally planted trees was 1.4 m. The mean annual temperature is 23 to 24°C, with a high of 38°C and a low of 16°C. Humidity ranges from 84 to 85% in spring and 90 to 100% in summer. Average rainfall is 1700 to 2200 mm $yr^{-1}$ with 130 to 140 rainy days per year on average (Tuan et al. 1999). The area is characterized by regular diurnal tides of 4 m amplitude and an average salinity of 10 to 11.2‰ (Tuan et al. 1999). The site of our field study was located adjacent to a small canal less then 100 m from the bordering, semi-intensive, shrimp farms.

**Sampling.** The *Kandelia candel* populations in northern Vietnam were visited in May 1999. We established plots of ca 100 and 3 $m^2$ in Gia Luan and Thai Thuy respectively, scaled to the widely different *K. candel* density in the sites (30-fold higher at Thai Thuy). Plots were set in triplicate in Gia Luan and 9 replicated plots were used at each of the thinned and unthinned stands in Thai Thuy. In Gia Luan, *K. candel* plots were established along the colonizing edge, where the 10 m × 10 m plots were separated by 15 to 25 m. The thinning at Thai Thuy was conducted as part of a previous experiment in August 1997, 21 mo before sampling.

At each location we selected 10 *Kandelia candel* saplings (>30 nodes each) and measured, to the nearest mm, the distances between nodes along the main axis, from the apical meristem down to the point where thickening rendered identification of the nodes undecipherable. At each location, we quantified the total number of meristems and the circumference (girth) of 54 plants encompassing the full range of sizes present. The size range was much narrower at Thai Thuy than at Gia Luan, as the largest tree in Thai Thuy was just 23.5 cm in circumference compared to 43.0 cm at Gia Luan. The circumference of the plants was measured to the nearest millimeter with a measuring tape around the base of the tree. For seedlings and saplings too small to allow accurate determination of circumference (girth <10 cm), the diameter was measured (using a caliper with an accuracy of ±0.25 mm) above the hypocotyl or any buttressing that may have developed secondarily at the base. The size distribution of the *K. candel* population in each plot was described by measuring the girth of every *K. candel* present.

In order to estimate the frequency of production of reproductive structures, we randomly selected about 15 to 20 reproductively active trees at each site. We then examined 3 randomly selected terminal branches in each tree to determine the percent of the nodes that produced inflorescences, as indicated by the presence of inflorescence scars (Fig. 1). The scaling of the frequency of inflorescences to the total production of reproductive organs was achieved by applying the frequency obtained to the number of meristems in the plot for plants larger than 12.5 cm in girth, since smaller plants were unlikely to be reproductively active.

About 40 fully-grown leaves were randomly selected and gathered from each site. The leaves were rinsed and kept refrigerated until dried to constant weight (80°C for 4 d). The leaves were then individually weighed on an electronic scale accurate to 0.1 g. About 30 inflorescences were gathered from Thai Thuy and kept refrigerated until dried to constant weight (80°C for 4 d). The dried inflorescences were weighed together, and the average weight per inflorescence was calculated as the ratio between the bulk weight and the number of inflorescences in the sample. For Gia Luan this was also done, but because the inflorescence were not yet in full bloom, only 2 fully developed inflorescence could be sampled.

**Data analysis.** The average number of nodes produced by each meristem annually was derived by identifying annual cycles based on the examination of the sequences of internodal lengths, as described in Duarte et al. (1999). Least-squares linear-regression was used to fit the allometric equation between total number of meristems per plant and plant girth, following logarithmic transformation of the variables.

## RESULTS

Seasonal cycles were clearly imprinted in all internodal length sequences in specimens of *Kandelia candel* examined (Fig. 2), resulting in an estimated average (±SE) number of internodes produced annually of 6.28 ± 0.22 and 5.96 ± 0.22 for Gia Luan and Thai Thuy, respectively.

The number of meristems was closely related to the girth of the plants (Fig. 3), as described by the regression equations:

$$\log M_{\text{tree}} = -0.35 + 1.83 \log \text{girth}$$
$(R^2 = 0.88, n = 54, p < 0.000001)$ (Thai Thuy)

$$\log M_{\text{tree}} = -0.91 + 2.23 \log \text{girth}$$
$(R^2 = 0.87, n = 54, p < 0.000001)$ (Gia Luan)

These equations reveal some differences in the development of meristems as a function of plant size, indicated by a faster increase in meristems with increasing girth in Gia Luan compared to Thai Thuy, where, in contrast, stems of small plants had a greater number of meristems than small plants at Gia Luan.

The size distribution of *Kandelia candel* was highly skewed at all sites, particularly at the unthinned stand at Thai Thuy (Fig. 4), so that the populations were numerically dominated by small plants, with an exponential decline in the number of plants as size increased.

Examination of inflorescence scars indicated the frequency of production of reproductive structures to be 0.31 and 0.22 inflorescences node$^{-1}$ at Gia Luan and Thai Thuy sites, respectively. This results in an annual rate of inflorescence production of 1.99 and 1.31 branch$^{-1}$ at Gia Luan and Thai Thuy sites, respectively. The average dry weight of individual leaves was 0.63 and 0.32 g, and that of the inflorescences was 0.5 and 0.43 g at Gia Luan and Thai Thuy respectively.

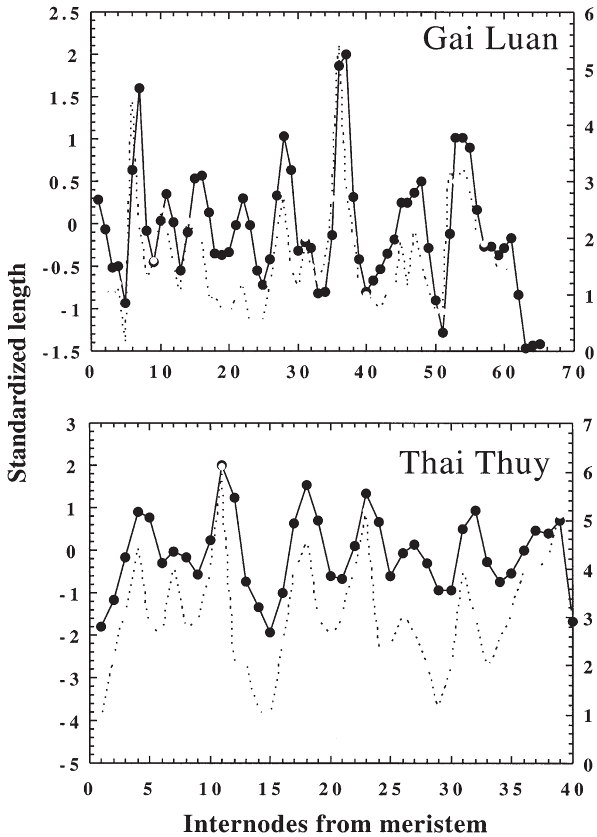


Fig. 2. *Kandelia candel.* Sequence of internodal length in stems for a representative plant from each site. Broken line and open circles: raw data; continuons line and filled circles: filtered data highlighting seasonal trend. Filtering of the internodal length sequences followed Duarte et al. (1999), whereby to remove subseasonal and interannual variability, the short-term and long-term filters were empirically set at 2 and 10 internodes respectively

The areal density of meristems in the stands was similar for Gia Luan and the thinned Thai Thuy stands, but was much greater for the unthinned stand (Table 1). These estimates were combined with those of the number of leaf pairs each meristem produces annually and the average weight of a fully-developed leaf to derive estimates of the net leaf production, as described above. The results obtained indicated a net leaf production (dry wt) ranging from 176.5 to 1338.7 g m$^{-2}$ yr$^{-1}$, being highest in the unthinned Thai Thuy population (Table 1). Similarly, we estimated the total inflorescence production to range from 0.9 to 101 g m$^{-2}$ yr$^{-1}$, again being highest for the unthinned Thai Thuy population (Table 1). Hence, inflorescence production represented about 10% of the combined leaf and inflorescence production, except for the thinned stand, where the removal of the larger, mostly reproductive,

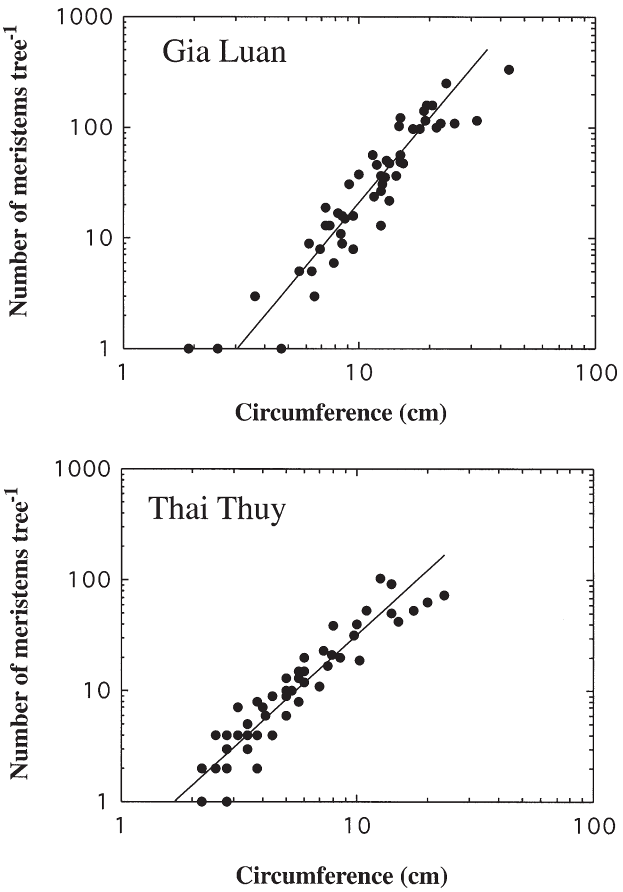


Fig. 3. *Kandelia candel.* Relationship between number of meristems and girth of plants at the sites studied in Vietnam. Lines represent the fitted regression equations

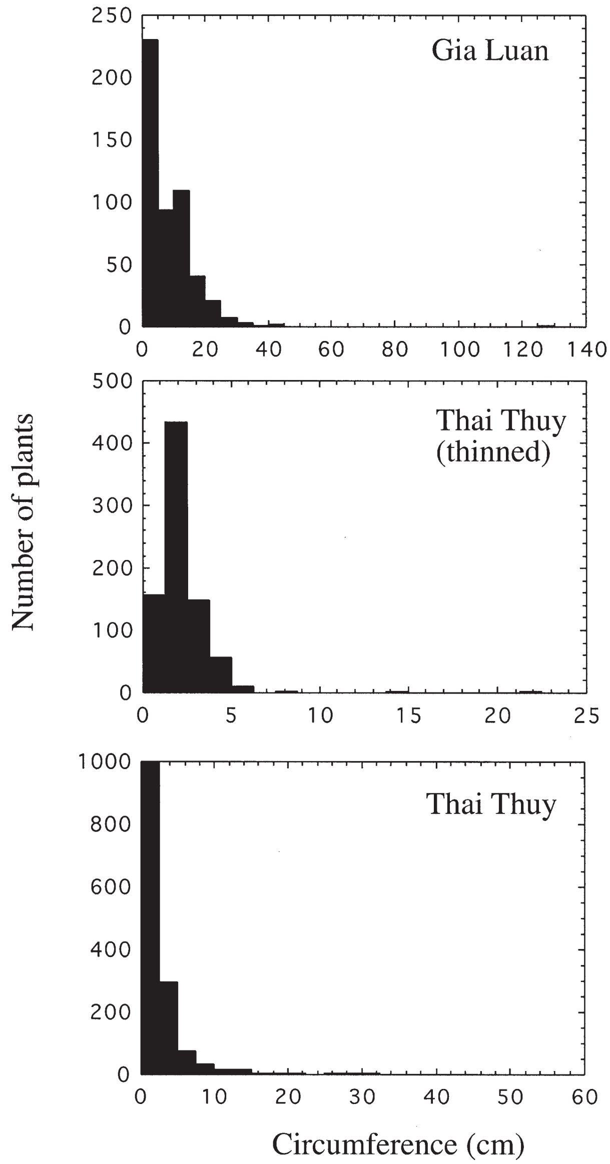


Fig. 4. *Kandelia candel.* Circumference distribution of plants at the sites studied in Vietnam. Sample size 512 for Gia Luan, and 1452 and 808 for unthinned and thinned stands, respectively, at Thai Thuy

trees resulted in a contribution of inflorescence production of only about 1% of the combined production (Table 1).

The method applied allowed the calculation of individual production per plant. These calculations revealed that the largest individuals, comprising 10% of the population, contributed the majority of the stand production, particularly at unmanaged stands, being responsible for 75 and 65% of the net leaf production at Gia Luan and Thai Thuy, respectively (Fig. 5). Thinning of the population in Thai Thuy resulted in a less uneven distribution of the contribution of the individual plants to the net leaf production, where the largest individuals, comprising 10% of the population, contributed about half of the production (Fig. 5).

## DISCUSSION

We have presented here a new approach to the estimation of net leaf production by the mangrove species *Kandelia candel* at 2 sites in Northern Vietnam. The net primary production at these sites differed by a factor of 5, reflecting the contrast between the monospecific nature of the Thai Thuy plantation and the mixed nature of the natural stand at Gia Luan. The extremely high density of *K. candel* at Thai Thuy (57 ind. m$^{-2}$ versus 1.7 ind. m$^{-2}$ at Gia Luan) further compounds this difference. This large discrepancy in density between the 2 sites was partially compensated by the much larger average tree size at Gia Luan (Fig. 4). The 30-fold difference in density only resulted in a 5-fold

Table 1. *Kandelia candel.* Meristem density, number of leaves and inflorescence produced, and their equivalent net production in stands sampled in Vietnam. Estimates followed the calculations described in 'Methods'

| | Gia Luan | Thai Thuy unthinned | Thai Thuy thinned |
|---|---|---|---|
| Meristem density (meristems $m^{-2}$) | 66 ± 7.5 | 350.5 ± 63 | 60.5 ± 7.5 |
| Leaves produced (number of leaves $m^{-2}$ $yr^{-1}$) | 829.3 | 4183.5 | 551.6 |
| Net leaf production (dry wt, g $m^{-2}$ $yr^{-1}$) | 525.8 | 1338.7 | 176.5 |
| Inflorescences produced (inflorescences $m^{-2}$ $yr^{-1}$) | 104.2 | 235.2 | 2.1 |
| Net inflorescence production (dry wt, g $m^{-2}$ $yr^{-1}$) | 46.4 | 101.1 | 0.9 |
| Leaf + inflorescence production (dry wt, g $m^{-2}$ $yr^{-1}$) | 572.2 | 1439.9 | 177.4 |

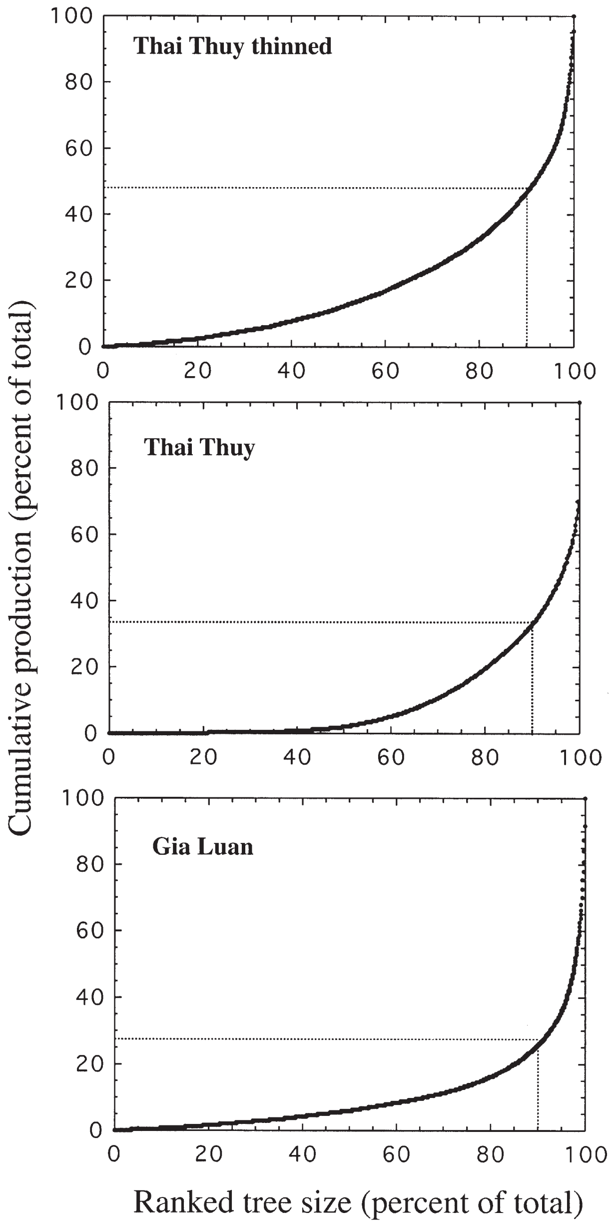


Fig. 5. *Kandelia candel.* Cumulative distribution of percent production with increasing tree size (also as percent) for populations at the sites studied in Vietnam

difference in production due to the fact that the number of meristems per tree increases as the square of the tree girth. Hence a few (10%) of the trees in Gia Luan contributed most (75%) of the net production (Fig. 5). The results obtained clearly illustrate that differences in age structure have a dominant influence over the net primary production of mangrove stands.

An additional source of variance between the 2 stands was the observed differences in the scaling of meristem development to tree size, which was fastest for Gia Luan. The differences between the allometric equations for Gia Luan and for Thai Thuy show that the trees in Thai Thuy branch more profusely at smaller diameters (i.e. at a younger age) than they do at Gia Luan. However, this tendency is reversed as the trees grow in circumference, for larger trees at Gia Luan branched more profusely, eventually exceeding the number of meristems for similar-sized trees in Thai Thuy. Indeed, variability in tree growth within a stand introduces error in the method. Although this source of uncertainty has a bearing on the precision of the estimates, it does not compromise the robustness of the results presented, for the error about the estimated meristem density (the component of the calculation influenced by variability about tree growth) is within 10 to 20% of the mean estimate.

The estimates of net leaf production (dry wt) obtained were comparable or higher than those previously derived from *Kandelia candel* populations in eastern Asia (an average of about 400 g $m^{-2}$ $yr^{-1}$ for *K.candel* populations growing in Southern China [Tam et al. 1998], and Hong Kong [Lee 1990]). These estimates, however, were derived using the litterfall technique compared to the allometric approach we used. Estimates of litterfall are available for the (unthinned) Thai Thuy stand, ranging between 190 g $m^{-2}$ $y^{-1}$ and 630 g $m^{-2}$ $yr^{-1}$, which are substantially lower than the estimate we obtained at the unmanaged stand, despite the fact that our estimates neglected the contribution of woody parts and of fruits. This difference may be largely explained by flaws in the assumptions of the litterfall method.

The litterfall method assumes populations to be in steady state, experiencing no significant increase or decrease in standing biomass with time. However, the planted stands at Thai Thuy are experiencing a rapid biomass accretion, particularly fast for 7 to 9 yr-old plants, for which biomass may increase by 21 to 45% annually (Tuan et al. 1999). Estimates derived from the litterfall method would have to be corrected by adding the net biomass gain of the stand; this would have largely bridged the gap between our production estimates and those derived from the litterfall method for this stand. Furthermore, the production of young seedlings, which were numerically dominant at the stands, is not incorporated in the litterfall estimates, for the nets are placed above the high-tide level, whereas the seedlings may be totally submerged at high tide. This is, however, a minor source of underestimation in the litterfall method, for seedlings, although numerically dominant, contribute a modest fraction to the production. Additional differences between the litterfall and realized net production may derive from material lost to wind, decomposition, animal activity or vandalism. The estimates derived here are also affected by particular sources of underestimation, primarily the fact that the estimates reported here did not include stem material nor fruits. These flaws can be, however, easily corrected by incorporating the weight of the stem material (which corresponds to the number of internodes produced annually) and that of the wood material resulting from the increase in girth of the plants in different size classes. Our observations also indicate that the development of fruits and eventually seedlings is associated with an increase in girth of the peduncle, resulting in a broader scar after it is shed. Hence, a calibration of scar size versus developmental stage and weight of the reproductive structures should allow the discrimination between inflorescence and fruit production at different stages.

Litterfall studies, although very popular in the assessment of mangrove productivity, only yield accurate estimates of net production (as opposed to litterfall production) when dealing with a steady-state forest. Estimates derived through litterfall analysis are based on what falls from the trees, not what the trees are actually producing, and therefore cannot provide an accurate estimate of production for a forest that is increasing its standing biomass.

In summary, we have presented and demonstrated the use of a new approach to estimate the net primary production of *Kandelia candel* using a retrospective, allometric approach. This approach should be applicable to other members of the Rhizophoraceae family, which bear similar imprints of their past growth history on their stems. The retrospective method presented here is based on a hierarchical approach to a demographic growth analysis of mangrove production. Demographic growth analysis focuses on the rate of production of plant modules (McGraw & Garbutt 1990), such as individual leaves or inflorescences. The production of individual modules must be scaled to the stand level, which requires an integration from the individual meristem (responsible for the production of leaves) to the entire tree and, ultimately, to the entire stand. This scaling exercise is implemented in the method presented through: (1) the use of allometric relationships to scale the activity of individual meristems to the entire plant, and (2) the integration of the individual plants using the distribution of plant size in the population, which is perhaps the single-most influential element in the analysis. This hierarchical approach, combined with some basic understanding of mangrove growth and architecture, allows the net production of the stands to be estimated in a reliable and inexpensive manner (in terms of resources and time). Use of this method in rapid assessment plans should allow for a more accurate evaluation of the effectiveness of regional mangrove afforestation plans in recovering the lost functions of these important ecosystems, which are partially dependent on their production.

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