Structure and productivity of a 20-year-old stand of *Rhizophora apiculata* Bl. mangrove forest

ONG JIN-EONG*[1], GONG WOOI KHOON[2] and B. F. CLOUGH[3] [1]*Centre for Marine and Coastal Studies,* [2]*School of Biological Sciences, Universiti Sains Malaysia, 11800 Penang, Malaysia & [3]Australian Institute of Marine Science, PMB 3 Townsville MC, Queensland 4810, Australia*

Abstract. Mangroves are dominant interface ecosystems between the land and the sea in the tropics, and are of importance in the economy of many of these regions in terms of mangrove-linked fisheries and forestry. Recently, mangroves have been of particular interest in relation to global change both because of the possible high carbon sequestration as well as being in the 'forefront' of any sea-level change, because of their location. To understand the impact of global change on these ecosystems (considered terrestrial and aquatic at the same time) and vice versa, it is necessary to obtain 'a more comprehensive and realistic picture of the terrestrial carbon cycle', which is one of the aims of the GCTE Programme. We therefore present here some of the results of our long-term study (started in the mid-1970s) on the carbon and nutrient budget of a mangrove ecosystem as a basis for further studies, including the proposed large-scale biogeochemical transects and climate models proposed by GCTE.

The tree density of the 20 m × 40 m plot in the 20-year-old stand was equivalent to 2425 stems per hectare (1975 live trees per hectare). Size (girth at breast height) of *Rhizophora apiculata* trees ranged from 9 to 75.5 cm with a mean at 39 cm. The smallest live tree weighed 10 kg and the biggest weighed 510 kg with a mean biomass of 122 kg. About 70% of the trees were below 100 kg but the 30% of the bigger trees

contributed to slightly more than half of the total biomass of the plot. The canopy had an average height of 21 m. The total standing biomass was 114 t C ha^{-1}; 74% of the biomass was in the trunk, 15% in the roots (10% in stilts and 5% below-ground) and 10.6% in the canopy (only 2.6% in leaves).

Using allometric regressions, we obtained a net productivity (root turnover and loss through leaching were not measured but only approximated as equal to small litter production) of 17 ± 5 t C ha^{-1} yr^{-1}. If greater accuracy (than $\pm 30\%$) is needed, direct measurements of root turnover and leaching from roots would be needed. Using the gas exchange method and using the mean value for a whole day's net photosynthesis measurements (averaged at 6 μmol m^{-2} s^{-1}), 1.5 μmol m^{-2} s^{-1} for leaf respiration, a leaf area index of 4, and assuming respiration of the non-leaf tissues to be the same as for leaves, we estimated net productivity to be 11.35 t ha^{-1} yr^{-1}, almost at the lower limit of the allometric estimate. Use of leaf to tree to stand models may improve the accuracy of this method. The main gaps are in fine root turnover and possible loss of carbon through leaching from the roots.

Key words. Mangrove, *Rhizophora apiculata*, biomass partitioning, productivity, CO_2 gas exchange, photosynthesis.

INTRODUCTION

Even where they dominate and are most luxuriant, in the wet tropics, mangroves comprise only approximately 2% of the total land area. Over the last 30 years or so, this coastal tropical ecosystem has been subjected to ever-increasing human population and economic pressures. Ong (1982) estimated that the loss of mangroves in Malaysia was about 1% per year over the past 20 years. Since then the rate of destruction has most likely increased. In Thailand, for example, most of the mangroves on the eastern coast have been 'reclaimed' (mainly converted to ponds for the culture of the tiger prawn, *Penaeus monodon*). Where human population pressures are minimal, the mangrove woodchips

industry continues to systematically degrade huge areas of pristine luxuriant mangroves (Ong, 1994).

Small as they may be in area, the mangrove ecosystem is still a dominant and important tropical coastal ecosystem and its contribution as a carbon sink may be several times that of most other ecosystems (Ong, 1993). Yet there is very little quantitative studies on mangroves.

The International Geosphere–Biosphere Programme: a Study of Global Change (IGBP) is a recently launched programme. The aims of one of its core projects, on Global Change and Terrestrial Ecosystems (GCTE), include obtaining a more comprehensive and realistic picture of the terrestrial carbon cycle. Among the studies to be undertaken is one of establishing large-scale biogeochemical transect studies. Land-use intensity transects are being established in a number of tropical regions, including Southeast Asia. These 'are designed to answer critical questions

*Corresponding author.

about the impact of land use change, such as forest conversion in the humid tropics, on fundamental ecosystem processes, particularly biogeochemical cycling' (GCTE, 1994). The selection of suitable sites is critical to the success of such studies. The climatic rain forest ecosystems are obvious choices but edaphic rain forests (such as mangrove and peat swamp forests ecosystems) although occupying smaller areas may be equally important because of their role as carbon sinks. Apart from their probable importance in sequestering atmospheric carbon, both mangrove (because they are on the seaward edge) and peat swamp (because they are in very low lying areas) forests are highly susceptible to any change in sea levels, yet these ecosystems are often overlooked.

This paper, describing work done on a 20-year-old stand of *Rhizophora apiculata* Bl. dominated mangrove forest, is to show that there have been fundamental studies carried out on such ecosystems in the humid tropics and that the GCTE Transects could benefit by making use of and supplementing such existing studies. The work described here centres on estimating biomass and productivity of a stand of managed forest. It is meant to show that this is not as simple a task as might at first be expected and that there are still a number of technically difficult gaps to fill. This work is part of a long-term study on the carbon and nutrient budget of a mangrove ecosystem (started in the mid-1970s).

SITE

The study site is located near Kuala Sepetang in the Matang Mangrove Forest Reserve (100° 36'N, 4° 50'E) and covers an area of 40,000 ha. This forest has been managed by the Perak State Forestry Department since the early part of this century. A description of the management system can be found in Haron & Hassan (1981) and Ong (1982). Since the Forestry Department keeps records on fellings, it is possible to estimate the age of any particular stand to within ± 2 years of the actual age.

This 20-year-old stand (in 1992) has been identified by the Forestry Department as a display area to enable better access for the public to the mangroves and there is a newly constructed walkway next to the site. The site is only inundated by high spring tides so comes under inundation class 4 of Watson (1928). *Rhizophora apiculata* grows best in inundation class 3 (inundated by all high tides) so this site is on the dry side for *R. apiculata*.

METHODS AND MATERIALS

A multi-platform scaffolding tower was constructed at the site which extends to just above the canopy. The top of the canopy is about 22 m high. The tower allows us to install light and temperature sensors for light and temperature profiles as well as to allow us to make photosynthesis and other measurements.

Environmental parameters

Silicon light sensors (calibrated against a LI-COR underwater PAR quantum sensor) and copper–constantan ther-

mocouples were placed at different heights from just above the canopy to just above ground level. These were connected to data-loggers to continuously record 10-min averaged readings. Data were downloaded to portable personal computers daily.

Soil salinity was measured by squeezing water from soil at different depths and measuring with a temperature compensated, hand-held refractometer (with a salinity scale).

Mangrove shoot water potential was measured using a specially constructed high pressure bomb.

Forest stand structure and standing biomass

Eight 10 m × 10 m plots (covering 20 m × 40 m) were established around the tower and the girth at breast height (g.b.h.) of all the trees was measured, noting the species and whether alive, dead or cut. The first measurements were made in June 1992 and the second measurements were made in September 1993.

The total above-ground weight, trunk weight, leaf weight and canopy (branches, twigs, buds, flowers and propagules) weight of every tree was calculated using the regressions obtained by Ong, Gong & Wong (1985) for *Rhizophora apiculata* in the Matang Mangrove Forest Reserve. These are:

$$W_{ag(total\ above-ground\ weight)} = 0.0135\ g.b.h.^{2.4243} \quad (1)$$
$$(kg) \qquad\qquad (cm)$$

$$W_{trunk(total\ trunk\ weight)} = 0.0067\ g.b.h.^{2.5414} \quad (2)$$
$$(kg) \qquad\qquad (cm)$$

$$W_{leaf(total\ leaf\ weight)} = 0.0161\ g.b.h.^{1.4363} \quad (3)$$
$$(kg) \qquad\qquad (cm)$$

$$W_{canopy(total\ canopy\ weight)} = 0.0140\ g.b.h.^{1.8453} \quad (4)$$
$$(kg) \qquad\qquad (cm)$$

where g.b.h. = girth at breast height (1.3 m).

Stilt weight was obtained by subtracting the trunk weight and canopy weight from the total above-ground weight.

The below-ground weight was calculated using the regression equation of Ong, Gong & Wong (unpublished). Total biomass was obtained by adding below-ground weight to total above-ground weight.

Photosynthetic assimilation

Net photosynthetic assimilation as well as a number of related parameters such as leaf temperature, stomatal water conductance, photosynthetically active radiation and relative humidity were measured using a LI-COR LI-6200 Portable Photosynthesis Meter. The LICOR LI-6200 measures net photosynthetic assimilation, i.e. total carbon dioxide taken in by the leaf minus respiration (including photo respiration, should this occur) of the leaf. This is different from net productivity because respiration of all the other plant parts (like those for branches, trunk and roots) have not been accounted for. It is thus a measure between gross and net productivity.

Measurements were made on three rosettes of leaves (the top two pairs of leaves were used for rosettes 1 and 2 and the top pair for rosette 3), two rosettes (1 and 2) of sun
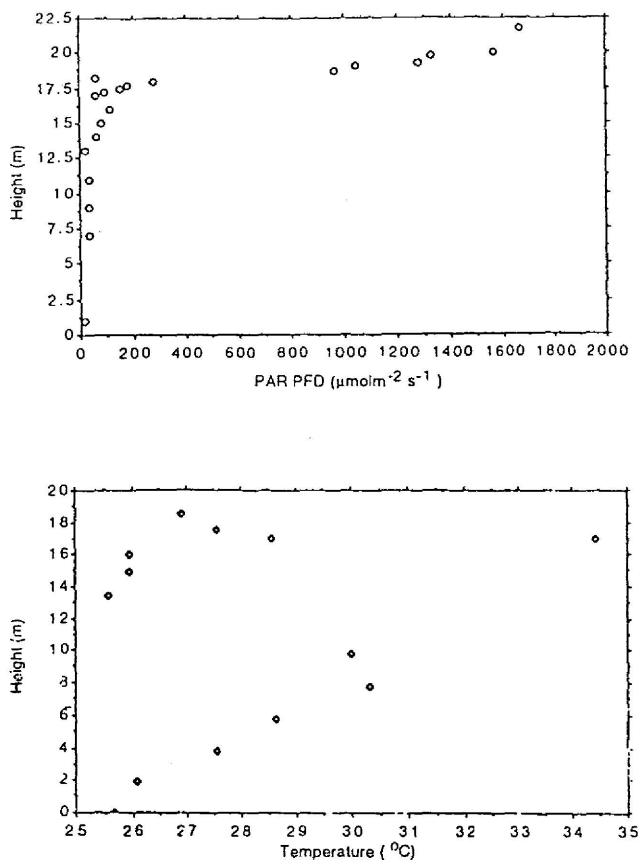
FIG. 1. Midday light (PAR) and temperature profiles. (a) Photosynthetically active radiation photon flux density profile in a 20-year-old forest stand. There are no leaves below about 10 metres from the crown. (b) Temperature profiles using copper–constantan thermocouples in the same forest stand.

leaves and one (rosette 3) of shade leaves, throughout the day (from about 06:50–20:00 h). The leaves in rosette 1 were measured eleven times, rosette 2 fourteen times and rosette 3 five times during the course of a day's measurements. There was thus a strong bias in sun leaves (measurements were made on shade leaves less than 5% of the time).

RESULTS

Environmental parameters

Light (PAR) and temperature profile. Fig. 1 shows typical (noon) light (PAR) and temperature profiles through the canopy. PFD ranged from 1670 μmol m^{-2} s^{-1} above the canopy to 14 μmol m^{-2} s^{-1} 1 m from the ground showing that just over 1% of the photosynthetically active radiation reaches the ground. The top sensor is above the canopy but the sensors located between about 10 m and 20 m are among the leaves of the crown of the tree, so exhibit a degree of variability. There are no leaves below about 10 m.

Temperature ranged from 34.5°C at the canopy to 25.6°C just off the ground. There is a great deal of variability, especially for the group of sensors in the crown (above 10 m). This is because these sensors are under leaves.

Soil salinity and shoot water potential. Fig. 2 shows a diurnal plot of shoot water potential and light. It can be seen that the predawn potential was around -1.96 MPa. This is approximately that of the osmotic potential of the soil salinity of 18.0 p.p.t. (at a depth of 10 cm at 06:30 h and 19:00 h). The shoot water potential decreased to -3.55 MPa, flattened off in the middle of the day and started to increase again at about 17:50 h dropping to -2.50 MPa, not quite reaching the predawn potential, suggesting that it takes a while for the plant to recover completely from water lost through transpiration.

Structure and standing biomass

The tree density (live, dead or cut) of the 20 m $\times$ 40 m plot was equivalent to 2425 stems per hectare. All were *Rhizophora apiculata*, apart from five small to medium-sized *Bruguiera parviflora* and a single very large (108.5 cm g.b.h.), *Bruguiera gymnorhiza* so that non-*Rhizophora apiculata* species constituted just over 3%; 18.5% of the trees were dead or had been recently cut so the density of live *Rhizophora apiculata* trees in the plot was equivalent to 1975 trees per hectare.

The size (g.b.h.) and biomass distribution of *Rhizophora apiculata* trees in the plot is shown in Fig. 3. The size of *Rhizophora apiculata* trees (both living and dead) ranged from 9 m to about 75.5 cm. Most (85%) of the trees were between 20 and 50 cm, with a peak (40%) at between 35 cm and 45 cm. The mean g.b.h. was 39 cm. The canopy had an average height of about 21 m.

The smallest (14.9 cm g.b.h.) live *Rhizophora apiculata* tree weighed 10 kg and the largest (75.5 cm g.b.h.) weighed 510 kg, with a mean biomass of 122 kg. About 70% of the trees were below 100 kg but 30% of the bigger trees contributed to slightly more than half of the total biomass of the plot. There was a large (g.b.h. = 108 cm) *Bruguiera gymnorhiza* tree weighing 1488 kg (aboveground biomass): about three times that of the largest *Rhizophora apiculata* tree. This plot was left out of the calculations on productivity because of the possible bias that this one large *B. gymnorhiza* tree may cause.

Very similar figures were given by Gong & Ong (1994) for a 18-year-old stand in the same forest. Figures were also very similar in terms of species composition and the proportion of dead trees. In terms of size distribution, the mean size of trees was slightly bigger for the 20-year-old stand and there was a group of large trees (65–75 cm g.b.h.) not found in the earlier study. This may be because the present stand is slightly older and there was no thinning at 15 years; consequently the present site had a higher standing biomass. Generally, a few large trees can contribute very significantly to increasing the total biomass.

Biomass partitioning

The partitioning of biomass is shown in Fig. 4. The total biomass was 114 t C ha^{-1}, of which 74% of the biomass was in the trunk, 15% in the roots (10% in stilt roots and 5% in below-ground) and 10.6% in the canopy (2.6% in leaves and 8% in branches, twigs, buds, flowers and propagules). The figure for below-ground roots is low compared with other studies and the reasons are as discussed by Clough (1992).

Productivity

Net productivity. Net productivity consists of four components: increment in biomass per unit time, the turnover of litter (leaves, small branches, fruits and flowers) and fine roots, herbivory and the loss of dissolved organic materials from the roots.

It can be seen from Fig. 4 that we have all the data for annual increase in standing biomass. Most of the increment is in the trunk (78%) and this is followed by roots (15%) both stilt roots (9%) and below-ground roots (6%); 7% (or about half the amount that went to roots) of the total annual increment in biomass went to the canopy (with only 1% going to leaf increment).

We only have productivity figures for small litter (leaf litter and branches, buds, flowers and propagules). Litterfall figures are those of Gong et al. (1984) for a 20-year-old in another site in the same Matang Mangrove Forest. Leaf litter productivity is fifty times standing leaf biomass increment. We do not have any data on fine root productivity but if it is anywhere near the fifty times standing biomass

increment figure for leaves, then this would be a very important 'missing' component.

We have no figures for herbivory but we have observed negligible herbivory during the 1 year and 3 months between the first and second measurements. In general, we have observed very little herbivory in *Rhizophora apiculata* and this may be because of its leathery leaves with its high phenolic content. We feel that it is safe to assume that herbivory did not decrease the productivity estimate of this stand of *Rhizophora apiculata* significantly.

We also have no figures on the possible loss of organic carbon through the roots. Since mangrove roots are tidally inundated, loss of organic carbon from roots could be significant (Clough, 1992). This is another important gap that needs filling.

Although only 1% of new biomass is allocated to leaves, a large proportion of the new biomass still goes to leaves in the form of leaf turnover (i.e. leaf litter production is 40% of total biomass increment). Turnover of trunk (perhaps some bark) and stilt root (above-ground) would be negligible but that of fine underground roots, for which we have as yet not been able to measure, may be very significant (perhaps as much, if not more than leaf turnover). As can be seen from Fig. 4, total net productivity in this 20-year-old stand of *Rhizophora apiculata* is at least (as we are as yet unable to measure fine root turnover) 12.24 t C ha^{-1} year^{-1}.

There is no estimate of all the components on net productivity for mangroves (Clough, 1992) and the figures reported here are as comprehensive as can be found for mangroves to date. The main gaps are for root turnover and for leaching of organic matter from the roots (through tidal
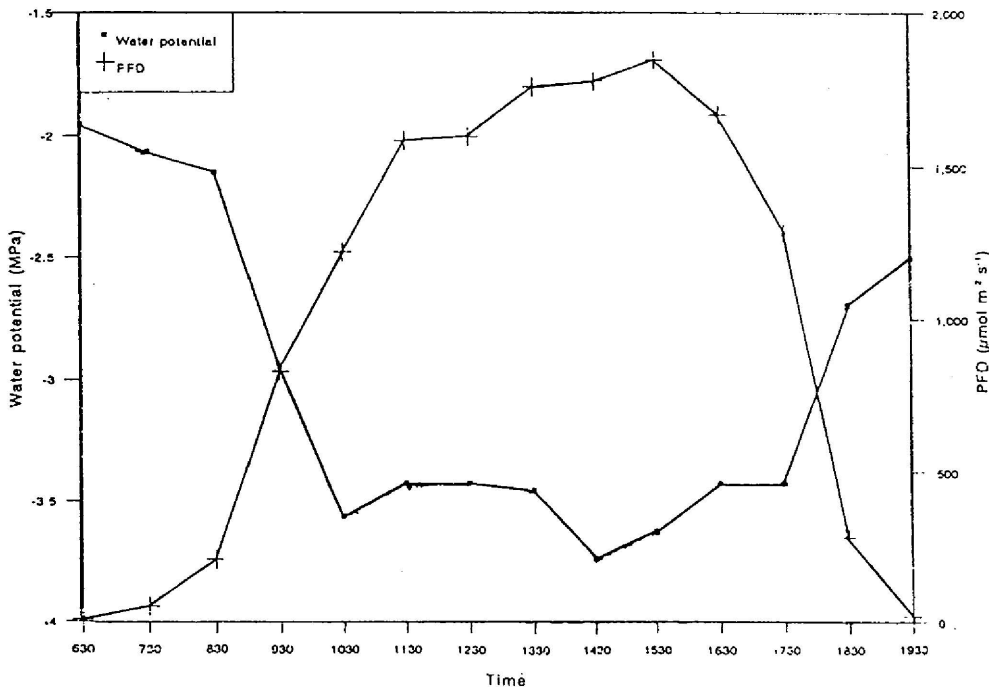

FIG. 2. Shoot water potential and light (PAR) characteristics through a day. ■- - - - -■, shoot water potential; +- - - - -+, PAR.
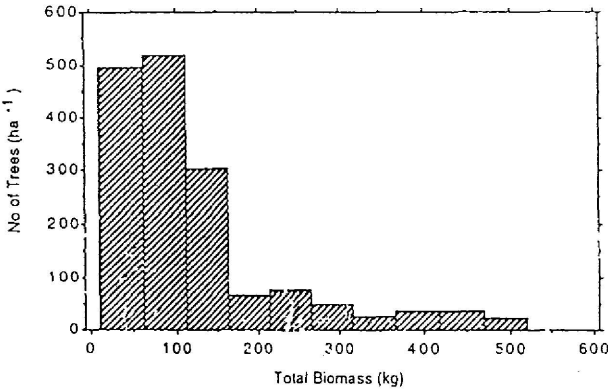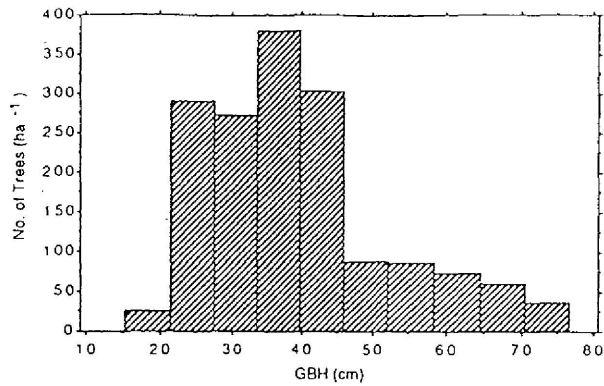
FIG. 3. Tree size distribution, based on girth (a) and biomass (b).

flushing). These are difficult gaps to fill but none the less need to be done if we are to determine the role of mangroves as carbon sources or sinks.

Photosynthetic assimilation

Fig. 5 shows measurements of net assimilation taken over a day. The mean photosynthetic assimilation (from all the readings taken through the day) was about 6 μmol m^{-2} s^{-1}.

Net assimilation was plotted against photosynthetically active radiation, leaf temperature, stomatal conductance and intercellular carbon dioxide. One striking feature is the large scatter of the data points. It is not our intention here to analyse or explain this data set in any detail, as Cheeseman *et al.* (1991) have done this most adequately with a similar study on another mangrove *Bruguiera parviflora*.

Assimilation/photosynthetically active radiation.
Despite the large scatter it is possible to discern that light saturation occurs at around 400 μmol m^{-2} s^{-1} and net assimilation levels off at about 15 μmol m^{-2} s^{-1}. Maximum assimilation recorded for the day was 23 μmol m^{-2} s^{-1}. Light compensation point was around 50 μmol m^{-2} s^{-1}. From measurements made in the dark, a mean rate of just under 1.5 μmol m^{-2} s^{-1} was obtained for dark respiration.

Assimilation/temperature.
There was also a large scatter with temperature but it can be seen that maximum net assimilation increased with temperature until about 38°C and decreased thereafter. Maximum leaf temperature recorded was a high 44°C.

Assimilation/conductivity.
The trend seen here is almost identical to that seen in the assimilation/PAR plot with net assimilation levelling off at about 15 μmol m^{-2} s^{-1}. A conductance above about 2.5 μmol H$_2$O m^{-2} s^{-1} will ensure optimum net assimilation.

Assimilation/intercellular carbon dioxide (C_i).
There is a very definite negative correlation between net assimilation and intercellular carbon dioxide ($r^2 = 0.59$). This negative correlation has been reported for another mangrove, *Bruguiera parviflora*, by Cheeseman *et al.* (1991) and is an exception rather than the rule (e.g. the biochemical model of von Caemmerer & Farquhar, 1981). Cheeseman *et al.* (1991) have attempted to explain this negative correlation but a completely satisfactory explanation is still lacking.

General

Basically, we have tried two approaches to finding an estimate of productivity.

The first is to estimate growth based on allometric regressions as well as the estimation of turnover of parts that are regularly shed (leaves and fine roots). It is clear that we are yet unable to get a reasonable figure for root turnover. Another gap concerns figures for the possible loss of dissolved organic material through leaching from roots. The net productivity figures we have (annual increment in standing biomass plus small litter production) come to 12.24 t C ha^{-1} yr^{-1} and if we assume that root turnover is about the same as canopy turnover then we are looking at a figure of around 17 t C ha^{-1} yr^{-1}. Unless leaching from roots is extremely high, we are very safe with a ± 5 t C ha^{-1} yr^{-1} error band and can confidently use the figure of 17 ± 5 t C ha^{-1} yr^{-1} net productivity for this 20-year-old stand of *Rhizophora apiculata*. We are completely confident with the lower limit but the upper limit may well be higher if loss of organic matter from roots is very significant. If we need to obtain an accuracy of better that the present ± 30%, then we need to try to directly measure root turnover as well as leaching from roots.

The second approach is to use the gas exchange method. As we pointed out earlier, the measurements we made were net leaf assimilation, giving a figure between gross and net productivity. If we know the respiration of the leaf (and we have some measurements of dark respiration) then we will be able to get an estimate of gross productivity. To obtain net productivity we would need to have an estimate of respiration of the whole plant. This we have not been able to measure, but we can start by making a few order of magnitude approximations.

First let us try to use the figures we have to see if we can arrive at some reasonable figures, based on a few approximations. Taking only daylight hours, assimilation ranged from 0–23 μmol m^{-2} s^{-1}. We will use the mean figure of 6 μmol m^{-2} s^{-1} that we mentioned earlier and the figure of 1.5 μmol m^{-2} s^{-1} for leaf respiration, so net productivity (not taking into account respiration of non-leaf tissues) is 4.5 μmol m^{-2} s^{-1}. If we assume respiration of the non-leaf tissues to be the same as for leaves, then the figure reduces to 1.5 μmol m^{-2} s^{-1}. Using a leaf area index of 4 (based on our non-destructive measurements made on four 0.5 m $\times$ 0.5 m quadrats around our scaffolding towers), the figure for net productivity comes out as 11.35 t C ha^{-1} yr^{-1}. This is close to the lower range of the 17 $\pm$ 5 t C ha^{-1} yr^{-1} net productivity obtained using the allometric method. It must be pointed out that the mean assimilation of 6.0 μmol m^{-2} s^{-1} may be an overestimate, since only 5% of the measurements were made on shade leaves. On the other hand, the leaf area index of 4 may have been an underestimate. Also, we could have overestimated respiration (of non-leaf parts) and loss through leaching. What this means is that our accuracy with the gas exchange method is worse than the $\pm$ 5 t C ha^{-1} yr^{-1} confidence band we estimated with the allometric method. Perhaps the use of models that allow us to move from the leaf to the whole tree and stand level could improve this resolution. Such models already exist (e.g. the MAESTRO model of Jarvis *et al.*, 1990). We have not tried these but are now in a position (in terms of the necessary data) to use our data on such a model.

Besides presenting the results obtained in this study which can now be used for existing models, this paper shows that much time and effort is required to acquire essential baseline data. Such baseline data may be readily available for some of the proposed transects of GCTE, while others may be absent or inadequate. It cannot be overemphasized that real data are necessary and that the best models are only as good as the data used. It is therefore important for international programmes such as GCTE to first establish what reliable data are already available and what the gaps are before wasting precious time and energy collecting new data or, worse, running models with inadequate data.

ACKNOWLEDGMENTS

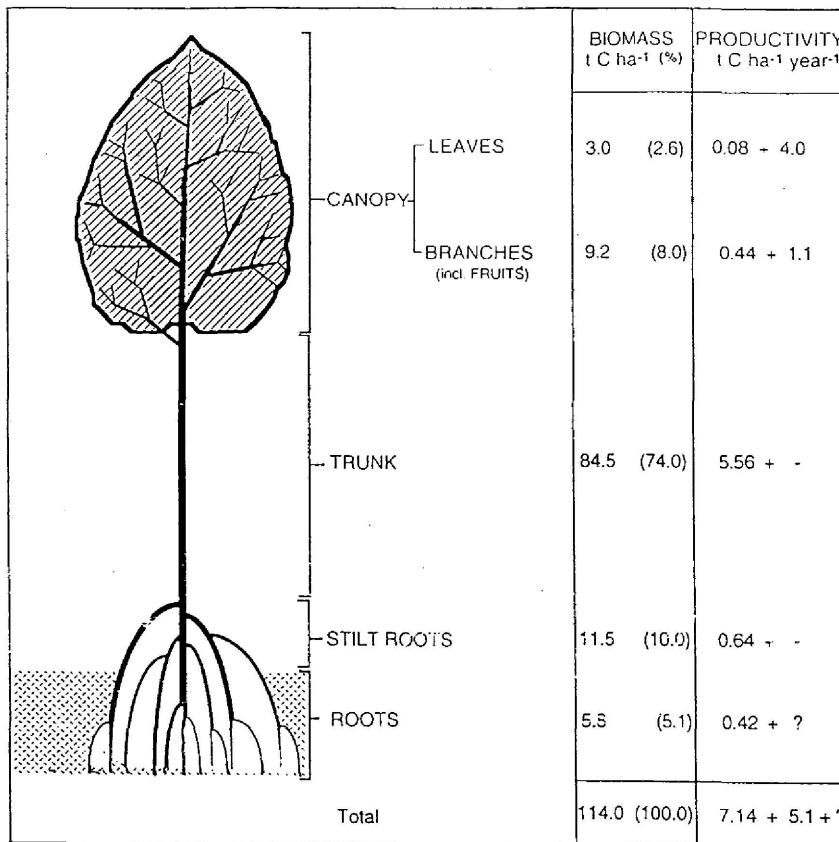|	BIOMASS t C ha^{-1} (%)		PRODUCTIVITY t C ha^{-1} year^{-1}
LEAVES	3.0	(2.6)	0.08 + 4.0
BRANCHES (incl. FRUITS)	9.2	(8.0)	0.44 + 1.1
TRUNK	84.5	(74.0)	5.56 + -
STILT ROOTS	11.5	(10.0)	0.64 + -
ROOTS	5.8	(5.1)	0.42 + ?
Total	114.0	(100.0)	7.14 + 5.1 + ?

FIG. 4. The partitioning of biomass, and net productivity (annual biomass increment and turnover) of a typical tree in a 20-year-old stand of *Rhizophora apiculata* mangrove forest. Turnover rates for underground roots were not available.
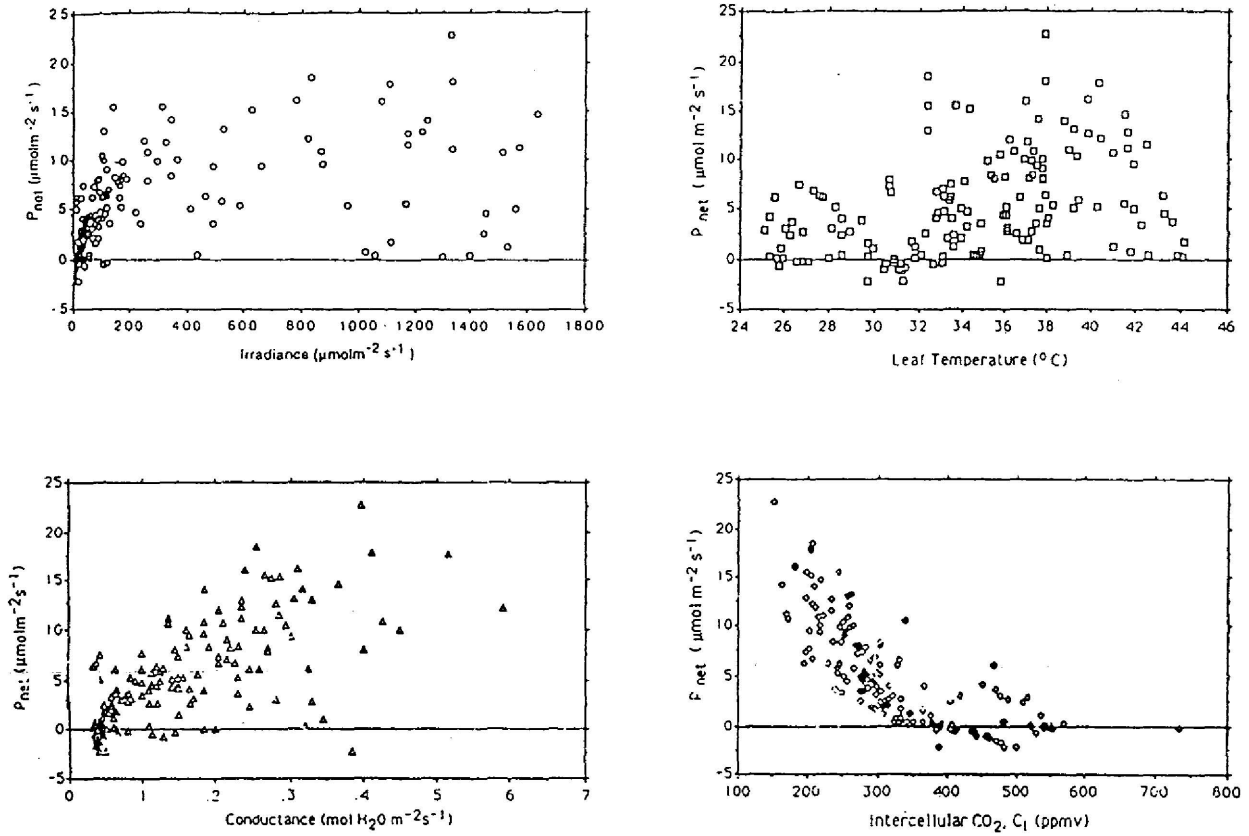
FIG. 5. Some characteristics of photosynthetic assimilation as measured using the LI-COR LI-6200 photosynthesis system. (a) Photosynthetic assimilation/light (PAR)/plot, (b) photosynthetic assimilation/leaf-temperature plot, (c) photosynthetic assimilation/stomatal conductance plot and (d) photosynthetic assimilation/intercellular carbon dioxide plot.

REFERENCES

Cheeseman, J.M., Clough, B.F., Carter, D.R., Lovelock, C.E., Ong Jin Eong & Sim, R.G. (1991) The analysis of photosynthetic performance in leaves under field conditions: a case study using *Bruguiera* mangroves. *Photosynth. Res.* **29**, 11–22.

Clough, B.F. (1992) Primary productivity and growth of mangrove forests. *Tropical mangrove ecosystems* (ed. by A. I. Robertson and D. M. Alongi), pp. 225–250. Coastal and Estuarine Studies 41, American Geophysical Union, Washington, DC.

GCTE (1994) *IGBP in Action: Work Plan 1994–998.* IGBP Report No. 28, Stockholm.

Gong, W.K. & Ong, J.E. (1994) The use of demographic studies in mangrove silviculture. *Hydrobiologia,* in press.

Gong, W.K., Ong, J.E., Wong, C.H. & Dhanarajan, G. (1984) *Productivity of mangrove trees and its significance in a managed mangrove ecosystem in Malaysia* (ed. by Soepadmo, E., Rao, A.N. and Macintosh, D.J.), pp. 216–225. Proceedings of the UNESCO Asian Symposium on Mangrove Environment: Research and Management, Universiti Malaya, Malaysia.

Haron, Hj. & Hassan, A. (1981) *A working plan for the second 30-year rotation of the Matang mangrove forest reserve Perak.* State Forestry Department, Perak. Rajan & Co. (Printers) Sdn. Bhd., Ipoh, Perak.

Jarvis, P.G., Barton, C.V.M., Dougherty, P.M., Teskey, R.O. & Massherder, J.M. (1990) MAESTRO. *Development and use of tree forest response models. Acidic Deposition: State of Science and Technology Report 17. NAPP* (ed. by A. R. Kiester), pp. 167–178. Government Printing Office, Washington DC 20402–9325, U.S.A.

Ong, J.E. (1982) Mangroves and aquaculture in Malaysia. *Ambio,* **11,** 252–257.

Ong, J.E. (1993) Mangroves—a carbon source and sink. *Chemosphere,* **27,** 1097–1107.

Ong, J.E. (1994) The ecology of mangrove conservation and management. *Hydrobiologia,* in press.

Ong, J.E., Gong, W.K. & Wong, C.H. (1985) Seven years of productivity studies in a managed Malaysian mangrove forest then what? *Coasts and tidal wetlands of the Australian mon-*

soon region (ed. by K. N. Bardsley, J. D. S. Davy and C. D. Woodroffe), pp. 231–223. Australian National University North Australia Research Unit Mangrove Monograph No. 1. Darwin, Australia.

Von Caemmerer, S. & Farquhar, G.D. (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, **153**, 376–397.

Watson, J.G. (1928) Mangrove forests of the Malay Peninsula. *Malay. For. Rec.* **6**, 1–275.