Carbon sequestration potential of *Rhizophora mucronata* and *Avicennia marina* as influenced by age, season, growth and sediment characteristics in southeast coast of India

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Abstract This work analysed the carbon sequestration potential in two species of mangroves (*Rhizophora mucronata* and *Avicennia marina*) along with their growth, biomass, sediment characteristics for four seasons of the year 2009–2010, in planted stands of different age (1–17.5 years) in the Vellar-Coleroon estuarine complex, India. The mangroves were recorded to store significant amount of biomass. *Avicennia marina* performed better to display 75 % higher rate of carbon sequestration than that in *Rhizophora mucronata*. This could be attributed to growth efficiency and high biomass production. For instance, *Avicennia marina* exhibited 2.7 fold higher girth, 24 % higher net canopy photosynthesis, 2 fold aboveground biomass (AGB), 40 % more belowground biomass (BGB) and 77.3 % higher total biomass, than *R. mucronata* did. Seasonally the rate of carbon sequestration was 7.3 fold higher in post-monsoon, 3.4 fold in monsoon, 73 % more in summer than that in pre-monsoon. The rate of carbon sequestration was positively correlated with age of planted site, tree height, tree diameter, net canopy photosynthesis, AGB, BGB, total biomass, carbon stock, growth efficiency, AGB/tree height tree girth, leaf area index, silt content ($p<0.01$). The carbon sequestration was negatively corrected with soil temperature and clay content ($p<0.05$). Mangroves were found to be a productive system and important sink of carbon in the tropical coastal zone, but increasing soil temperature due to global warming would have a negative impact on carbon sequestration potential of the mangroves.

Keywords Carbon sequestration · Mangroves · *Avicennia* · *Rhizophora* · Biomass · Sediment

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Introduction

Mangrove forests contribute significantly to the global carbon, although they colonise only 0.7 % of global coastal zone. The mangroves are known to remove CO_2 from the atmosphere through photosynthesis. This perhaps reduces the problems that go with the 'green house gases' and global warming. They fix greater amounts of CO_2 per unit area, than what the phytoplankton do in the tropical oceans (Kathiresan and Bingham 2001). Mangroves also respond well to high CO_2. For example, *Rhizophora mangle* shows greater accumulation of biomass under high CO_2 conditions (Farnsworth et al. 1996). The mangroves contribute to 10 % of total net primary production and 25 % of carbon burial in the global coastal zone (Alongi 2007). A recent assessment of global mangrove carbon budget, based on published data, indicates that global mangrove primary production is 218 trillion grams of carbon annually and this contributes carbon to the ocean through the processes of export, sediment burial and mineralization of carbon fixed by net primary production of the mangrove forests. It appears that >50 % of the carbon fixed by mangrove vegetation is unaccounted for (Bouillon et al. 2008).

Because the mangroves fix and store significant amounts of carbon, their loss may have impact on global carbon budget. According to Cebrain (2002), a loss of about 35 % of the world's mangroves has resulted in a net loss of 3.8×10^{14} g C stored as mangrove biomass. It must be kept in mind that mangroves are among the most productive ecosystems and their carbon stock per unit area can be enormous (Twilley et al. 1992). Rehabilitating degraded mangrove areas will contribute to carbon sequestration to mitigate the global warming threat. It is expected that new counter-

measure of global warming is by restoration of lost mangrove forests. This requires much more studies on the potential of such restored sites for carbon sequestration.

It is difficult to study biomass changes of mangrove forests by harvesting the trees from planted or mature forests. In this regard, the allometric method is comparatively better one to estimate the weight of a tree from measurable tree dimension, including trunk diameter and height. This is also a non-destructive method and easy to study temporal changes of biomass (Komiyama et al. 2008). Therefore, allometric equations for mangroves have been developed for several decades to estimate biomass and subsequent growth (Clough et al. 1997; Chave et al. 2005; Komiyama et al. 2005; Dahdouh-Guebas and Koedam 2006). Estimation of the potential of a forest in sequestrating carbon involves calculating the total biomass per hectare, and then applying appropriate conversion factors to get the carbon equivalents.

There are knowledge gaps in mangrove sequestration potential in planted mangroves in relation to growth attributes, age of plantation and seasonal changes and sediment characterizations. In this regard, only dearth of published data is available. Therefore, the present study was made on the carbon sequestration potential in two species of mangroves (*Rhizophora mucronata* and *Avicennia marina*) along with their growth, biomass, sediment characteristics for four seasons, in the planted mangrove stands of different ages.

Materials and methods

The study area is the Vellar-Coleroon estuarine complex, located along the Bay of Bengal on the southeastern coast of the state of Tamil Nadu, India (Fig. 1). There are four seasons prevailing in the area: post-monsoon (Jan.–Mar.), summer (Apr.–June), Pre-monsoon (July–Sep.) and monsoon (Oct.–Dec.). The tides are semi-diurnal with a range of tidal amplitude from 15 to 100 cm, reaching maximum during monsoon and a minimum in summer. The depth of the water ways ranges from 0.3 to 3 m. The mean annual temperature of this area is 27 °C and annual precipitation is 1465 mm with 52 rainy days (Kathiresan 2000).

In the study area, 17 experimental sites planted with two species of mangroves—*Avicenna marina* (Forssk.) Vierh and *Rhizophora mucronata* Poir., of different age from 1 to 17.5 year old stands were fixed. Eleven plots along the Vellar estuary (Lat. 11° 29′ 19.1–25.2″ N; Long. 79° 45′ 51.9–57.3″ E) and six plots in Pichavaram (Lat. 11° 29′ 21.9–28.3″ N; Long. 79° 46′ 27.2–57.3″ E) were used for experimental study. Although all the experimental sites were located in the same area of similar environmental conditions, there was spatial variation in addition to age of plant growth of the sites. Three healthy plant individuals of *R. mucronata* and *A. marina* were selected from each of the experimental plots.

The individual plants were measured for height in meters, girth in cm at 130 cm of breast height, light intensity at

Fig. 1 Location of mangrove forests of different age (1–6 plots in Pichavaram and 7–17 plots in Vellar estuary) sampled in four seasons
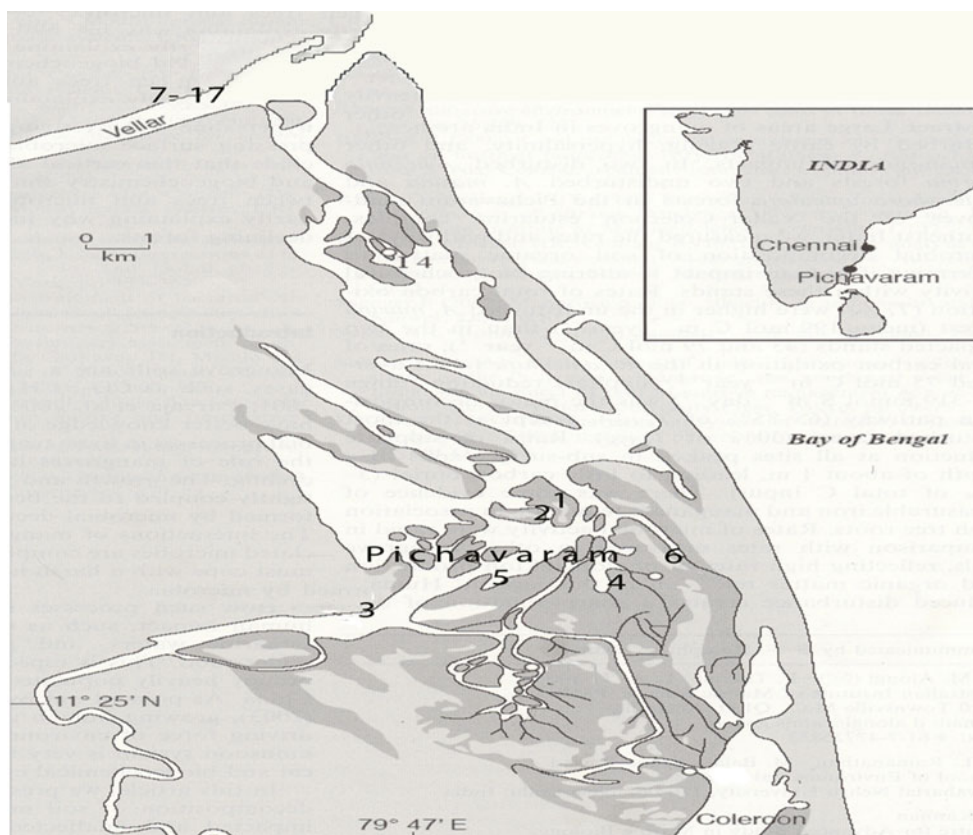
above canopy and below canopy using a lux meter. From these measures, leaf area index, net canopy photosynthesis, biomass of aboveground (AGB), belowground (BGB), total and AGB/BGB were calculated using the Internationally recognized scientific techniques recommended by the Australian Institute of Marine Sciences (AIMS) (English and Wilkinson Basker 1997). The measurement was made for four seasons: summer (May 2009), premonsoon (July 2009), monsoon (Dec.2009) and post monsoon (Jan. 2010) in all the 17 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 1,000 and 1,400 h were used to estimate leaf area index, L ($=m^2$ leaf area m^{-2} ground area) using the formula.

$$L = \left[\log_e(I)_{mean}\right] - \left[\log_e(I_\sigma)_{mean}\right]/-k$$

Where, $(I)_{mean=}$the mean photosynthetically active radiation (PAR) under the canopy; $(I_\sigma)_{mean=}$incident PAR; and k = canopy light extinction coefficient (0.5). L was corrected to a solar zenith angle (θ) for the latitude of the 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, $\underline{d}$ = day length (hrs) and A = average rate of photosynthesis per unit leaf area are 0.3456 for *R. apiculata*, 0.4752 for *A. marina* (Clough et al. 2000).

The biomass was estimated using the following allometric equation, proposed by Komiyama et al. (2005).

Leaf weight $= 0.135\rho\ D_B^{1.696}$
Above$-$ground weight $= 0.251\rho\ D^{2.46}$
Below$-$ground weight $= 0.199\rho^{0.899}D^{2.22}$

Where D – Trunk diameter in centimeter at breast height at 30 cm above ground in *R. mucronata* and at 130 cm above ground in *A. marina*

D_B Trunk diameter in centimeter at the lowest living branch
H Tree height in meter
P Wood density of trunk in ton per m^3

The total biomass per tree was converted to carbon biomass per tree by multiplying with a factor 0.42, as the average carbon content is 42 % of total biomass, as found for the present study using in CHN/O analyser (Perkin Elmer-series II 2400). The latter was converted to carbon biomass per year, based on the forest age, as the rate of carbon sequestration in the tree biomass.

Sediment samples were collected from rhizosphere soil of individual trees of each of the sampling plots in four seasons: summer (May 2009), pre-monsoon (July 2009), monsoon (Dec.2009) and post-monsoon (Jan. 2010). The samples were drawn using a 1.5 m long stainless steel corer during low tide and analysed in situ for temperature, hydrogen ion concentration (*p*H) and redox potential (Eh), and salinity of pore water. Temperature was measured by using a thermometer with 0.5 °C accuracy; *p*H and redox potential (Eh) by using a millivoltmeter with platinum electrode (*p*H 315i/SET, Wissenschaftlich Technische Werkstatten, Germany) and pore water salinity by using a hand refractometer (Erma INC, Tokyo). In the laboratory, the sediment samples were analyzed for contents of silt, clay and sand using pipette method (Buchanan 1984).

Statistical procedures

A suite of statistical analysis (SPSS 11.5) was made to assess the significance for each variable between the plant age groups or mangroves species or season of analysis. Post hoc multiple comparison test (Tukey's, S-N-K), were also used to identify significance between different combinations. Correlation was made between carbon sequestrations and other variables and significant ones ($p<0.05$) are shown in figs.

Results

Plant height varied significantly between species or age of plantation ($p<0.01$), but not between season of analysis. The plant height was 8 % higher in *Rhizophora mucronata* than that in *Avicennia marina*. It ranged from 0.41 to 8.75 m respectively in 1 year and 16.3 year old plantations (Table 1). Thus, there was 21 fold increase in tree height within 15.3 years of plantation; in other words, the growth was 4.6 cm per month or 55.2 cm per year.

Tree girth at breast height varied significantly between mangrove species or age of plant or seasons of analysis ($p<0.01$) (Table 1). *Avicennia marina* had 2.7 fold higher girth than *R. mucronata*. Tree diameter at breast height was significantly different between species, age and seasons ($p<0.01$) (Table 1). It ranged from 2.61 to 10.22 cm respectively in 7- and 11.1 years of plant growth that was 3.9 fold higher growth within 4.1 years, that was 1.9 cm per year and 0.2 cm per month.

Net canopy photosynthesis varied between mangrove species or age of growth or seasons (Table 1). *Avicennia marina* exhibited 24 % higher net canopy photosynthesis (65.43 tC $ha^{-1}year^{-1}$) than *R. mucronata* (52.64 tC ha^{-1} $year^{-1}$). Leaf area index (LAI) did show variation between

Table 1 Height, girth at breast height of 1.3 cm (gbh), diameter at breast height (dbh), leaf area index, net canopy photosynthesis, AGB, BGB and AGB/BGB ratio in two mangrove species (*A. marina* and *R. mucronata*) in different forest age under four seasons

Source	Height (m)	Gbh (cm)	Dbh (cm)	Leaf area index (m^2/m^2 area)	Net canopy photosynthesis (tC/ha/year)	Biomass of above ground (AGB) (t/ha)	Biomass of below ground (BGB) (t/ha)	AGB/BGB ratio
Species								
Avicennia marina	4.29 ± 0.28^{a}	31.85 ± 4.48^{b}	9.34 ± 0.75^{a}	5.66 ± 0.31^{a}	65.43 ± 3.81^{b}	117.65 ± 40^{b}	43.00 ± 9.40^{b}	2.73 ± 0.88^{b}
Rhizophora mucronata	4.64 ± 0.37^{b}	11.87 ± 0.77^{a}	3.55 ± 0.24^{b}	5.14 ± 0.34^{a}	52.64 ± 3.54^{a}	59.95 ± 15.75^{a}	30.65 ± 7.00^{a}	1.95 ± 0.21^{a}
Age								
1	0.41 ± 0.05^{a}	—	—	4.91 ± 1.24^{b}	52.31 ± 10.12^{c}	1.20 ± 0.35^{a}	1.25 ± 0.75^{a}	0.96 ± 0.20^{b}
2	0.57 ± 0.08^{a}	—	—	4.89 ± 1.11^{b}	46.95 ± 7.92^{b}	1.35 ± 0.50^{a}	1.45 ± 0.45^{a}	0.93 ± 0.22^{a}
3	0.87 ± 0.12^{a}	—	—	3.33 ± 0.25^{a}	37.27 ± 3.97^{a}	4.85 ± 1.80^{b}	3.15 ± 1.05^{b}	1.53 ± 0.40^{a}
7	2.46 ± 0.025^{b}	8.17 ± 1.32^{a}	2.61 ± 0.42^{a}	5.49 ± 1.09^{c}	44.53 ± 8.58^{b}	6.70 ± 2.55^{c}	4.25 ± 1.65^{c}	1.57 ± 0.24^{a}
8	3.55 ± 0.04^{c}	12.47 ± 0.72^{b}	3.99 ± 0.23^{a}	4.42 ± 0.74^{b}	45.59 ± 6.18^{b}	5.50 ± 0.60^{b}	2.90 ± 0.55^{b}	1.89 ± 0.45^{a}
9	3.54 ± 0.43^{c}	19.62 ± 6.68^{c}	6.28 ± 2.13^{b}	4.73 ± 0.67^{b}	50.32 ± 5.88^{c}	14.65 ± 5.35^{d}	8.55 ± 2.85^{c}	1.71 ± 0.12^{a}
11.5	4.46 ± 0.30^{d}	23.85 ± 6.14^{d}	7.63 ± 1.96^{c}	5.67 ± 1.01^{c}	63.22 ± 12.25^{d}	44.60 ± 28.90^{e}	23.05 ± 10.1^{d}	1.93 ± 0.34^{a}
11.9	4.15 ± 0.18^{d}	23.66 ± 7.50^{d}	7.57 ± 2.40^{c}	5.63 ± 0.60^{c}	63.85 ± 8.96^{d}	30.15 ± 13.45^{e}	16.00 ± 6.45^{d}	1.88 ± 0.98^{a}
11.10	5.72 ± 0.09^{e}	31.96 ± 8.29^{e}	10.22 ± 2.65^{d}	6.09 ± 0.94^{d}	70.49 ± 13.25^{e}	103.85 ± 64.80^{g}	48.80 ± 26.95^{e}	2.12 ± 0.23^{b}
11.11	5.45 ± 0.16^{e}	23.03 ± 4.61^{d}	7.37 ± 1.47^{c}	5.22 ± 1.01^{c}	56.68 ± 10.75^{c}	75.25 ± 43.45^{f}	37.25 ± 17.85^{d}	2.02 ± 0.76^{b}
12.1	3.00 ± 1.16^{c}	19.92 ± 7.73^{c}	6.37 ± 2.47^{b}	4.07 ± 1.60^{b}	52.68 ± 20.70^{c}	101.50 ± 63.85^{g}	46.65 ± 27.85^{e}	2.17 ± 0.69^{b}
14.9	5.66 ± 0.28^{e}	28.82 ± 7.46^{e}	8.98 ± 2.50^{d}	5.31 ± 1.23^{c}	56.60 ± 13.72^{c}	222.75 ± 112.35^{h}	105.50 ± 43.80^{f}	2.11 ± 0.46^{b}
15.2	6.26 ± 0.14^{f}	24.98 ± 5.06^{d}	8.11 ± 1.53^{d}	6.17 ± 1.08^{d}	69.73 ± 13.74^{d}	34.05 ± 18.45^{e}	17.55 ± 8.30^{d}	1.94 ± 0.63^{a}
15.3	4.68 ± 0.29^{d}	29.41 ± 6.86^{e}	9.70 ± 2.08^{d}	6.32 ± 0.6^{d}	75.44 ± 11.11^{e}	46.35 ± 20.20^{e}	23.80 ± 10.30^{d}	1.94 ± 0.87^{a}
16.3	8.75 ± 1.28^{g}	53.75 ± 33.82^{f}	6.55 ± 0.80^{b}	5.66 ± 1.14^{c}	60.53 ± 11.45^{d}	211.70 ± 103.25^{gh}	99.90 ± 41.10^{f}	2.11 ± 0.14^{b}
16.8	8.12 ± 0149^{g}	24.86 ± 5.35^{d}	7.70 ± 1.69^{c}	5.81 ± 0.86^{c}	60.08 ± 11.01^{d}	350.50 ± 158.5^{i}	57.45 ± 32.50^{e}	1.10 ± 0.17^{a}
17.5	6.17 ± 0.19^{f}	23.36 ± 4.28^{d}	7.47 ± 1.35^{c}	5.98 ± 0.80^{c}	61.16 ± 10.57^{d}	224.60 ± 68.75^{h}	112.85 ± 27.75^{f}	1.99 ± 0.46^{a}
Season								
Summer	4.13 ± 0.45^{a}	24.46 ± 8.45^{b}	5.37 ± 0.83^{a}	3.02 ± 0.28^{a}	35.87 ± 3.67^{a}	34.55 ± 10.05^{b}	22.65 ± 5.90^{b}	1.52 ± 0.08^{a}
Pre-monsoon	4.25 ± 0.47^{a}	14.39 ± 2.05^{a}	4.82 ± 0.64^{a}	4.22 ± 0.42^{a}	50.15 ± 5.04^{b}	23.75 ± 7.55^{a}	13.40 ± 4.10^{a}	1.77 ± 0.05^{a}
Monsoon	4.25 ± 0.45^{a}	22.64 ± 3.63^{b}	7.24 ± 1.16^{b}	7.36 ± 0.41^{b}	69.25 ± 6.25^{c}	84.80 ± 30.10^{c}	40.40 ± 12.40^{c}	2.09 ± 0.23^{a}
Post-monsoon	4.72 ± 0.47^{a}	23.30 ± 2.70^{b}	7.16 ± 0.88^{b}	6.50 ± 0.33^{b}	72.35 ± 3.76^{d}	205.05 ± 76.35^{d}	67.20 ± 16.90^{d}	3.05 ± 0.47^{a}
Species	**	**	*	NS	**	**	**	*
Age	**	**	**	**	*	*	**	NS
Season	NS	*	*	**	*	**	**	NS
Species X Age	**	NS	NS	NS	NS	NS	NS	*
Species X Season	*	NS	NS	*	NS	*	*	*
Age X Season	NS	NS	NS	**	NS	NS	NS	NS

Values are mean ± standard error, the alphabets of the superscript varied within the group ($p<0.05$)

NS not significant

$**p<0.01$; $*p<0.05$

seasons or age of growth ($p<0.01$; Table 1). It varied from 3.33 to 6.32 in one and 15.3 years of plantations respectively, and thus there was 90 % increase in LAI within 14.3 year; in other words, LAI increased at a rate of 0.2 per year and 0.02 per month. Seasonally, LAI was higher in monsoon (7.36) and post-monsoon (6.5) than that in pre-monsoon (4.22) and summer (3.02) (Table 1); and its value was 2.4 fold higher in monsoon and 2.2 fold in post-monsoon, 40 % higher in pre-monsoon than that in summer.

Aboveground biomass (AGB) exhibited significant difference between mangrove species ($p<0.01$) or seasons or age of growth ($p<0.05$). AGB was 2 fold higher in *A. marina* (117.65 t ha^{-1}) than *R. mucronata* (59.95 t ha^{-1}). Seasonally, AGB was highest in post-monsoon (48.5 t ha^{-1}), followed by monsoon (16.96 t ha^{-1}), summer (6.91 t ha^{-1}) and lowest in pre-monsoon (4.75 t ha^{-1}) (Table 1) and its value was 10.2 fold higher in post-monsoon and 3.6 fold more in monsoon than that in pre-monsoon.

Belowground biomass (BGB) did exhibit significant variation between mangrove species or age of growth or seasons ($p<0.01$; Table 1). BGB was 40 % higher in *A. marina* (43 t ha^{-1}) than *R. mucronata* (30.65 t ha^{-1}). It ranged from 1.25 to 112.85 t ha^{-1} respectively in 1 year and 16.8 year-old plantations and thus its value was 90 fold higher within 16.5 years of growth. Seasonally, AGB was highest in post-monsoon (67.2 t ha^{-1}), followed by monsoon (40 t ha^{-1}), summer (22.65 t ha^{-1}) and lowest in pre-monsoon (13.4 t ha^{-1}). BGB was 5 fold higher in post-monsoon, 3 fold more in monsoon and 69 % higher in summer than that in pre-monsoon. The ratio between AGB and BGB displayed variation only between species ($p<0.05$). The ratio was 2.73 in *A. marina* and 1.95 in *R. mucronata* (Table 1) and it was 40 % higher in the former than in the later.

Total biomass varied significantly between mangrove species or seasons ($p<0.01$) or age of growth ($p<0.05$) or interactive effects of species x age and species x seasons ($p<0.01$) (Table 2). There was 77.3 % higher biomass in *A. marina* (160.65 t ha^{-1}) than that in *R. mucronata* (90.6 t ha^{-1}). Total biomass ranged from 2.5 to 407.95 t/ha respectively in 1- and 16.8 years of plantations and thus it was 163 fold higher within 15.8 years of growth, that was 25.7 t/ha/year and 2.1 t/ha/month.

Carbon stock of the total biomass did exhibit variation between age of growth or mangrove species ($p<0.05$) or seasons ($p<0.01$) (Table 2). The carbon stock was 77 % higher in *A. marina* (67.47 t ha^{-1}) than that in *R. mucronata* (38.05 t ha^{-1}). Carbon stock ranged from 1.05 to 171.33 t/ha in one and 16.8 years of plantations respectively and there was 163 fold higher biomass within 15.8 years of growth, that was 10.3 t/ha/year or 0.86 t/ha/month. Carbon stock was highest in post-monsoon (114.36 t ha^{-1}) followed by monsoon (52.58 t ha^{-1}), summer (24.02 t ha^{-1}) and lowest in pre-monsoon (15.6 t ha^{-1}) and there was 7.3 fold higher

value in pre-monsoon, 3.4 fold in monsoon, 54 % more in summer than in pre-monsoon.

Rate of carbon sequestration varied between mangrove species or age of growth or seasons ($p<0.01$) or between the interactive effects of species x seasons ($p<0.05$) (Table 2). The rate of carbon sequestration was 75 % higher in *A. marina* (4.8 t ha^{-1}year^{-1}) than that in *R. mucronata* (2.75 t ha^{-1}year^{-1}). Seasonally the rate of carbon sequestration was the highest in post-monsoon (8 t/ha/year), followed by monsoon (3.75 t ha^{-1}year^{-1}), summer (1.9 t ha^{-1}year^{-1}) and the least in pre-monsoon (1.1 t ha^{-1}year^{-1}) and thus the value was 7.3 fold higher in post-monsoon, 3.4 fold in monsoon, 73 % more in summer than that in pre-monsoon.

Growth efficiency varied between age of growth or seasons or their interactive effects ($p<0.01$), but not between mangrove species (Table 2). It ranged from 0.02 to 1.32 t ha^{-1}year^{-1} in 2 and 14.9-years of plantations respectively and thus there was 66 fold increase in growth efficiency within 12.9 years of growth. The growth efficiency was highest in summer (0.53 t ha^{-1}year^{-1}) followed by post-monsoon (0.38 t ha^{-1}year^{-1}), monsoon (0.15 t ha^{-1}year^{-1}) and lowest in pre-monsoon (0.13 t ha^{-1}year^{-1}) and there was 4 fold increase in summer, 2.9 fold in post-monsoon, 15 % more in monsoon than that in pre-monsoon.

Leaf longevity varied between mangrove species or age of growth or seasons, ($p<0.05$); it was the highest (6.9 months) in post-monsoon, followed by monsoon (3.58 months), summer (3.39 months) and least (2.92 months) in pre-monsoon, and thus leaf longevity was high by 2.4 fold, 23 % and 16 % respectively, as compared to pre-monsoon. Leaf turnover rate exhibited significant variation between mangrove species, age of growth or seasons ($p<0.05$). The leaf turnover rate was 2.6 fold higher in *R. mucronata* than that in *A. marina*. It ranged from 0.64 per year in 11.1 year of plant growth and 7.8 per year in 15.2 year of growth with 12 times increase of leaf turnover rate within 4.1 years. The leaf turn over rate also varied seasonally with 2 times greater value in pre-monsoon, 85 % higher in monsoon, and 81 % more in summer than that in post-monsoon. The ratio between AGB and tree height varied only between mangrove species ($p<0.01$) or seasons ($p<0.05$) (Table 2). The ratio was 2 fold higher in *A. marina* (27.42 t ha^{-1}m^{-1}) than that in *R. mucronata* (12.92 t ha^{-1}m^{-1}) and it was 7.8 fold higher in post-monsoon (43.44 t ha^{-1}m^{-1}), 3.6-fold in monsoon (19.95 t ha^{-1}m^{-1}) and 50 % more in summer (8.36 t ha^{-1}m^{-1}) than that in pre-monsoon (5.58 t ha^{-1}m^{-1}).

Soil temperature showed significant difference between mangrove species or seasons ($p<0.05$) (Table 3) and it was 5.8 % higher in *R. mucronata* than that in *A. marina*. The soil temperature ranged from 24.24 °C in monsoon to 31.52 °C in summer with an increase of 30 % in the latter. Soil pH and did not show any significant difference between mangrove species or seasons or age of growth. Soil salinity varied seasonally ($p<0.05$) from 20.61 ppt in monsoon to 36.91 ppt in

Table 2 Total biomass, carbon stock, rate of carbon sequestration, growth efficiency, leaf longevity, leaf turnover rate and AGB/tree height in two mangrove species (*A. marina* and *R. mucronata*) in different forest age under four seasons

Source	Total biomass (t/ha)	Carbon stock (t/ha)	Rate of carbon sequestration (tC/ha/year)	Growth efficiency (t/ha/year)	Leaf longevity (month)	Leaf turnover rate (year^{-1})	AGB/Tree height (t/ha/m)
Species							
Avicennia marina	160.65±47.8[b]	67.47±20.09[b]	4.80±1.25[b]	0.36±0.09[b]	3.36±0.42[b]	3.46±1.20[a]	27.42±2.34[b]
Rhizophora mucronata	90.6±22.7[a]	38.05±9.53[a]	2.75±0.55[a]	0.25±0.08[a]	1.32±0.18[a]	9.06±1.38[b]	12.92±1.78[a]
Age							
1	2.5±0.95[a]	1.05±0.39[a]	1.05±0.39[b]	0.30±0.19[a]	–	–	2.92±0.98[b]
2	2.85±0.75[a]	1.19±0.31[a]	0.59±0.15[a]	0.02±0.01[a]	–	–	2.36±1.03[b]
3	8.05±2.85[b]	3.38±1.19[b]	1.12±0.39[b]	0.10±0.03[a]	–	–	5.57±2.34[c]
7	11±4.2[b]	4.62±1.76[c]	0.66±0.25[a]	0.04±0.01[a]	–	–	2.72±1.98[b]
8	8.45±1.1[b]	3.54±0.46[b]	0.44±0.05[a]	0.03±0.01[a]	–	–	1.54±1.02[a]
9	23.2±8.15[c]	9.74±3.42[d]	1.08±0.38[b]	0.07±0.03[a]	–	–	4.13±1.24[c]
11.5	67.7±38.8[d]	28.43±16.29[f]	2.47±1.41[c]	0.15±0.06[a]	3.42±0.17[c]	3.50±1.22[d]	10.00±2.54[d]
11.9	46.2±19.95[d]	19.40±8.37[e]	1.63±0.70[b]	0.08±0.03[a]	4.43±1.02[d]	2.70±0.98[c]	7.26±1.76[d]
11.10	152.65±91.75[e]	64.11±38.53[h]	5.77±3.47[d]	0.29±0.14[a]	18.75±2.08[g]	0.64±0.08[a]	18.15±2.34[e]
11.11	112.55±61.25[e]	47.27±25.72[g]	4.25±2.31[d]	0.27±0.11[a]	7.63±1.08[f]	1.57±1.92[b]	13.80±2.76[e]
12.1	148.15±91.7[e]	62.22±38.51[h]	5.14±3.18[d]	0.20±0.13[a]	1.92±0.19[a]	6.22±0.48[e]	33.83±3.45[f]
14.9	328.3±155.9[f]	137.88±65.47[i]	9.25±4.39[e]	1.37±0.63[b]	2.66±0.55[b]	4.50±2.21[d]	39.35±4.35[f]
15.2	51.65±26.7[d]	21.69±11.21[f]	1.42±0.73[b]	0.10±0.04[a]	1.55±0.81[a]	7.80±1.09[e]	5.43±1.24[c]
15.3	70.15±31.05[d]	29.46±13.04[f]	1.92±0.85[b]	0.09±0.03[a]	4.00±1.02[d]	3.00±1.08[d]	9.90±2.35[d]
16.3	311.6±144.85[f]	130.87±60.83[i]	8.02±3.73[e]	1.01±0.45[b]	3.31±0.15[c]	3.61±0.92[d]	24.19±2.54[e]
16.8	407.95±325.35[g]	171.33±136.64[i]	10.19±8.13[e]	0.58±0.45[a]	5.57±0.89[e]	2.15±0.48[c]	43.16±5.67[f]
17.5	337.45±96.15[f]	141.72±40.38[i]	8.09±2.30[e]	0.39±0.10[a]	4.17±0.58[d]	2.87±0.56[c]	36.40±4.98[f]
Season							
Summer	57.2±15.96[b]	24.02±6.70[b]	1.90±0.4[a]	0.53±0.19[d]	3.39±1.04[b]	3.53±0.92[b]	8.36±1.24[b]
Pre-monsoon	37.15±11.65[a]	15.60±4.89[a]	1.10±0.25[a]	0.13±0.05[a]	2.92±0.93[a]	4.09±1.08[c]	5.58±1.43[a]
Monsoon	125.2±42.5[c]	52.58±17.85[c]	3.75±1.15[b]	0.15±0.05[b]	3.58±0.69[b]	3.60±0.42[b]	19.95±2.76[c]
Post-monsoon	272.3±90.2[d]	114.36±37.88[d]	8.00±2.35[c]	0.38±0.12[c]	6.91±0.13[c]	1.95±0.18[a]	43.44±7.98[d]
Species	**	**	**	*	*	*	**
Age	*	*	*	*	*	*	*
Season	**	**	**	**	*	*	*
Species X Age	**	**	NS	NS	NS	*	NS
Species X Season	**	**	*	NS	NS	*	NS
Age X Season	NS	NS	NS	**	NS	*	NS

Values are mean ± standard error, the alphabets of the superscript varied within the group ($p<0.05$)

NS not significant

**$p<0.01$; *$p<0.05$

summer. Silt content of soil also showed variation between season ($p<0.01$) ranging from 17.29 % in pre-monsoon to 24.91 % in monsoon with 14 % increase between the two seasons. Clay content varied between mangrove species ($p<0.01$) or seasons ($p<0.05$) and it was 30 % more in *R. mucronata* than that in *A. marina*. It ranged from 42.41 % in summer to 53.52 % in monsoon with 26 % increase between the seasons. Sand content showed significant difference between age of growth ($p<0.05$) or seasons ($p<0.05$) and it was 48.75 % in 2 year old plantation and 12 % in 11.1 year-old plantations with a 4 fold decline of sand as the plantation aged. Sand ranged from 19.32 % in monsoon to 41.58 % in pre-monsoon with 2.2 fold increase between the seasons.

Rate of carbon sequestration was positively correlated with age of plant growth (Fig. 2a), tree height (Fig. 2b), tree girth (Fig. 2c), tree diameter (Fig. 2d) ($p<0.01$), leaf area index (Fig. 2e; $p<0.05$), net canopy photosynthesis (Fig. 2f), AGB (Fig. 2g), BGB (Fig. 2h), total biomass (Fig. 2i), carbon stock

Table 3 Temperature, pH, redox potential (Eh), silt, clay and sand contents of sediment of two mangrove species (*A. marina* and *R. mucronata*) in different forest age under four seasons

Source	Soil Temperature (°C)	Soil pH	Soil Eh (mV)	Pore water salinity (ppt)	Silt (%)	Clay (%)	Sand (%)
Species							
Avicennia marina	27.30±0.45[a]	6.75±0.02[a]	5.01±2.29[a]	37.19±1.79[a]	22.10±1.42[a]	40.27±1.91[a]	27.75±2.94[a]
Rhizophora mucronata	28.89±0.47[b]	6.84±0.03[a]	4.64±1.81[a]	39.28±2.10[a]	21.28±0.83[a]	52.17±1.24[b]	29.06±1.93[a]
Age							
1	30.63±1.74[a]	6.96±0.03[a]	6.37±0.13[b]	33.5±6.27[a]	14±3.71[a]	42.75±6.57[a]	47.87±9.16[c]
2	30.66±1.73[a]	6.75±0.11[a]	6.83±0.76[b]	32.5±6.97[a]	14±3.64[a]	41.5±6.96[a]	48.75±8.73[c]
3	29.5±1.41[a]	6.77±0.12[a]	1.05±0.56[a]	34.12±7.04[a]	14.12±3.7[a]	42±7.16[a]	47.12±8.83[c]
7	29.9±1.93[a]	6.65±0.21[a]	2.57±0.16[a]	34.37±6.40[a]	14.25±3.69[a]	41.12±6.8[a]	47.75±8.79[c]
8	28.38±1.22[a]	6.72±0.11[a]	10.35±0.62[d]	36±7.25[a]	14.25±3.74[a]	41.62±6.95[a]	48.00±8.75[c]
9	27.62±0.98[a]	6.73±0.14[a]	5.77±0.92[b]	32±6.71[a]	14.87±4.10[a]	39.25±6.62[a]	48.25±9.02[c]
11.5	27.18±1.34[a]	6.83±0.06[a]	5±0.29[b]	39±5.49[a]	24.87±1.44[b]	50.25±3.72[a]	26.25±5.71[b]
11.9	26.65±1.28[a]	6.78±0.08[a]	5±0.79[b]	31.62±5.1[a]	25.87±1.44[b]	49±2.71[a]	24.62±3.85[b]
11.10	13.25±5.03[a]	7.38±1.36[a]	2.23±0.86[a]	20±8.29[a]	12.62±4.89[a]	24.75±9.58[a]	12.00±5.86[a]
11.11	27.03±0.96[a]	6.75±0.10[a]	2.23±0.44[a]	37.25±4.3[a]	24.25±1.52[b]	49.37±2.67[a]	25.75±4.65[b]
12.1	27.12±1.05[a]	6.8±0.07[a]	15.01±0.45[e]	38.12±5.16[a]	23.87±1.99[b]	49.37±3.07[a]	26.5±4.82[b]
14.9	27.5±1.86[a]	6.75±0.05[a]	8.98±0.76[c]	38.75±5.91[a]	23.12±1.31[b]	54±3.59[a]	23.62±4.52[b]
15.2	27.8±1.29[a]	6.83±0.02[a]	3.35±0.37[a]	38.62±3.84[a]	24.25±1.06[b]	52.37±4.51[a]	25.62±6.45[b]
15.3	27.06±1.46[a]	6.8±0.06[a]	11.81±0.02[d]	37.5±4.46[a]	24.75±1.58[b]	49.12±3.10[a]	26.5±3.86[b]
16.3	27.76±1.23[a]	6.82±0.02[a]	6.63±0.23[c]	32.75±5.93[a]	25.62±1.75[b]	49.12±3.71[a]	27.5±5.97[b]
16.8	28.01±1.33[a]	6.83±0.03[a]	8.4±0.39[d]	35.37±4.74[a]	25.12±1.44[b]	51.12±2.76[a]	22.75±3.61[b]
17.5	27.63±1.04[a]	6.78±0.08[a]	5.22±0.54[b]	39.87±4.97[a]	25.75±1.42[b]	47.81±5.41[a]	23.62±4.86[b]
Season							
Summer	31.52±1.04[c]	6.52±0.10[a]	4.35±3.12[a]	36.91±1.75[d]	18.82±1.07[a]	42.41±1.46[a]	35.97±1.87[b]
Pre-monsoon	27.05±1.00[b]	6.69±0.18[a]	8.26±2.29[c]	33.38±2.27[c]	17.29±1.41[a]	43.79±2.54[b]	41.58±3.10[c]
Monsoon	24.24±0.77[a]	6.62±0.13[a]	6.07±2.79[b]	20.61±1.22[a]	24.91±1.78[b]	53.52±3.69[c]	19.32±4.95[a]
Post-monsoon	26.28±0.98[b]	6.51±0.20[a]	8.08±2.75[c]	27.94±1.66[b]	20.29±1.53[b]	42.51±2.46[a]	33.11±2.96[b]
Species	*	NS	*	NS	NS	**	NS
Age	NS	NS	*	NS	*	NS	*
Season	*	NS	*	*	**	*	*
Species X Age	*	NS	NS	NS	NS	*	**
Species X Season	NS	NS	NS	NS	*	*	*
Age X Season	NS	NS	NS	NS	NS	NS	NS

Values are mean ± standard error, the alphabets of the superscript varied within the group ($p<0.05$)

NS not significant

**$p<0.01$; *$p<0.05$

(Fig. 2j), growth efficiency (Fig. 2k), AGB/tree height (Fig. 2 l) ($p<0.01$), silt (Fig. 2n). The rate of carbon sequestration was negatively corrected with soil temperature (Fig. 2 m), and clay (Fig. 2 0) ($p<0.05$).

Discussion

The rate of carbon sequestration was 75 % higher in *Avicennia marina* than that in *Rhizophora mucronata*

(Table 1). This could be attributed to higher growth efficiency and biomass production of *A. marina*. For instance, the growth efficiency was 43 % higher in *A. marina* than that in *R. mucronata* (Table 2). Similarly the biomass density was 2.1 fold greater in *A. marina* than in *R. mucronata* (Table 2). In most mangroves, the biomass density appears to be higher than in terrestrial forests (Teas 1979).

In the present study, above ground biomass (AGB) was higher in *Avicennia marina* (117.65 t.ha^{-1}) than that in *Rhizophora mucronata* (59.95 t.ha^{-1}), which was similar
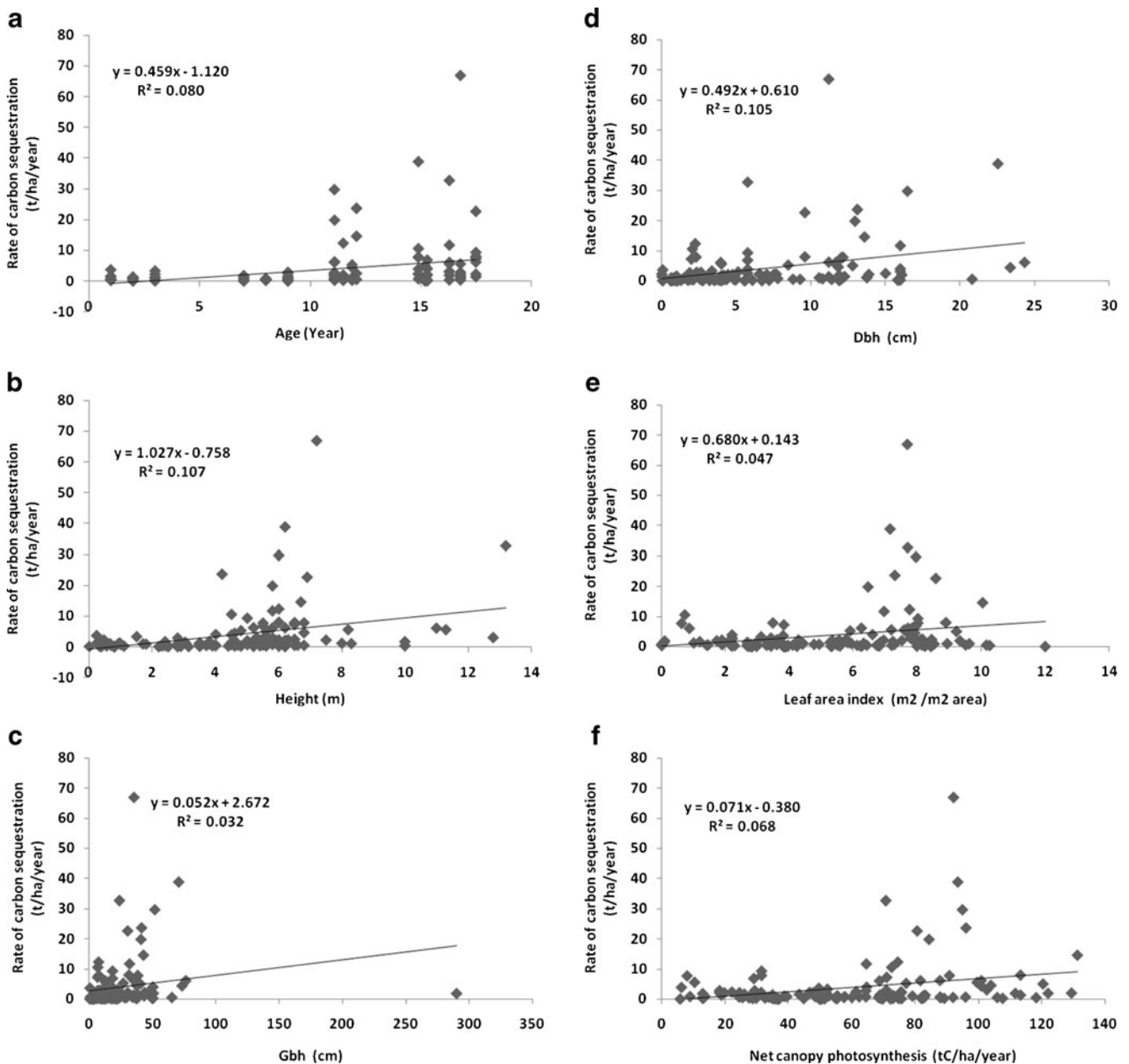
Fig. 2 Regression between rate of carbon sequestration in mangrove biomass and forest age (**a**), tree height (**b**), gbh (**c**), dbh (**d**), leaf area index (**e**), net canopy photosynthesis (**f**), AGB (**g**), BGB (**h**), total biomass (**i**), carbon stock (**j**), growth efficiency (**k**), AGB/tree height (**l**), soil temperature (**m**), silt (**n**), and clay (**o**)

to the trend of carbon sequestration in the mangrove species (Table 1). However, AGB values vary with the mangrove forest: 281 t ha^{-1} in *Rhizophora* forest (Tamai et al. 1986), 357 t ha^{-1} in *Sonneratia* forest (Komiyama et al. 1987) and 315 t ha^{-1} in *Avicennia germinans* (Fromard et al. 1998), 94.8 t ha^{-1} in a secondary mangrove forest of *R. mucronata* and *Bruguiera gymnorrhiza* (Suzuki and Tagawa 1983) and 62.9 t ha^{-1} in a *R. mangle* forest (Golley et al. 1962). The AGB are reportedly more than 300 t.ha^{-1} in Malaysia (Putz and Chen 1986), Indonesia (Komiyama et al. 1988) and French Guiana (Fromard et al. 1998). The AGB is also

reportedly less than 100 t ha^{-1} in most secondary forests and primary forests of high latitude areas (>24°23′N or S) (Mackey 1993). The lowest AGB reported is 7.9 t ha^{-1} for a *Rhizophora mangle* forest in Florida, USA (Lugo and Snedaker 1974).

In the present study, belowground biomass (BGB) was higher in *A. marina* (43 t ha^{-1}) than that in *R. mucronata* (30.65 t ha^{-1}), similar to the trend of carbon sequestration in the mangrove species (Table 1). The values are closer to 32.4 t ha^{-1} in the *Sonneratia* forest (Komiyama et al. 1987). However, the values are much
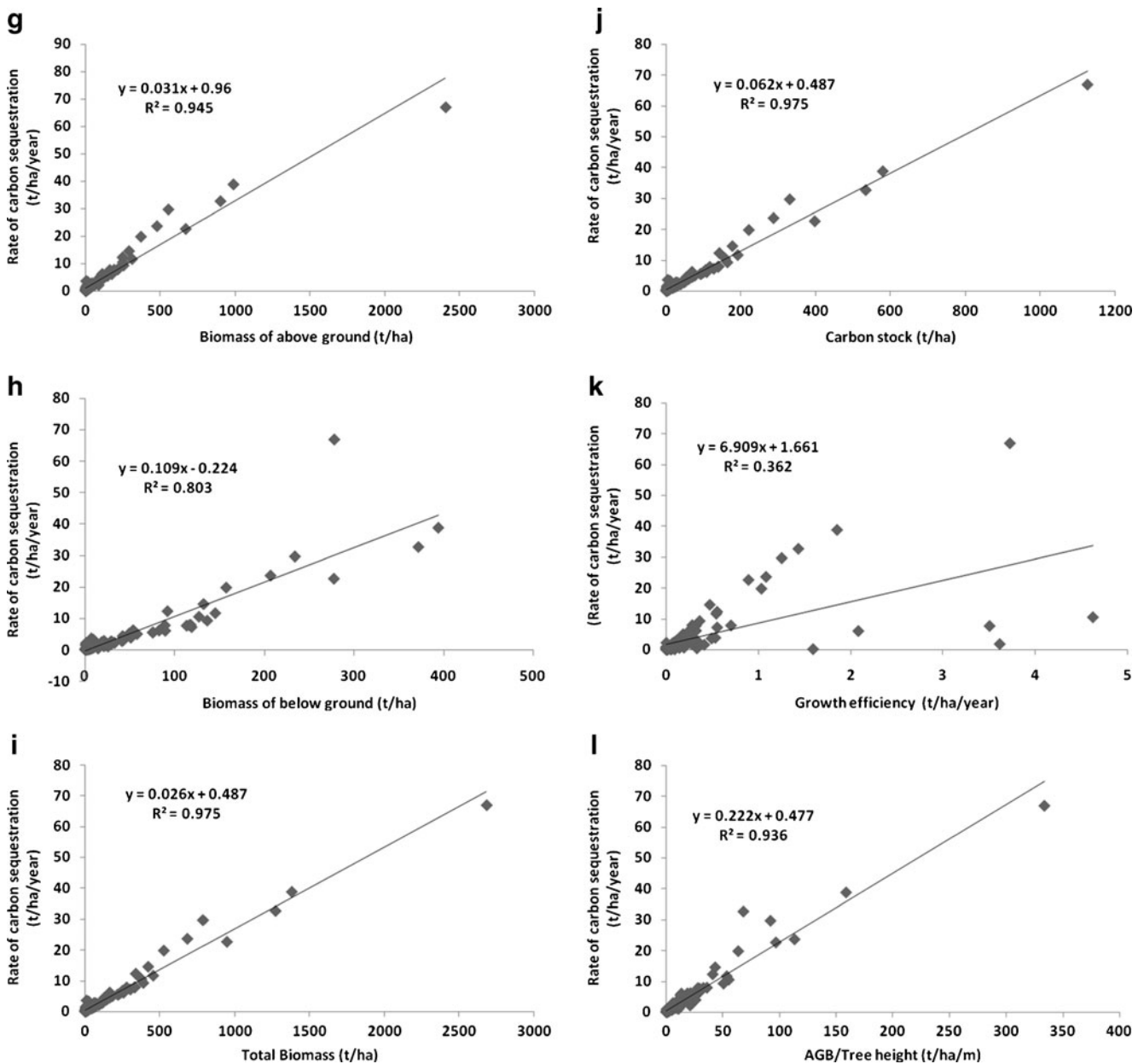
Fig. 2 (continued)

lower than that of other mangrove forests: 106–173 t ha^{-1} for *Bruguiera*, 187–273 t ha^{-1} for *Rhizophora* (Komiyama et al. 1987) and 87.5 t ha^{-1} in the *Ceriops tagal* (Komiyama et al. 2000).

Generally mangroves show relatively high amount of root biomass than other forms of forests (Saintilan 1997a, b; Komiyama et al. 2000). It is noteworthy that the large biomass allocated to the underground roots in the mangroves as revealed by the low ratio in the present study (Table 1). Mangroves are usually coping with the stresses of high water tables, salty soil and less mechanical support due to soft muddy substrate. Mangroves are unable to mechanically support their

above-ground weight without a heavy root system. Therefore, a large allocation of the net production into roots is necessary. In addition, soil moisture may cause increased allocation of biomass to the roots with enhanced cambial activity induced by ethylene production under submerged conditions (Yamamoto et al. 1995). Most mangrove species are highly sensitive to variation in nutrient availability (Boto and Wellington 1988; Feller 1995; Koch 1997; Feller et al. 2007; Lovelock et al. 2005, 2007; Naidoo 2006). Enhanced allocation to root biomass relative to shoot biomass is a common adaptation to low nutrient availability. Species of Rhizophoraceae are more tolerant to low nutrient
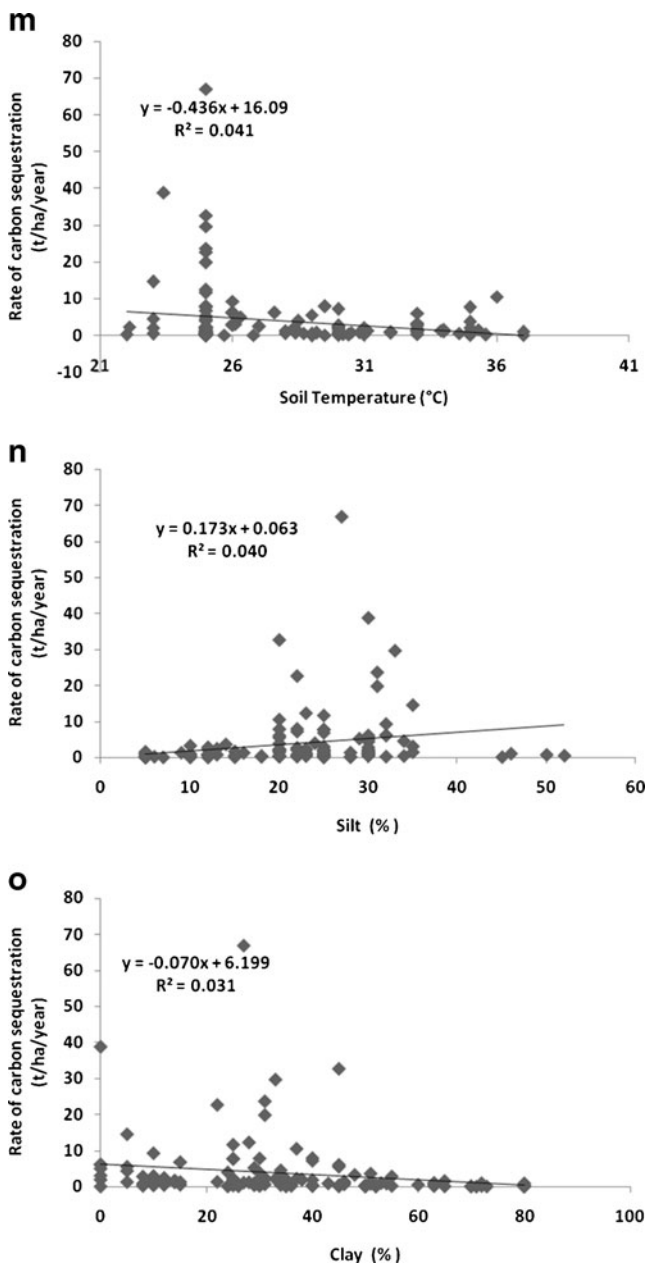
Fig. 2 (continued)

conditions than other mangrove species (Komiyama et al. 2000; Krauss et al. 2008), as was substantiated in the present study by low ratio of AGB/BGB in *R. mucronata*, as compared to *A. marina* (Table 1). This ratio between AGB and BGB was 2.73 for *A. marina* and 1.95 for *R. mucronata* in the present study (Table 1). The ratio is much higher than other reports: 1.12 in *Kandelia obovata* (Khan et al. 2009), 1.05 in *Ceriops tagal* (Komiyama et al. 2000), 1.72 in *A. marina* (Mackey 1993), but is closer to 2.27 in a *Rhizophora* forest (Tamai et al. 1986). In tropical inland forests the ratio which ranges from 5.1 to 10.7 is higher

than that in mangroves (Ogawa et al. 1965; Hozumi et al. 1969).

In the present study, the growth variables exhibited significant variation largely between mangrove species rather than mangrove sites. This finds the support of Komiyama et al. (2005) who have suggested that the allometric equations of mangrove species are highly species-specific but less site-specific. For example, the present study recorded leaf area index in a range of 3.33–6.32 (Table 1). A similar range of leaf area index is reported in other mangrove areas: 3.3 to 4.9 in *R. apiculata* in Mekong Delta, Vietnam (Clough et al. 2000) and 1.6 to 5.1 in Sawi Bay, Southern Thailand (Along and Dixon 2000). The present study registered net canopy photosynthesis in a range of 37.27 to 75.44 tC ha^{-1}year^{-1} (Table 1). A similar range of the net canopy photosynthesis has been recorded in other mangrove areas: from 24.5 tC ha^{-1}year^{-1} in 5 year old forest to 76.6 tC ha^{-1}year^{-1} in 25 year old forest in Sawi Bay (Along and Dixon 2000).

The rate of carbon sequestration recorded in present study was in a range between 1.1 and 8 t C ha^{-1}year^{-1} (Table 2). This value is lower than previous report: 13.57 t C ha^{-1}year^{-1} in 20-year old stand of *Rhizophora apiculata* in Peninsular Malaysia (Ong et al. 1995). In the Matang of Malaysia, total standing biomass was 114 t C ha^{-1} for *R. apiculata* (Ong et al. 1995) as against 90.6 t C ha^{-1} in *R. mucronata* in the present study (Table 2). Similarly, the 20 year old stand of *Rhizophora apiculata* in Matang of Malaysia shows the girth at breast height (gbh) of 30 cm and the average height of 21 m with biomass ranging from 10 to 510 kg with a mean biomass of 122 kg (Ong et al. 1995). However in the present study, all these values were low for *R. mucronata*, showing the mean gbh value of 11.87 cm, tree height of 4.64 m with a mean biomass of 8.53 kg (Table 1). The reason for these low values is that the present site is experiencing high salinity, high wind action, lack of freshwater, and man-made pressures (Kathiresan 2000; Alongi et al. 2005a, 2005b), whereas the Malaysian mangrove forest has been well-managed and it has moderate salinity and all other environmental conditions, favourable for growth of mangrove species (Ong et al. 1995).

The organic carbon burial rate in mangrove sediment is estimated at 1.39 t C ha^{-1}year^{-1} (Duarte et al. 2005). This value is lower than the carbon sequestered in the form of mangrove standing biomass, as evident in the present study (Table 2). Relatively high primary production of tree biomass is considered to bring about unusual carbon dynamics (Komiyama 2006). Therefore, mangroves forest is a highly efficient carbon sink in the tropics. However, the global warming may hit the efficiency of carbon sequestration by mangroves, as evident by a negative correlation between carbon sequestration and soil temperature (Fig. 2m).

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