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Carbon dioxide emission through soil respiration in a secondary mangrove forest of eastern Thailand

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Abstract: Carbon dioxide emission through soil respiration is an important component of the carbon balance in forest ecosystems. However, little information is available on the rates of soil respiration in mangrove forests. We studied the rate of soil respiration in a secondary mangrove forest in eastern Thailand on an estuary of the Trat River during both the wet and dry seasons. A study site of 40 × 110 m was established and a series of vegetation zones identified: *Sonneratia*, *Avicennia*, *Rhizophora* and *Xylocarpus*, in order of increasing elevation inland. Soil respiration was measured during low tide, using an infrared gas analyser connected to a respiratory chamber, by excluding the respiration of above-ground roots from the chamber. At least 19 measurements were performed in each zone for each season. The rate of soil respiration significantly increased with increasing soil temperature. The soil temperature which was usually lower than that of sea water showed a trend that decreased with distance from the river in both wet and dry seasons. The relative land elevation causes different periods of inundation among the vegetation zones. The period was longest in the *Sonneratia* zone located on the river fringe, and became shorter moving inland. Thus, the elevation and relevant period of inundation are considered to be causal factors warming the soil. Consequently, the difference in soil temperature caused significantly different rates of soil respiration among the vegetation zones in the mangrove forest. Overall, the average rate of soil respiration ranged from 0.456 to 0.876 μmol CO_2 m^{-2} s^{-1}, supporting the view that mangrove forests have lower rates of soil respiration than do upland forests.

Key Words: CO_2 emission, mangrove zonation, soil respiration, soil temperature

INTRODUCTION

Forest ecosystems play an important role in regulating atmospheric CO_2 concentration (Dixon *et al.* 1994, Houghton 2002). A forest with high net primary production (NPP) would be a strong carbon sink if the transfer from biomass increment to carbon uptake is efficient at the ecosystem level. Small losses of carbon via soil respiration would strengthen this assumption. For mangroves, which are highly productive in terms of annual biomass increment (Amarasinghe & Balasubramaniam 1992, Christensen 1978, Day *et al.* 1987, Ong *et al.* 1995, Sherman *et al.* 2003), loss of carbon via soil respiration may theoretically counter high rates of primary productivity in assessment of the source or sink strength for atmospheric carbon of mangrove ecosystems.

While the NPP of mangrove forests has received much attention (Putz & Chan 1986, Robertson *et al.* 1991, Ross *et al.* 2001, Sherman *et al.* 2003), only a few studies have considered the soil respiration rate of mangroves (Alongi *et al.* 2001, Kristensen *et al.* 1995, Lovelock 2008, Mall *et al.* 1991). Most of these studies reported a low rate of soil respiration, possibly caused by the anaerobic conditions of mangrove soils.

Mangrove forests, periodically inundated by seawater, are formed into vegetation zones with the dominant tree species changing with distance from the seashore (Bunt 1996, Youssef & Saenger 1999). Potential causes for the vegetation zones include plant succession and physiological adaptation to physico-chemical gradients in mangrove forest (Smith 1992). The physical condition of mangrove soil differs among vegetation zones due to

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inundation patterns and changes in elevation. However, few studies have compared the rate of soil respiration among vegetation zones.

In the present study, the magnitude of CO_2 emission through soil respiration is compared among four zones dominated respectively by *Sonneratia*, *Avicennia*, *Rhizophora* and *Xylocarpus* species in a secondary mangrove forest in both the wet and dry seasons. The soil temperature is also compared among them. We hypothesized that rates of soil respiration differ among the vegetation zones and seasons. Moreover, the relationship between soil respiration and temperature is examined. We discussed the zonal variation in soil temperature by causal factors such as elevation and inundation.

METHODS

Site description

The study site was a secondary mangrove forest on an estuary of the Trat River, Trat Province, eastern Thailand (12° 12′N, 120° 33′E, Figure 1a). This forest was formerly used for timber and charcoal production. Since the 1980s, Mangrove Forest Research and Development Station No. 4 (Department of Marine and Coastal Resources, Thailand) has managed this area. The annual precipitation and temperature at Trat were 5214 mm and 27.6 °C from 2003 to 2006 (Department of Meteorology, Thailand). In 2006, the precipitation in the wet season (May–October) was 89% of the total for the year.

A study plot (40 × 110 m) was established in 2001. Tree density (diameter at breast height, dbh > 4.0 cm) was 1682 stems ha^{-1}, and average dbh and height were 11.7 cm and 10.8 m, respectively. The dominant tree species changed with distance from the river, and the forest was divided into four vegetation zones based on dominant tree species (Figure 1b). The river fringe was occupied by a narrow belt of *Sonneratia* in very soft and deep mud. This zone formed a pure stand of *S. caseolaris* with regularly distributed conically shaped, 20–30-cm-high pneumatophores. Inland of the *Sonneratia* zone was the *Avicennia* zone, with many tall (height = 17 m) *A. alba* trees that produced a high density of short, slim pneumatophores. The soil was soft mud but shallower than that of the *Sonneratia* zone. Next was a zone mainly composed of dense stands of *Rhizophora apiculata* and *R. mucronata*, which produced many stilt roots in a soft mud substrate approximately 5–10 cm deep. A dense root necromass had formed below that depth. The fourth zone, farthest from the river, was the *Xylocarpus* zone, comprising *X. granatum*, *Bruguiera gymnorrhiza* and *Ceriops tagal*, with small buttresses. Large amounts of root necromass were densely accumulated in the *Xylocarpus* zone soils.

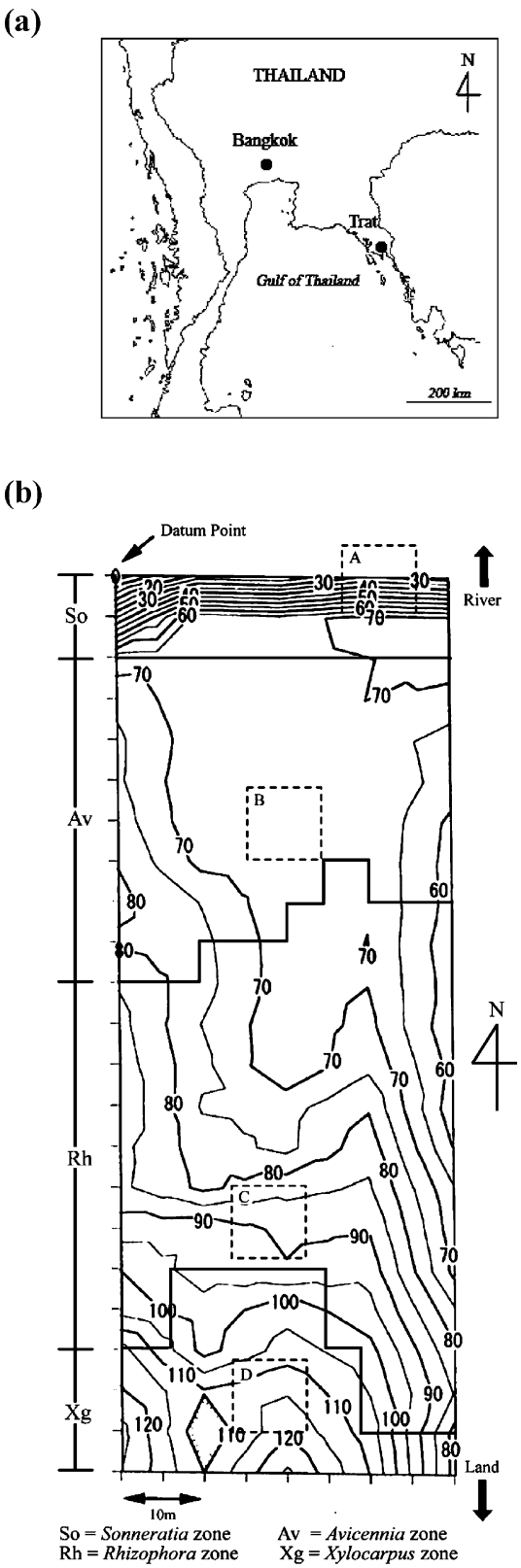

Figure 1. Study site and sample plot. Location of the study site (a), sample plot (40 × 110 m) (b). Contour lines show the relative elevation from the datum point. The four survey areas (A, B, C and D) represent the sites where soil respiration and temperature were measured in the respective zones.

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Table 1. Average rates of CO_2 emission via soil respiration in the mangrove forest.

	CO_2 emission via soil respiration (μmol CO_2 $m^{-2}s^{-1}$)	
	Mean ± SD	Range
Wet season 2006		
Avicennia zone (n = 12)	0.852 ± 0.169	0.597–1.16
Rhizophora zone (n = 19)	0.383 ± 0.146	0.165–0.704
Xylocarpus zone (n = 20)	0.586 ± 0.353	0.133–1.37
Wet season 2007		
Sonneratia zone (n = 19)	0.786 ± 0.246	0.445–1.25
Avicennia zone (n = 20)	0.747 ± 0.335	0.218–1.67
Dry season 2007		
Sonneratia zone (n = 19)	0.966 ± 0.479	0.359–2.26
Avicennia zone (n = 20)	0.645 ± 0.260	0.281–1.29
Rhizophora zone (n = 20)	0.526 ± 0.182	0.270–0.887
Xylocarpus zone (n = 19)	0.600 ± 0.323	0.205–1.17

The elevation of the study site was relatively low in the *Sonneratia* zone, with the slope gradually increasing toward the inland zones to a total 1.2-m difference in elevation between the riverside and the most inland zone (Figure 1b). The range of elevation in each plot was 0–0.3 m in the *Sonneratia* zone, 0.6–0.8 m in *Avicennia*, 0.6–0.9 m in *Rhizophora* and 0.9–1.2 m in the *Xylocarpus* zone.

The study site is generally affected by a single tide, as is most of the mangrove forest area of the Trat River estuary (Royal Thai Navy, Thailand). The highest tide level in the wet season at the various zone elevations is typically around 1.5, 0.9, 0.7 and 0.3 m in the *Sonneratia*, *Avicennia*, *Rhizophora* and *Xylocarpus* zones, respectively.

Measurement of soil respiration

To measure soil respiration, we established four survey areas in each vegetation zone (*c.* 50 m^2 each; Figure 1b). Measurements in the 2006 wet season for *Avicennia*, *Rhizophora* and *Xylocarpus* were taken on 11–12 August 2006. Measurements in the 2007 wet season for *Sonneratia* and *Avicennia* were taken on 8–12 August 2007. Measurements in the 2007 dry season for all vegetation zones were taken on 21–30 March 2007. At least 19 measurements of soil respiration were made in each area for each season (Table 1).

Measurements were done during low-tide periods using a closed system consisting of a chamber and an infrared gas analyser (model LI-840, LI-COR Biosciences, USA). The open area of the chamber was 78.5 cm^2. A 10-cm-tall PVC collar was carefully inserted about 1 cm into open and non-disturbed soil surfaces with no above-ground roots, such as pneumatophores, stilt roots or buttresses, and remained in place 10 min before the chamber was attached. An elastic ring gasket was inserted between the chamber and collar to prevent air leaks. We used platforms to avoid soil disturbance around the chamber. The CO_2 concentration in the chamber was measured at 1-s intervals continuously for 15 min. The data were recorded with a computer connected to the gas analyser. Differential CO_2 concentrations were calculated for each second. The soil respiration rate of each measurement was then obtained by averaging the differential CO_2 concentrations (60 s × 15 min). During soil respiration measurements, the soil temperature at a 5-cm depth was measured near the chamber, with the temperature recorded at 0, 5, 10 and 15 min, using a temperature sensor and recorder (Model TR-71U, T&D Co., Ltd.). The temperatures were averaged to obtain a mean temperature for each soil respiration measurement.

Measurement of environmental factors

Twelve temperature sensors and loggers (Thermochron G-type, KN Laboratories Inc., Japan, and TidbiT v2 Temp logger, Onset Computer Co., Ltd.) were buried at a depth of 5 cm from the soil surface in each study plot (Figure 1b), and measurements of soil temperature were taken at 30-min intervals from August 2006 to August 2007. Another sensor measured the water temperature of the river in front of the study plot. Unfortunately, the data loggers recording the August 2006–February 2007 temperature of the *Xylocarpus* zone were lost. The temperature sensors and loggers for all zones were reset in March 2007. Therefore, no temperature data were available for any zone in early March.

The inundation period between the low and high tides was investigated on 15 August 2006 (wet season) and 22 March 2007 (dry season). We recorded the time when the tide started to move inland from the river edge, and then periodically recorded as it reached each part of the study plot. The water table was assessed during low tides

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on 22–23 August 2006. Two-cm-diameter plastic pipes were placed in the soil 0, 35, 80 and 105 m from the river. The distance between the soil surface and the water in the pipes was measured using a ruler.

Statistical analysis

All statistical analyses were performed using SPSS 13.0 for window (SPSS Inc., USA). The difference in soil temperature across the vegetation zones was tested by one-way ANOVA and Duncan's multiple range test. Two-way ANOVA was used to test for effects of vegetation zone and season on rate of soil respiration. The analysis of significant differences in rate of soil respiration was tested by Games-Howell test (Day & Quinn 1989). The relationship between soil temperature and respiration was tested by regression analysis.

RESULTS

Inundation pattern and water table of vegetation zones

On 15 August 2007 (wet season), the single-tide inundation of seawater started at 12h25 in the *Sonneratia* zone. The *Avicennia* zone was completely submerged 20 min later. The seawater flooded the end of the *Xylocarpus* zone at 14h40. On 22 March 2007 (dry season), inundation began at 09h00 and slowly reached the *Xylocarpus* zone at 14h10. On this day, a section of the *Xylocarpus* zone was never submerged. Thus, the daily inundation period of the *Sonneratia* zone was longer than that of the innermost *Xylocarpus* zone, totalling at least 2 h 15 min in the wet season and 5 h 10 min in the dry season.

The water table (Figure 2) at the riverside in the *Sonneratia* zone had a relatively wide range of 5–15 cm depth below the soil surface. However, 35, 80 and 105 m from the river, the water table was stable, usually varying only slightly (0–3 cm depth).

Soil temperature

The soil temperatures were calculated by averaging the soil temperature across all four vegetation zones from August 2006 to August 2007, these were 28.19 °C in the dry (November to April) and 27.21 °C in the wet (May to October) seasons. We compared the average March–August 2007 soil temperatures among the four vegetation zones (Figure 3), because of the lost data from *Xylocarpus* zone mentioned above. Soil temperatures differed among the zones (ANOVA, $F_{4,680} = 83.4$, $P < 0.01$). The average soil temperatures tended to decrease with increasing distance from the river and were 30.14 °C, 29.63 °C, 28.38 °C and 27.71 °C for *Sonneratia*, *Avicennia*, *Rhizophora* and *Xylocarpus*, respectively. The average water temperature was 30.05 °C, which was not significantly different from the soil temperature in the *Sonneratia* zone (Duncan's multiple range test, $P = 0.985$) but significantly higher than soil temperatures of the other three zones (Duncan's multiple range test, $P < 0.01$) as shown in Figure 4.

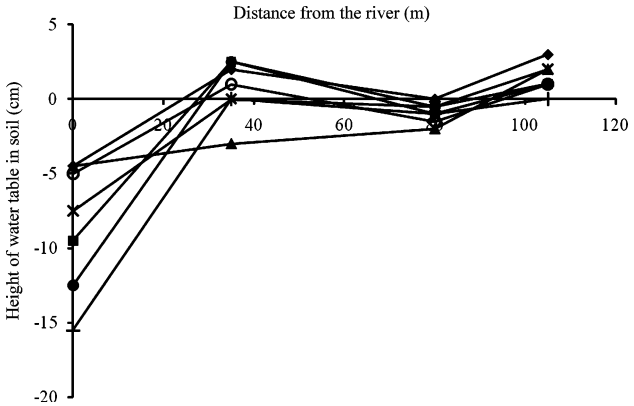

Figure 2. Relative water table at four points from the river during low tide on 22 August 2006 at 09h20 (♦) and 13h30 (■); and 23 August 2006 at 10h00 (▲), 10h30 (×), 10h45 (◯), 11h30 (●) and 11h45 (+). Negative values indicate that the water level was lower than the soil surface.

Soil respiration

The average rates of soil respiration in the wet and dry seasons of each zone are shown in Table 1. The rate of soil respiration in the *Avicennia* zone did not differ significantly between 2006 and 2007 in the wet season (ANOVA, $F_{1,30} = 1.02$, $P = 0.320$) or across all zones between the wet and dry seasons (two-way ANOVA, $F_{1,160} = 3.35$, $P = 0.069$). There was no significant interaction between zone and season (two-way ANOVA, $F_{3,160} = 0.79$, $P = 0.053$). However, the difference in soil respiration was significant (two-way ANOVA, $F_{3,160} = 14.4$, $P < 0.001$) among the four vegetation zones in both seasons. When the average rate of soil respiration in each zone (Table 1) was calculated regardless of season, the average rate was higher in the *Sonneratia* zone (0.876 μmol CO_2 m^{-2} s^{-1}) than in either the *Rhizophora* or *Xylocarpus* zones (0.525 μmol CO_2 m^{-2} s^{-1}), but did not differ from the zone immediately adjacent (*Avicennia*: 0.732 μmol CO_2 m^{-2} s^{-1}). The rate of soil respiration for the *Rhizophora* zone was lower than both the *Sonneratia* and *Avicennia* zones, roughly tracking the pattern of soil elevation change (Figure 4) and water table depth (Figure 2).

We checked the overall relationship between soil respiration and the temperature obtained in each

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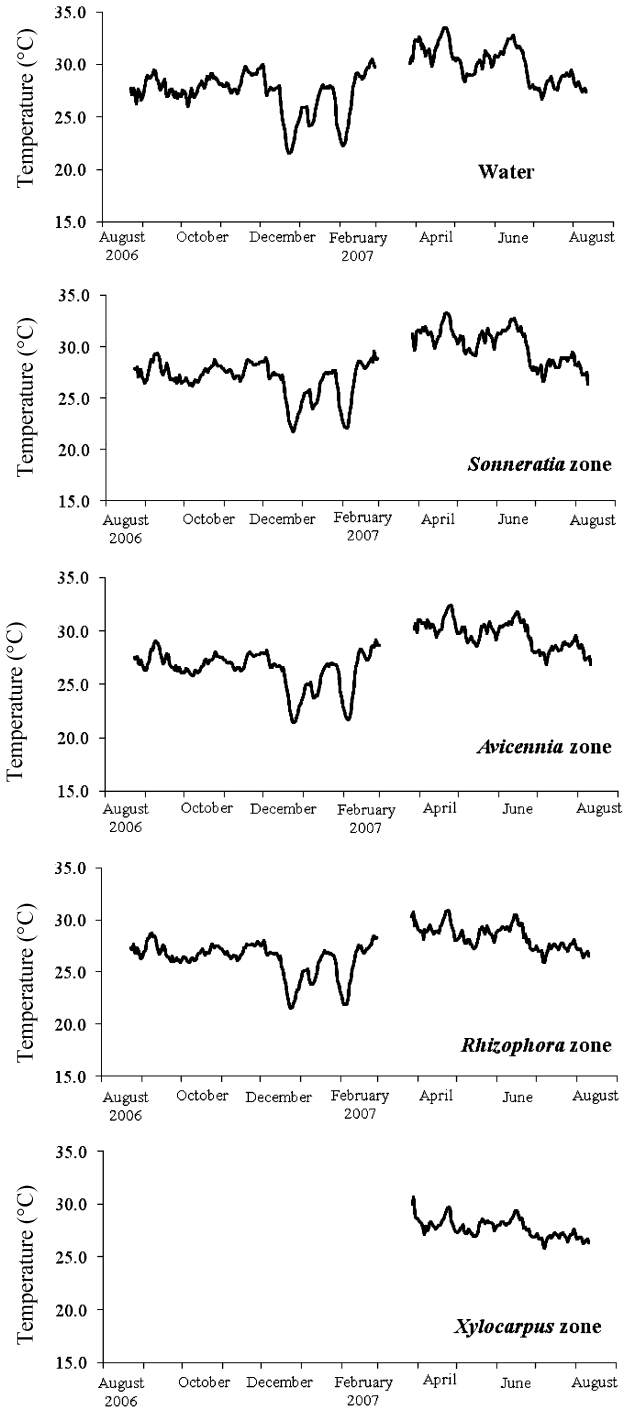

Figure 3. Daily soil temperature for each zone and river water temperature during August 2006–August 2007. The *Xylocarpus* zone data of August 2006–February 2007 were not available because the data loggers were lost. For all vegetation zones, no data were obtained in early March due to the reset and preparation of the temperature sensors and loggers.

measurement (n = 168). Although the relationship was significant in both linear ($F_{1,167} = 17.5$, $P = 0.00004$) and power function ($F_{1,167} = 20.3$, $P = 0.00001$), the coefficient of determination (R^2) of regression line fitted a power function rather than that of a linear regression (0.109 vs. 0.0953). Therefore, we adopted the relationship between soil respiration and temperature fitted by a power function (Figure 5).

DISCUSSION

Carbon dioxide emission via soil includes CO_2 efflux from roots and heterotrophic respiration (Hanson *et al.* 2000, Lee *et al.* 2003). Recently, Komiyama *et al.* (2008) suggested a method of balancing net ecosystem production (NEP) without taking root respiration into consideration. Consequently, the NPP and heterotrophic respiration in soil allow estimation of NEP. The mangroves we studied develop peculiar root systems, in which the aerenchymatous tissue of underground roots is connected with lenticels on pneumatophores, prop roots, and buttresses above the ground (Tomlinson 1986). Scholander *et al.* (1955) clarified the process of gas exchange through these lenticels under submerged conditions. Most metabolic respiration from underground roots is released through the lenticels. The underground roots likely make only a small contribution to soil respiration when measured via respiration chambers placed to avoid above-ground roots. Therefore, the soil CO_2 efflux obtained in the present study would be close to the CO_2 released from heterotrophic respiration.

The soil temperature at the study site fluctuated in a relatively small range by season, although exceptionally low soil temperatures occurred during two short periods (Figure 3) in mid-December and early February, due to cold air masses from high-latitude regions. Soil temperature in tropical zones usually fluctuates in a narrow range (Hashimoto *et al.* 2004, Kosugi *et al.* 2007) compared with that in temperate zones (Hirata *et al.* 2007).

The rate of soil respiration basically depends on soil temperature (Davidson *et al.* 1998, Lee *et al.* 2003, Martin *et al.* 2007, Nakane *et al.* 1983). While we found a strong relationship between soil temperature and soil respiration (Figure 5), temperature dissimilarity between the wet and dry seasons assessed was apparently not sufficient to drive seasonal difference in soil respiration rate. Hashimoto *et al.* (2004) also reported that the difference in soil respiration rate was not significant between dry and rainy seasons in a tropical forest in northern Thailand, and showed a small change in soil temperature throughout the year.

Some studies on soil respiration in tropical forests are shown in Table 2. This provides evidence pointing to generally lower rates of soil respiration in mangrove forests than in tropical upland forests. The water table at our study site was high (Figure 2), and the soil respiration rate is negatively correlated to soil water

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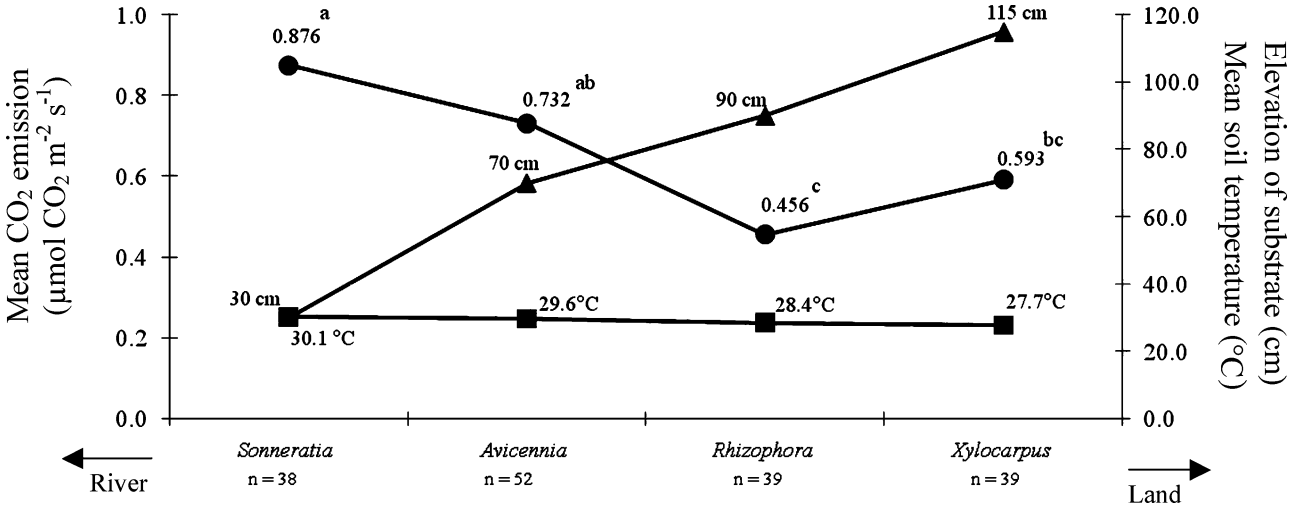

Figure 4. Mean CO_2 emission (●), soil temperature (■), and elevation of the substrate (▲) among the four vegetation zones. Values with the same letters are not significantly different. The soil temperature of each zone was obtained by averaging the daily soil temperature from March to August 2007.

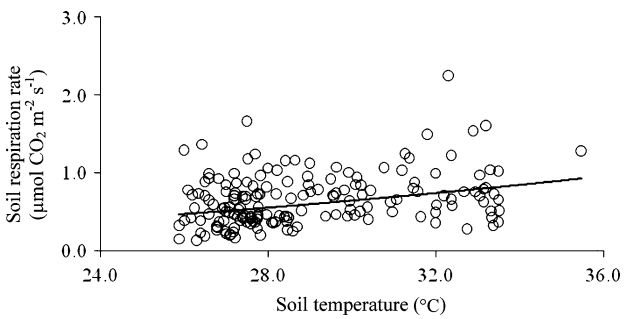

Figure 5. Response of soil respiration to soil temperature in the mangrove forest. The regression line was fitted to a power function as $Y = 0.0004 X^{2.204}$, $R^2 = 0.109$.

content (Davidson *et al.* 1998, Kosugi *et al.* 2007, Scott-Denton *et al.* 2003). Moreover, mangrove soils often experience anaerobic conditions (Lawton *et al.* 1981, McKee *et al.* 1988), which may restrict the activity and respiration of microbes and benthic organisms in mangrove forests compared to other terrestrial forests.

It is noteworthy that the difference in soil respiration rate was significant among the four vegetation zones. The rate was highest in the *Sonneratia* zone at the riverside and trended lower in the more inland zones (Figure 4, Table 1). On the other hand, soil temperature tended to decrease with distance from the river (Figure 4). Thus, the spatial difference in soil respiration over the zones can be explained by the variation in soil temperature.

We considered the effect of the temperature of inundating seawater on soil temperature over the mangrove vegetation zones. At the study site, the seawater temperature was usually higher than that of the soil (Figure 3), and therefore the water warmed the soil when it invaded the forest.

The period of inundation depends on microtopography, especially elevation (Figure 1b). The *Sonneratia* zone near the river had the lowest elevation among the four

Table 2. Published ranges of soil respiration rates in tropical forests.

Location	Soil respiration rate (μmol CO_2 $m^{-2}s^{-1}$)	Temperature (°C)	Reference
Mangrove forest			
Eastern Thailand	0.456–0.876	27.7–30.1	Present study
Southern Thailand	0.61	–	Kristensen *et al.* 1995
Australia	0.048–1.47	–	Alongi *et al.* 2000
Southern Thailand	0.193–0.611	–	Alongi *et al.* 2001
Australia and New Zealand	0.371–0.511	15 – 35	Lovelock 2008
Terrestrial forest			
Tropical rain forest in Asia	3.96– 9.94	–	Yoda 1971
Tropical rain forest in Australia	7.16	–	Maggs & Hewett 1990
Eastern Amazonia, Brazil	2.54–5.07	22–31	Davidson *et al.* 2000
Northern Thailand	2.13–14.1	19	Hashimoto *et al.* 2004
Pasoh, Malaysia	2.5–6.5	24.6–25.7	Kosugi *et al.* 2007

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vegetation zones, and thus was submerged for the longest period of time each day, with the long period of inundation sustaining the higher temperature of the soil. In contrast, *Xylocarpus*, the most inland zone, was submerged for the shortest period of time. The time spent submerged differed by approximately 2–5 h d^{-1} between the *Sonneratia* and *Xylocarpus* zones. The difference was longest in the dry season, possibly due to the low specific gravity (salt concentration) of the inundating seawater in the wet season.

In conclusion, the magnitude of CO_2 emissions through soil respiration is low in mangrove forests compared with other tropical upland forests. Moreover, we found that the rate of soil respiration differed by vegetation zone. Zones at lower elevations, which are submerged for long periods by warm seawater, show higher rates. Therefore, the decomposition process of organic matter may be closely related to the inundation pattern or elevation of mangrove forests. This may help to explain the zonation patterns of mangroves in terms of soil formation and soil properties.

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LITERATURE CITED

ALONGI, D. M., TIRENDIA, F. & CLOUGH, B. F. 2000. Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* along the arid coast of Western Australia. *Aquatic Botany* 68:97–122.

ALONGI, D. M., WATTAYAKORN, G., PFITZNER, J., TIRENDI, F., ZAGORSKIS, I., BRUNSKILL, G. J., DAVIDSON, A. & CLOUGH, B. F. 2001. Organic carbon accumulation and metabolic pathways in sediments of mangrove forests in southern Thailand. *Marine Geology* 179:85–103.

AMARASINGHE, M. D. & BALASUBRAMANIAM, S. 1992. Net primary productivity of two mangrove forest stands on the northwest coast of Sri Lanka. *Hydrobiologia* 247:37–47.

BUNT, J. S. 1996. Mangrove zonation: an examination of data from seventeen riverine estuaries in tropical Australia. *Annals of Botany* 78:333–341.

CHRISTENSEN, B. 1978. Biomass and primary production of *Rhizophora apiculata* mangrove forest in southern Thailand. *Aquatic Botany* 4:43–52.

DAVIDSON, E. A., BELK, E. & BOONE, R. D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology* 4:217–227.

DAVIDSON, E. A., VERCHOT, L. S., CATTANIO, J. H., ACKERMAN, I. L. & CARVALHO, J. E. M. 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* 48:53–69.

DAY, J. W., CONNER, W. H., LEY, L. H., DAY, R. H. & NAVARRO, A. M. 1987. The productivity and composition of mangrove forests, Laguna de Terminons, Mexico. *Aquatic Botany* 27:267–284.

DAY, R. W. & QUINN, G. P. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59:433–463.

DIXON, R. K., BROWN, S., HOUGHTON, R. A., SOLOMON, A. M., TREXLER, M. C. & WISNIEWSKI, J. 1994. Carbon pool and flux of global forest ecosystems. *Science* 263:185–190.

HANSON, P. J., EDWARDS, N. T., GRATEN, C. T. & ANDREWS, J. A. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48:115–146.

HASHIMOTO, S., TANAKA, N., SUZUKI, M., INOUE, A., TAKISAWA, H., KOSAKA, I., TANAKA, K., TANTASIRIN, C. & TANGTHAM, N. 2004. Soil respiration and soil CO_2 concentration in a tropical forest, Thailand. *Journal of Forest Research* 9:75–79.

HIRATA, R., HIRANO, T., SAIGUSA, N., FUJINUMA, Y., INUKAI, K., KITAMORI, Y., TAKAHASHI, Y. & YAMAMOTO, S. 2007. Seasonal and interannual variations in carbon dioxide exchange of a temperate larch forest. *Agricultural and Forest Meteorology* 147:110–124.

HOUGHTON, R. A. 2002. Magnitude, distribution and causes of terrestrial carbon sinks and some implications for policy. *Climate Policy* 2:71–88.

KOSUGI, Y., MITANI, T., ITOH, M., NOGUCHI, S., TANI, M., MATSUO, N., TAKANASHI, S., OHKUBO, S. & NIK, A. R. 2007. Spatial and temporal variation in soil respiration in a Southeast Asian tropical rainforest. *Agricultural and Forest Meteorology* 147:35–47.

KOMIYAMA, A., ONG, J. E. & POUNGPARN, S. 2008. Allometry, biomass, and productivity of mangrove forests: a review. *Aquatic Botany* 89:128–137.

KRISTENSEN, E., HOLMER, M., BANTA, G. T., JENSEN, M. H. & HANSEN, K. 1995. Carbon nitrogen and sulfur cycling in sediments of the Ao Nam Bor mangrove forest, Phuket, Thailand: a review. *Phuket Marine Biology Center Research Bulletin* 60:37–64.

LAWTON, J. R., TODD, A. & NAIDOO, D. K. 1981. Preliminary investigations into the structure of root of mangroves *Avicennia marina* and *Bruguiera gymnorrhiza*, in relation to ion uptake. *New Phytologist* 88:713–722.

LEE, M. S., NAKANE, K., NAKATSUBO, T. & KOIZUMI, H. 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. *Plant and Soil* 255:311–318.

LOVELOCK, C. E. 2008. Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems* 11:342–354.

MAGGS, J. & HEWETT, B. 1990. Soil and litter respiration in rainforests of contrasting nutrient status and physiognomic structure near Lake Eacham, north-east Queensland. *Australian Journal of Ecology* 15: 329–336.

MALL, L. P. SINGH, V. P. & GARGE, A. 1991. Study of biomass, litter fall, litter decomposition and soil respiration in monogeneric mangrove

and mixed mangrove forests of Andaman Islands. *Tropical Ecology* 32:144–152.

MARTIN, D., BERINGER, J., HUTLEY, L. B. & MCHUGH, I. 2007. Carbon cycling in a mountain ash forest: analysis of below ground respiration. *Agricultural and Forest Meteorology* 147:58–70.

MCKEE, K. L., MENDELSSOHN, I. A. & HESTER, M. W. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany* 75:1352–1359.

NAKANE, K., YAMAMOTO, M. & TSUBOTA, S. 1983. Estimation of root respiration rate in a mature forest ecosystem. *Japanese Journal of Ecology* 33:397–408.

ONG, J. E., GONG, W. K. & CLOUGH, B. F. 1995. Structure and productivity of a 20-year-old stand of *Rhizophora apiculata* Bl. Mangrove forests. *Journal of Biogeography* 22:417–427.

PUTZ, F. & CHAN, H. T. 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. *Forest Ecology and Management* 17:211–230.

ROBERTSON, A. I., DANIEL, P. A. & DIXON, P. 1991. Mangrove forest structure and productivity in the Fly River estuary, Papua New Guinea. *Marine Biology* 111:147–155.

ROSS, M. S., RUIZ, P. L., TELESNICKI, G. J. & MEEDER, J. F. 2001. Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (USA). *Wetlands Ecology and Management* 9:27–37.

SCHOLANDER, P. F., VAN DAM, L. & SCHOLANDER, S. I. 1955. Gas exchange in the roots of mangroves. *American Journal of Botany* 42:92–98.

SCOTT-DENTON, L. E., SPARKS, K. L. & MONSON, R. K. 2003. Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest. *Soil Biology and Biochemistry* 35:525–534.

SHERMAN, R. E., FAHEY, T. J. & MARTINEZ, P. 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems* 6:384–398.

SMITH, T. J. 1992. Forest structure. Pp. 101–136 in Robertsons, A. I. & Alongi, D. M. (eds.). *Tropical mangrove ecosystems, coastal and estuarine studies*. American Geophysical Union, Washington DC.

TOMLINSON, P. B. 1986. *The botany of mangroves*. Cambridge University Press, Cambridge. 419 pp.

YODA, K. 1971. *Forest ecology*. Tsukiji-Shokan, Tokyo. 331 pp. (in Japanese).

YOUSSEF, T. & SAENGER, P. 1999. Mangrove zonation in Mobbs Bay – Australia. *Estuarine, Coastal and Shelf Science* 49:43–50.