

MANGROVE PRIMARY PRODUCTION AND ABOVE- AND BELOW-GROUND BIOMASS IN SAWI BAY, SOUTHERN THAILAND

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ABSTRACT

Above- and below-ground biomass and primary productivity of mangroves was estimated at two 3-yr old, one 5-yr old and one 25-yr old forest in southern and northern Sawi Bay. Mean stand density (5402 stems ha⁻¹), diameter at breast height (11 cm) and above-ground biomass (344 t DW ha⁻¹) were significantly greater at the oldest forest. Among the three younger stands, tree densities ranged from 9623 to 15,067 stems ha⁻¹, diameter at breast height ranged from 3 to 4 cm, and above-ground biomass ranged from 42 to 65 t DW ha⁻¹. The bulk of above-ground biomass in all four forests was vested in stems (63–78% of total biomass). Vertical distribution of fine roots indicated live roots constituted only 3 to 16% of total below-ground biomass. Below-ground biomass was significantly greater at the oldest forest (35.6 t DW ha⁻¹) than at the other three stands (range: 8.1–23.1 t DW ha⁻¹). Total living below-ground biomass accounted for 9 to 35% of total living biomass among the four forests. Estimates of leaf area index (LAI) varied from 1.6 to a maximum of 5.1 at the oldest forest. Net canopy primary production ranged from a minimum of 24.5 tC ha⁻¹ yr⁻¹ at the 5 yr-old forest to a maximum of 76.6 tC ha⁻¹ yr⁻¹ at the 25 yr-old forest. Of the two 3 yr-old forests, the *Rhizophora* forest was more productive (53.7 tC ha⁻¹ yr⁻¹) than the adjacent *Ceriops* stand (33.3 tC ha⁻¹ yr⁻¹). Extrapolating to the entire area of mangroves in Sawi Bay (3225 ha) based on similar forest types and subtracting canopy respiration, total canopy net carbon fixation averages 34 tC ha⁻¹ yr⁻¹ for a grand mean of 109,650 tC yr⁻¹. Compared with other Southeast Asian mangroves, the forests of Sawi Bay are highly productive.

INTRODUCTION

Mangrove forests are usually very productive ecosystems thought to be important sources and sinks of carbon within the tropical coastal zone (Twilley *et al.*, 1992; Ong, 1993; Alongi, 1998). In Southeast Asia, mangroves are an important source of wood for many socioeconomic purposes, but the growth of human populations, coastal aquaculture and agriculture, and tourism has placed increasing pressure on the survival of these tidal forests. Thailand, for instance, lost mangroves at the rate of ~13,000 ha yr⁻¹ from 1979 to 1986, and although the destruction rate has declined, the country is still losing forests at an alarming rate (Aksornkoae *et al.*, 1993). The effect of mangrove losses on the alteration of carbon cycling along such impacted tropical coastlines is unknown.

For this reason, a large-scale project was initiated to identify sources of carbon fixation and

storage in relatively pristine and in moderately impacted tropical coastal ecosystems (see Preface, this issue). In the pristine ecosystem (Hinchinbrook Channel, Australia), mangroves were identified as the largest single source of organic carbon, accounting for 56% of total carbon input (Alongi *et al.*, 1998). Further, it was estimated that most mangrove carbon was available for export to the adjacent coastal zone. The mangroves of Hinchinbrook Channel are composed mostly of mature stands of *Rhizophora stylosa* Griff., *Rhizophora apiculata* Bl. and *Ceriops australis* C.T.W. (Bunt and Bunt, 1999) with rates of biomass accumulation ranging from 2.6 to 11.7 t DW ha⁻¹yr⁻¹ (Clough, 1998).

The moderately impacted ecosystem chosen for study was Sawi Bay in Chumphon Province of southern Thailand. Sawi Bay is a more open, similar-sized (160 km²) coastal embayment compared to Hinchinbrook Channel. Sawi Bay is a shallow (~3 m depth), crescent-shaped

embayment fringed by mostly *Rhizophora* and *Ceriops* plantations. The watershed consists of intensive aquaculture, mussel culture, fisheries and various agricultural activities; the bay is also subjected to sewage loading and other human perturbations.

In this paper, we estimate rates of primary production and above- and below-ground biomass in some mangrove stands of different age in northern and southern Sawi Bay. As part of a broader effort to estimate mass balance of carbon, we extrapolate our results to estimate the contribution of mangrove forests to carbon cycling within the entire bay.

MATERIALS AND METHODS

Study sites

Four mangrove stands were chosen in Sawi Bay (Fig. 1) for our biomass and productivity

measurements. Below-ground root biomass measurements were made in October 1999 and estimates of above-ground biomass and primary productivity were made in April 2000.

Forests S1 and S2 were located on opposite sides of a small tidal river, Khlong Sawi, in the southern part of the bay. Stn S1 ($10^{\circ}16.8'N$, $99^{\circ}9.8'E$) is a mid-intertidal *Rhizophora apiculata* forest that was partially clear-felled once 15 yrs ago, and allowed to regenerate naturally. The mature trees in this stand are ~ 25 yrs old. The forest is inundated by tides $\sim 50\%$ on a monthly average.

Stn S2 ($10^{\circ}16.7'N$, $99^{\circ}9.8'E$) is a high-intertidal *R. apiculata* plantation (with *A. alba* Blume and *C. tagal* (Perr.) C.B. Robinson as subdominants), manually planted 5 yrs ago and maintained by the Royal Forest Department. This forest is inundated $\sim 10\%$ on a monthly average. The canopy is more open than at Stn S1, to the extent that $\sim 75\%$ of

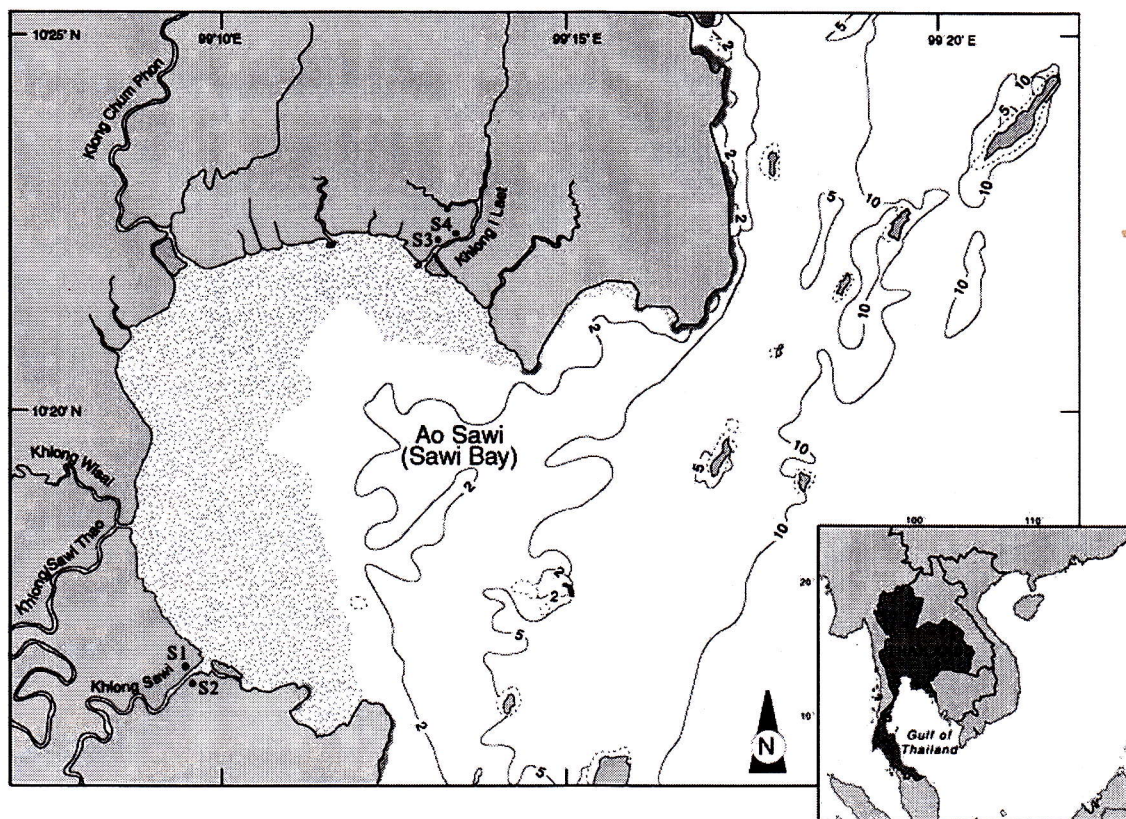


Figure 1 Location of the four mangrove forests within Sawi Bay, and Sawi Bay in relation to the southern coast of Thailand. Darkened areas depict mangrove forests, dotted areas depict intertidal sand-flats.

the forest floor is colonized by a mixture of cyanobacterial, and green and red macroalgal mats.

Stns S3 (10°22.4'N, 99°13.2'E) and S4 (10°22.4'N, 99°13.3'E) adjoin within the same plantation located on a small tidal estuary, Khlong I Laet, in the northern part of Sawi Bay. This plantation was originally the site of a failed shrimp pond, and was manually replanted 3 yrs ago. Stn S3 is a *R. apiculata* stand within the mid-intertidal zone (~25% monthly tidal inundation frequency). Stn S4 is located in the high-intertidal zone (~15% monthly tidal inundation frequency) and is inhabited by *Ceriops decandra* (Griff.) Ding Hou.

Below-ground biomass estimates

Below-ground fine root biomass in each forest was estimated by taking three replicate cores (6 cm i.d.) in each plot to a maximum sediment depth of 1 m. Each core was subdivided by 2 cm intervals to 40 cm, then by 5 cm intervals to 1 m. In the laboratory, roots were washed of sediment and debris, and live and dead roots were separated using the colloidal silica method of Robertson and Dixon (1993).

Above-ground biomass and productivity estimates

Within each forest, three separate sets of measurements were made for species identification, basal area and diameter at breast height (DBH) using the angle count cruising method (Cintron and Novelli, 1984; Clough, 1997). These data were used to calculate stem density (stem ha⁻¹) which in turn was used to estimate biomass (t ha⁻¹) based on the allometric relationships for each species in Clough and Scott (1989) for single-stemmed trees and in Clough *et al.* (1997) for multi-stemmed trees.

Within these same plots, net canopy production was estimated using the light interception method of Bunt *et al.* (1979) as modified by Clough (1997). Measurements of light absorption by the forest canopy (100–250 light readings per plot on a sunny day between 1000 and 1400 hrs) were used to estimate leaf area index, L (= m² leaf area m⁻² ground area) using the formula,

$$L = [\log_e (I)_{mean}] - [\log_e (I_0)_{mean}] / -k$$

where, $(I)_{mean}$ = the mean photosynthetically active radiation (PAR) under the canopy; $(I_0)_{mean}$ = incident PAR; and k = canopy light extinction coefficient (0.5). L was corrected to a solar zenith angle (θ) of 10° for the latitude of these forests.

The leaf area index (L) was then converted to net canopy photosynthesis (P_N) using the formula,

$$P_N = A \times \underline{d} \times L$$

where, \underline{d} = daylength (hrs) and A = average rate of photosynthesis per unit leaf area. A , was measured in Sawi Bay forests by Clough *et al.* (2000a). The empirical values are 0.3456 for *Rhizophora apiculata*, 0.4752 for *Avicennia alba* and 0.2592 for *Ceriops tagal*; the last value was assumed to be valid for *C. decandra*.

RESULTS AND DISCUSSION

Estimates of stand density, basal area and diameter at breast height (Table 1) show that the oldest forest (Stn. S1) was composed of larger diameter trees (mean DBH: 11.2 cm) of greater above-ground biomass than in the younger forests (Stns S2, S3 and S4; Tables 2–4). The younger stands were, however, more dense; mean stand densities and basal areas ranged from 9623 to 15,067 stems ha⁻¹ and from 34.7 to 44.7 m² ha⁻¹. The oldest forest (Stn. S1) was less dense, averaging 5402 trees ha⁻¹ with a mean basal area of 33.3 m² ha⁻¹ among replicate plots (Table 1).

Total above-ground biomass (tonnes dry weight ha⁻¹) averaged 344.2 t DW ha⁻¹ at Stn. 1 (Table 5) with significantly (ANOVA, $P < 0.05$) less biomass at the three plantation forests (range: 42.0–65.4 t DW ha⁻¹; Tables 2–4). Most above-ground biomass was vested in stems (63–78% of total biomass) than in leaves, branches and, in the case of *Rhizophora*, prop roots. Among the three *Rhizophora* forests (Stns. S1–S3), proportionally more above-ground biomass was vested in prop roots within the oldest forest (19% of total above-ground biomass) than in the two younger forests where leaf biomass was a greater proportion of

Table 1 Stand density (stems ha⁻¹), DBH (cm), BA (basal area, m² ha⁻¹) and total and component above-ground biomass (t ha⁻¹) in three replicate plots at forest S1.

	Stand density	DBH	BA	Total Biomass	Leaf Biomass	Branch Biomass	Stem Biomass	Prop Root Biomass
Plot 1	2776	12.9	29	278.8	8.4	33.8	171.8	57.3
Plot 2	5404	10.5	35	311.4	10.6	37.7	196.9	58.3
Plot 3	8025	10.3	36	442.5	15.2	53.6	280.4	82.2
Mean±1SE	5402±1239	11.2±0.7	33.3±1.8	344.2±40.9	11.4±1.6	41.7±5.0	216.4±26.8	65.9±6.7

Table 2 Stand density (stems ha⁻¹), DBH (cm), BA (basal area, m² ha⁻¹) and total and component above-ground biomass (t ha⁻¹) in three replicate plots at forest S2. Values in plot 1 for DBH, BA and biomass include all species.

	Stand density	DBH	BA	Total Biomass	Leaf Biomass	Branch Biomass	Stem Biomass	Prop Root Biomass
Plot 1	12,000*	3.4	30	30.8	2.8	3.4	21.4	3.2
Plot 2	17,600	3.0	44	36.5	2.5	4.3	26.0	3.8
Plot 3	15,600	3.8	39	58.8	3.6	7.0	41.4	6.8
Mean±1SE	15,067±1339	3.4±0.2	37.7±3.3	42.0±7.0	2.9±0.3	4.9±0.9	29.3±5.1	4.6±0.9

* *Rhizophora apiculata* = 9600; *Avicennia alba* = 1600; *Ceriops tagal* = 800 stems ha⁻¹

Table 3 Stand density (stems ha⁻¹), DBH (cm), BA (basal area, m² ha⁻¹) and total and component above-ground biomass (t ha⁻¹) in three replicate plots at forest S3.

	Stand density	DBH	BA	Total Biomass	Leaf Biomass	Branch Biomass	Stem Biomass	Prop Root Biomass
Plot 1	10,857	4.1	38	48.7	2.9	5.9	34.6	5.9
Plot 2	17,778	4.4	32	101.5	5.7	12.3	71.3	12.9
Plot 3	11,000	3.9	34	45.8	2.8	5.6	43.7	5.5
Mean±1SE	13,212±1865	4.1±0.1	34.7±1.4	65.4±14.7	3.8±0.8	7.9±1.8	46.2±10.3	8.1±1.9

Table 4 Stand density (stems ha⁻¹), DBH (cm), BA (basal area, m² ha⁻¹) and total and component above-ground biomass (t ha⁻¹) in three replicate plots at forest S4.

	Stand density	DBH	BA	Total Biomass	Leaf Biomass	Branch Biomass	Stems Biomass
Plot 1	10,571	4.3	37	61.3	2.8	8.8	47.8
Plot 2	6964	3.7	39	28.7	0.4	4.0	22.4
Plot 3	11,334	3.8	58	48.4	2.3	6.7	637.6
Mean±1SE	9623±1100	4.0±0.2	44.7±5.5	46.0±7.7	1.8±0.6	6.5±1.1	35.9±6.0

total biomass (6–7%) than at Stn. S1 (3%). At all four forests, branches constituted 12 to 14% of the total above-ground biomass (Tables 1–4).

The vertical distribution of fine-roots at all four forests (Fig. 2) showed that most fine roots were dead, with large subsurface accumulations of dead

roots below 40 cm depth at Stns. S1, S3 and S4. The distribution of living roots showed little, if any, significant change among depth intervals at all four forests. Living root biomass was significantly greater at Stns S1 and S2 than at Stns S3 and S4 (ANOVA, $P < 0.05$)

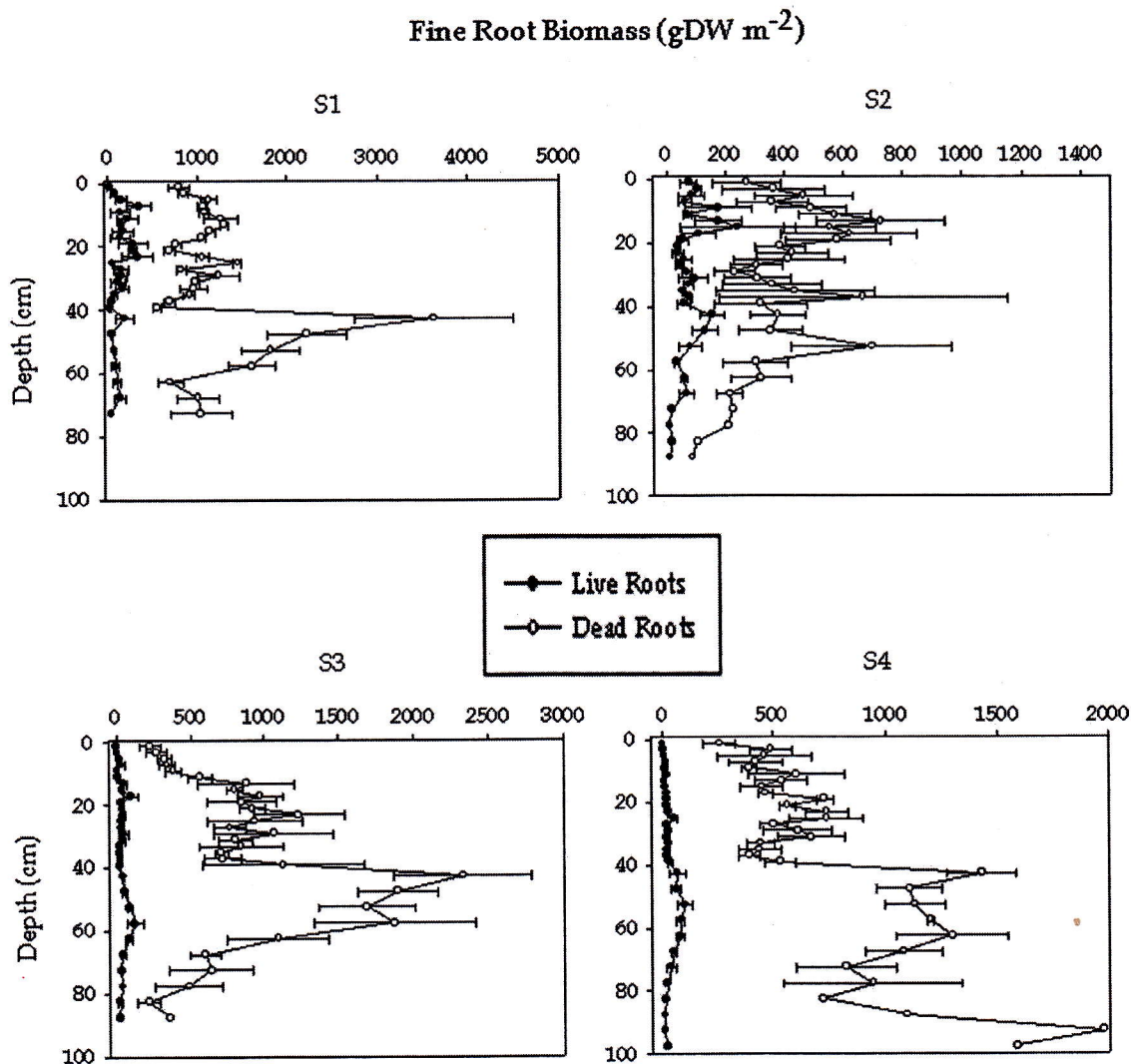


Figure 2 Vertical distribution of live and dead fine roots, expressed as g DW m⁻², at all four mangrove forests. Values are mean \pm 1 S.E.

Total living below-ground biomass ranged from 8.1 to 35.6 tonnes dry weight ha⁻¹ among the forests (Table 5), constituting only 9 to 35% of total living biomass and 3 to 16% of total living + dead, below-ground biomass.

Estimates of leaf area index (LAI) varied from 1.6 at Stn. S2 to a maximum of 5.1 at the oldest forest (Table 6). Net canopy primary production ranged from a minimum of 24.5 tC ha⁻¹ yr⁻¹ at S2 to a maximum production rate of 76.6 tC ha⁻¹ yr⁻¹ at S1 (Table 6). At the I Laet Creek plantation, the *Rhizophora* forest was more productive (53.7 tC ha⁻¹ yr⁻¹) than the *Ceriops* stand (33.3 tC ha⁻¹ yr⁻¹).

The measurements of light attenuation under the forest canopy and leaf photosynthetic rates (Clough *et al.*, 2000a) indicate that the *Rhizophora* and *Ceriops* forests of Sawi Bay are very productive. In a review of carbon flow in coastal ecosystems, Gattuso *et al.* (1998) estimated that mangrove canopy primary production ranges worldwide from 12 to 143 mol C m⁻² yr⁻¹, with a grand mean of 58 mol C m⁻² yr⁻¹. Mangrove primary production in Sawi Bay ranged from 204 to 638 mol C m⁻² yr⁻¹—several times greater than previous estimates. These differences are, however, mainly a reflection of improvements to the original method

Table 5 Mean above- and below-ground biomass (tonnes DW ha⁻¹) at each of the four forests.

	S1	S2	S3	S4
Total above-ground biomass	344.2	42.0	65.4	46.0
Total living below-ground biomass	35.6	23.1	11.2	8.1
Total dead below-ground biomass	317.1	117.5	258.7	249.5
Total living biomass	379.8	65.1	76.6	54.1
Total biomass (living + dead, above- and below-ground)	696.9	182.6	335.3	303.6

Table 6. Estimates of leaf area index (LAI) and net canopy primary production (NPP) in the four forests at Sawi Bay, April 2000. Values are mean \pm 1 S.E. (n = 3 plots per forest).

Forest	LAI	NPP (t C ha ⁻¹ yr ⁻¹)
S1	5.1 \pm 0.5	76.6 \pm 7.5
S2	1.6 \pm 1.1	24.5 \pm 16.8
S3	3.6 \pm 1.0	53.7 \pm 14.9
S4	2.9 \pm 1.9	33.3 \pm 21.8

of Bunt *et al.* (1979) upon which the bulk of the measurements cited by Gattuso *et al.* (1997) were made. Clough (1997) and Clough *et al.* (1997) suggested that the earlier measurements underestimate true canopy production by a factor of at least 5, and perhaps as by as much as tenfold. Comparing the Sawi Bay estimates with those using the improved method of Clough (1997) in mangroves of Western Australia (Alongi *et al.*, 2000) and Vietnam (Clough *et al.*, 2000b), the mangroves of Sawi Bay are still among the most productive forests measured in SE Asia.

The high rate of production is likely due to the relatively young age of these forests, although there appears to be no clear link between stand age and net primary production among the four Sawi Bay stands. The oldest forest (Stn. 1) is approximately 25 yrs old, and is the most productive. For *Rhizophora apiculata*, measurements in Vietnam (Clough *et al.*, 2000b) and in Malaysia (Ong, 1993) suggest that leaf area index and net primary production generally declines with age —as in terrestrial forests (Gower *et al.*, 1996). One reason why such a decline was not observed in this study may be the confounding effects of differences in soil types, nutrient concentrations and intertidal position. For example, the less productive forests (Stns. S2 and S4) were

located higher in the intertidal zone than the other two forests. However, Stns S2 and S4 had comparatively low and high concentrations of soil nitrogen, respectively.

Rates of primary production were linked to above-ground biomass ($r^2 = 0.89$; $P < 0.1$) but not significantly to below-ground living biomass. The above-ground biomass of Stn. S1 (Table 5) was greater than most other *Rhizophora*-dominated forests of similar age in Malaysia (Ong *et al.*, 1995; Tanouchi *et al.*, 2000), Thailand (Christensen, 1978; Aksornkoae *et al.*, 1993), Australia (Clough, 1998) and in comparison to mangroves at 10° latitude worldwide (Saenger and Snedaker, 1993). The three younger forests in Sawi Bay were expectedly smaller in size, given their age.

A comparison of below-ground biomass to other forests is problematic, given the lack of information not only of total below-ground biomass, but also of what proportion of below-ground roots are alive. In Ranong, Thailand, an extensive study of root distribution and biomass was conducted in mature mangrove forests by Komiyama *et al.* (1987). Total root biomass within the *Rhizophora apiculata* forest at Ranong averaged 509.5 tonnes DW ha⁻¹ with fine roots comprising 46.4% of the total, but live and dead roots were not distinguished. In Cuban mangroves, Fiala and Hernandez (1993) distinguished live from dead fine roots in *Rhizophora mangle* L. and *Avicennia germinans* (L.) Stern forests. Live roots constituted 47 to 55% of total below-ground biomass within the *R. mangle* forest; unlike our study, the greatest amount of total root biomass was concentrated in the 10–25 cm soil horizon. Total live root biomass averaged 17.05 t ha⁻¹ and total below-ground biomass within the *Rhizophora* forest averaged 32.3 t ha⁻¹ (to a depth of 40 cm). Extrapolating to 100 cm, these figures equate to

42.6 and 78.3 t ha⁻¹, respectively. In Sawi Bay, total below-ground biomass (living and dead fine roots) ranged from 140.6 t ha⁻¹ to 352.7 t ha⁻¹ at the mature forest, and from 140.6 to 269.9 t ha⁻¹ at the three younger stands. However, 84 to 97% of the total below-ground biomass was dead. These recent studies suggest that most earlier data (Golley *et al.*, 1962, 1975; Briggs, 1977; Komiyama *et al.*, 1987) of below-ground biomass in mangrove forests are overestimates (Fiala and Hernandez, 1993).

To extrapolate our results to the entire mangrove ecosystem of Sawi Bay, we used Ratanasermping *et al.* (2000) estimate of the total area of mangroves of 3225 hectares, and the estimate by Clough *et al.* (2000a) that canopy respiration accounts for ~31% of total whole canopy fixation in these stands. Using these estimates and extrapolating our results to the area of similar forest types within the bay (Ratanasermping *et al.* 2000), we estimated that total annual whole canopy carbon fixation in Sawi Bay averaged 50 tC ha⁻¹yr⁻¹, which subtracting canopy respiration, is equivalent to a net fixation

rate of 34 tC ha⁻¹yr⁻¹. This latter figure is the amount carbon available for leaf, wood and root growth and wood respiration. Multiplying this figure by 3225 hectares, gives a total annual whole canopy net carbon fixation of 109,650 tC yr⁻¹, or 9.1×10^9 mol C yr⁻¹. Canopy respiration, estimated to be ~16 tC ha⁻¹ yr⁻¹, extrapolates to 51,600 tC yr⁻¹, or 4.3×10^9 mol C yr⁻¹ for the entire mangrove ecosystem of Sawi Bay.

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REFERENCES

- Aksornkoae S., N. Paphavasit and G. Wattayakorn. 1993. Mangroves of Thailand: present status of conservation, use and mangement. In: B.F. Clough (ed). The Economic and Environmental Values of Mangrove Forests and Their Present State of Conservation in the South-East Asia/Pacific Region, pp. 83–134. Mangrove Ecosystems Technical Reports, Vol. 1. International Society for Mangrove Ecosystems, Okinawa.
- Alongi, D.M. 1998. Coastal Ecosystem Processes. CRC Press, Boca Raton. 429p.
- Alongi, D.M., T. Ayukai, G.J. Brunskill, B.F. Clough and E. Wolanski. 1998. Sources, sinks and export of organic carbon through a tropical, semi-enclosed delta (Hinchinbrook Channel, Australia). *Mangr. Salt Marsh.* **2**: 237–242.
- Alongi, D.M., F. Tirendi and B.F. Clough. 2000. Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora* and *Avicennia* along the arid coast of Western Australia. *Aq. Bot.* **68**: 97–122.
- Briggs, S.V. 1977. Estimates of biomass in a temperate mangrove community. *Aust. J Ecol.* **2**: 369–373.
- Bunt, J.S., K.G. Boto and G. Boto. 1979. A survey method for estimating potential levels of mangrove forest primary production. *Mar. Biol.* **52**: 123–128.
- Bunt, J.S. and E.D. Bunt. 1999. Complexity and variety of zonal pattern in the mangroves of the Hinchinbrook area, Northeastern Australia. *Mangr. Salt Marsh.* **3**: 165–176.
- Christensen, B. 1978. Biomass and primary production of *Rhizophora apiculata* Bl. in a mangrove in southern Thailand. *Aq. Bot.* **4**: 432–452.

- Cintron, G. and Y.S. Novelli. 1984. Methods for studying mangrove structure. **In:** S.C. Snedaker and J.G. Snedaker (eds.). *The Mangrove Ecosystem: Research Methods*, pp. 91–113. UNESCO, Paris.
- Clough, B.F. 1997. Mangrove ecosystems. **In:** S. English, C. Wilkinson and V. Baker (eds.). *Survey Manual for Tropical Marine Resources*, 2nd ed. pp. 119–196. Australian Institute of Marine Science, Townsville.
- Clough, B.F. 1998. Mangrove forest productivity and biomass accumulation in Hinchinbrook Channel, Australia. *Mangr. Salt Marsh.* **2**: 191–198.
- Clough, B.F., P. Dixon and O. Dalhaus. 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Aust. J. Bot.* **45**: 1023–1031.
- Clough, B.F. and K. Scott. 1989. Allometric relationships for estimating above-ground biomass in six mangrove species. *Forest Ecol. Manag.* **27**: 117–127.
- Clough, B.F., P. Patanaporpaiboon and S. Pongpan. 2000a. Forest structure and carbon fixation by mangroves at Chumphon, southern Thailand. **In:** D.M. Alongi and T. Ayukai (eds.). *Carbon Fixation and Storage in Coastal Ecosystems-Phase 2*, pp.10–16. Final Report to the Kansai Electric Power Co., Japan, Australian Institute of Marine Science, Townsville.
- Clough, B.F., D.T. Tan, D.X. Phuong and D.C. Buu. 2000b. Canopy leaf area index and litter fall in stands of the mangrove *Rhizophora apiculata* of different ages in the Mekong delta, Vietnam. *Aq. Bot.* **66**: 311–320.
- Fiala, K. and L. Hernandez. 1993. Root biomass of a mangrove forest in southwestern Cuba (Majana). *Ekologia (Bratislava)* **12**: 15–30.
- Gattuso, J.-P., M. Frankignoulle and R. Wollast. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annu. Rev. Ecol. Syst.* **29**: 405–434.
- Golley, F.B., H.T. Odum and R.F. Wilson. 1962. The structure and metabolism of a Puerto Rico red mangrove forest in May. *Ecology* **43**: 9–19.
- Golley, F.B., J.T. McGinnis, R.G. Clements, G.I. Child and M.J. Duever. 1975. *Mineral Cycling in a Tropical Moist Forest Ecosystem*. Univ. of Georgia Press, Athens, 248p.
- Gower, S.T., R.E. McMurtrie and D. Murty. 1996. Aboveground net primary production decline with stand age: potential causes. *Trend Ecol. Evol.* **11**: 378–382.
- Komiyama, A., K. Ogino, S. Aksornkoae, and S. Sabhasri. 1987. Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. *J. Trop. Ecol.* **3**: 97–108.
- Ong, J.E. 1993. Mangroves—a carbon source and sink. *Chemosphere* **27**: 1097–1107.
- Ong, J.E., W.K. Gong and B.F. Clough. 1995. Structure and productivity of a 20-year-old stand of *Rhizophora apiculata* Bl. mangrove forest. *J. Biogeogr.* **22**: 417–424.
- Ratanasermpong, S., D. Disbunchong., T. Charupatt and S. Ongsomwang. 2000. Assessment of mangrove ecosystem change using remote sensing and GIS technology in Ao Sawi–Thung Kha, Chumphon, Thailand. *Phuket mar. biol. Cent. Spec. Publ.* **22**: 3–14.
- Robertson, A.I. and P. Dixon. 1993. Separating live and dead fine roots using colloidal silica: an example from mangrove forests. *Plant Soil* **157**: 151–154.
- Saenger, P. and S.C. Snedaker. 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia* **96**: 293–299.
- Tanouchi, H., S. Nakamura, Y. Ochiai and A. Hassan. 2000. Stand structure and aboveground biomass of a mangrove forest in Matang, peninsular Malaysia. **In:** JIRCAS International Workshop on Brackish Water Mangrove Ecosystems-Productivity and Sustainable Utilization, pp.35–38. Tsukuba International Congress Center, Japan.
- Twilley, R.R., R.H. Chen and T. Hargis. 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water Air Soil Pollut.* **64**: 265–288.