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Soil Respiration and Belowground Carbon Allocation in Mangrove Forests

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Abstract

Mangrove forests cover large areas of tropical and subtropical coastlines. They provide a wide range of ecosystem services that includes carbon storage in above- and below ground biomass and in soils. Carbon dioxide (CO_2) emissions from soil, or soil respiration is important in the global carbon budget and is sensitive to increasing global temperature. To understand the magnitude of mangrove soil respiration and the influence of forest structure and temperature on the variation in mangrove soil respiration I assessed soil respiration at eleven mangrove sites, ranging from latitude 27°N to 37°S. Mangrove soil respiration was similar to those observed for terrestrial forest soils. Soil respiration was correlated with leaf area index (LAI) and aboveground net primary production (litterfall), which should aid scaling up to regional and global estimates of soil respiration. Using a carbon balance model, total belowground carbon allocation (TBCA) per unit litterfall was similar in tall mangrove forests as observed in terrestrial forests, but in scrub mangrove forests TBCA per unit litter fall was greater than in terrestrial forests, suggesting mangroves allocate a large proportion of their fixed carbon below ground under unfavorable environmental conditions. The response of soil respiration to soil temperature was not a linear function of temperature. At temperatures below 26°C Q10 of mangrove soil respiration was 2.6, similar to that reported for terrestrial forest soils. However in scrub forests soil respiration declined with increasing soil temperature, largely because of reduced canopy cover and enhanced activity of photosynthetic benthic microbial communities.

Key words: aboveground primary production; total belowground carbon allocation; leaf area index; climate change; *Avicennia marina*; *Avicennia germinans*; *Ceriops tagal*; *Rhizophora lamarkii*; *Rhizophora mangle*.

Introduction

Carbon dioxide efflux from soil or soil respiration is an important component of the global carbon budget and is predicted to be strongly influenced by current and future increases in global temperature (Lloyd and Taylor 1994; Boone and others 1998; Valentini and others 2000; Rustad and others 2000; Schlesinger and Andrews 2000). Wetlands are an important ecosystem influencing global carbon budgets because of their high productivity and the high carbon (C) stocks in wetland soils (Raich and Schlesinger 1992; Raich and Tufekcioglu 2000). The contribution of different wetland ecosystems, for example, temperate peatlands, salt marshes and mangrove forests, and the factors that influence CO_2 emissions from wetland soils are not well known, particularly for tropical ecosystems (Raich and Schlesinger 1992; Grace and Rayment 2000).

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The sensitivity of soil respiration to temperature variations was proposed to be higher in cooler compared to warmer environments (Lloyd and Taylor 1994; Raich and Schelsinger 1992) and has been proposed to be particularly important in determining whether soils will be long-term sources or sinks of C (Grace and Rayment 2000) although this has been disputed (for example, Melillo and others 2002). In this study I use natural variation over a wide range of sites to investigate broad scale patterns in soil respiration of mangrove forests and to understand the factors that are important in determining the magnitude of soil respiration in mangrove forests.

In terrestrial forests, soil respiration increases linearly with aboveground primary production (ANPP) reflecting the importance of plant productivity and allocation to roots, root microbial symbionts and exudates in determining soil respiration (Raich and Nadelhoffer 1989; Högberg and others 2001; Davidson and others 2002; Ruess and others 2003; Jianwu Tang and others 2005). The proportion of total photosynthetically fixed carbon (C) allocated belowground tends to decline with increasing ANPP (Giardina and others 2003), consistent with the predictions of models where environments with abundant belowground resources (water and nutrients) result in relatively smaller investment in roots and root symbionts (Brouwer 1962; Chapin 1991; Cannell and Dewer 1994; Raich 1998). Establishing relationships between ANPP, total belowground carbon allocation (TBCA) and soil respiration are important for building models to estimate regional and global carbon budgets for forests and for establishing the value of the ecosystems services they provide (Raich and Nadelhoffer 1989; Raich and Schlesinger 1992, Giardina and Ryan 2000; Giardina and others 2003).

Mangrove forests occupy the interface between land and sea on sheltered tropical and subtropical coasts over a broad latitudinal range (30°N to 38°S, Duke and others 1998). Global coverage of mangroves is extensive, covering 1.7–1.8 $\times 10^5$ km^2 of the coastal zone (Spalding and others 1997; Valiela and others 2001). They have important roles in sustaining tropical and subtropical coastal productivity (Ewel and others 1998) and sequester large amounts of C below ground (Twilley and others 1992; Chmura and others 2003). Mangrove forests make a significant contribution to the world tropical peat storage (MacIntyre and others 1995; McKee and others 2007; Chimner 2004) and C stores in mineral soils are also large, significantly greater than temperate salt marsh soils (Chmura and others 2003).

Large C stores in mangrove soils occur because C deposition in mangrove soils is high; both from allochthanous and autochthonous sources, and rates of C oxidation within mangrove soils is low, due to anaerobic conditions (Twilley and others 1992). Mangrove forests are notable for their conspicuous aerial root systems (pnuematophores and stilt roots) with abundant aerenchyma. Due to high primary production rates of some mangrove forests (Clough 1992; Saenger and Snedaker 1993) and the conspicuous root systems and highly organic soils, it has been proposed that mangroves allocate a large portion of their fixed carbon to roots (Lugo and Snedaker 1974; Hutchings and Saenger 1987; Komiyama and others 1987). In some settings, for example within the Belizean barrier reefs, mangrove islands consist of up to 12 m of peat comprised of mangrove root tissue that have been deposited during recent Holocene sea level rise (MacIntyre and others 1995; McKee and Faulkner 2000). Due to difficulties in extracting live roots from mangrove soils, data on standing stocks of roots and root growth are very limited (but see Komiyama and others 1987; Robertson and Dixon 1993; McKee 2001; McKee and others 2007). The few estimates of standing stocks of live roots reveal that mangrove live root biomass per unit area of soil can be relatively low compared to other forested ecosystems (Clough 1992). Fine root respiration per unit biomass is low (McKee 1996; Lovelock and others 2006), and root turnover is also very slow compared to other tree species (McKee and others 2007). Together these data suggest that TBCA in mangroves could be lower than expected on the basis of the C stores in soils, and that respiration of mangrove soils would also be low compared to other forest types.

In this study I assess the magnitude of soil respiration in mangrove forests over a range of sites, which encompass wide variation in forest structure, ANPP, and climate. The study forests vary from dwarf and scrub stands (<2 m in height), associated with soil anoxia, hypersalinity and low nutrient availability to taller stands fringing channels and open water (>3 m in height). I use this data set to test whether TBCA in mangrove forests follows the predictions of carbon allocation models developed for terrestrial forests (Raich and Nadelhoffer 1989; Giardina and Ryan 2002; Giardina and others 2003). I assess whether soil respiration is higher in taller forests compared to dwarf forests, reflecting differences in aboveground productivity. I also assess whether TBCA in mangrove forests is related to ANPP with a similar relationship as it is in terrestrial forests, and whether shorter stature forests,

many of which are nutrient limited (Feller and others 2002; Feller and others 2003; Lovelock and others 2004; 2007a, b) have proportionally higher TBCA than taller forests.

Site Descriptions

This study was conducted using 11 mangrove forest sites (Table 1); three sites are from the Caribbean, and six sites from Australia and two sites from New Zealand. Sites vary from latitude 37°S to 27°N, ranging in average minimum temperatures from 11 to 27°C, and maximum temperatures from 19 to 32°C. Sites also span a large variation in average annual rainfall from 0.3 m in Exmouth to over 3.0 m in Bocas del Toro, Panamá. Many of the sites comprise forests of different stature. Most of the sites were dominated by species within the genera *Rhizophora* or *Avicennia*, with the exception of the Hinchinbrook Channel in Queensland where *Ceriops tagal* (Rhizophoraceae) dominates the dwarf forests. Tidal range was microtidal in the Caribbean sites (approximately 0.5–1 m) and mesotidal in the Australian and New Zealand sites (1.6–2.4 m). Soils also varied, from fine silts in New Zealand, Port Douglas and Cape Cleveland, sand in dwarf forest in Florida, Moreton Bay and the Hinchinbrook Channel to highly organic soils (mangrove peat) that are more than 60% carbon in Twin Cays, Belize and Bocas del Toro, Panamá.

Complete site descriptions have been previously published for Belize (McKee and others 2002; Feller and others 2003), Florida (Feller and others 2003), and Bocas del Toro (Lovelock and others 2004; Lovelock and others 2005; Lovelock and others 2006). In Moreton Bay, the study was conducted at Myora Springs on North Stradbroke Island. The forest was dominated by *A. marina*, ranging in height from 7 to 13 m. General site characteristics, and mangrove forest description for Moreton Bay are available in Davie (1984) and Manson and others (2003). In the Hinchinbrook Channel, the site is on the landward edge of the Channel at a site 25 km south of the town of Cardwell. There is a narrow fringing forest of *Rhizophora larmarkii* growing on highly organic soils, which gives way to an extensive stand of dwarf (<1.5 m) *Ceriops tagal* growing on coarse quartz sand. A description of the mangroves of the Hinchinbrook Channel can be found in Robertson and others (1992) and Clough (1998). In Exmouth, one site was situated in Mangrove Bay on the western side of the North West Cape. A general site description for Mangrove Bay is available in Alongi and others (2003). Another site was situated in Giralia Bay on the eastern side of the Exmouth Gulf. The mangroves in Mangrove and Giralia Bays are dominated by *A. marina.* In Mangrove Bay the study site was in a patch of small (<1.5 m) trees, whereas in Giralia Bay taller fringing (3–5 m) and shorter landward stands (<2 m) were studied. The Exmouth region (including Giralia) is arid (<30 cm rainfall per year). Two sites from New Zealand were studied, both having monospecific stands of *A. marina* (Lovelock and others 2007a, b). Waikopua is close to the city of Auckland. The site is muddy due to high rates of sediment deposition due to clearing and agricultural land use in the adjacent terrestrial ecosystem. A full site description of Waikopua can be found in Ellis and others (2004). The second site in New Zealand was situated in the Whangapoua estuary. This site is not heavily impacted by sedimentation and soils are coarse to fine sands. A general site description can be found in Schwarz (2004).

Materials and Methods

Soil respiration was measured at low tide at each site using a LiCor 6400 portable photosynthesis system configured with the LiCor Soil Respiration chamber (LiCor Corp, Lincoln, NE, USA). The chamber was set to penetrate only 0.5 mm into the soil to avoid damaging surface roots. Settings for measurement were determined at each site following the procedure described by the manufacturer. In some instances soils were absorbing CO_2. In these cases data were manually logged at 2-min intervals for three cycles, and flux rates calculated manually following the equations in the manufacturer's manual. Soil temperature was measured at 2 cm depth simultaneously with soil respiration. Measurements were made between 2004 and 2006 (Table 1).

Where a conspicuous microbial mat or biofilm was present on the soil surface, for example in the New Zealand sites, Port Douglas and the Hinchinbrook Channel, soil respiration was initially measured on intact soil, after which the top 0.5–1 cm of soil was gently removed with a spatula to avoid wounding surface roots. Soil respiration was then re-measured in the same location.

Variation in forest structure over the sites was measured by assessing Leaf Area Index (LAI) using a gap fraction method and by measuring tree heights. A hemispherical photo was taken with a Nikon Coolpix digital camera (model 995, Nikon, Tokyo, Japan) fitted with a fisheye lens under the canopy either on cloudy days or early in the morning. Images were processed using the computer program Hemiview Canopy Analysis Software (version 2.1,

Table 1. Locations and Climatic Characteristics of Sites, Dominant Species, Tree Stature, Numbers of Trees or Sampling Points Used, and Source of Litterfall Data

Site	Lat. Long.	Average annual min. and max. air temp in °C and rainfall (m)	Tidal range (m)	Soil	Species	Tree stature	Number of trees or samples	Month and year of soil respiration measurements	Human influences identified at the site	Source of litterfall data
Bocas del Toro, Panama	9°21′ N, 82°15′W	27–30 (~4.0)	0.7	Organic-peat	*R.mangle*	3–5 m	9	April 2004	Undisturbed	Guzman and others 2005
				Organic-peat	*R.mangle*	2–4 m	9			NA
				Organic-peat	*R.mangle*	<1.5 m	9			NA
				Organic-peat	*R.mangle*	7–12 m	9			NA
Port Douglas, Queensland, Australia	16°30′ S, 145° 27′ E	20.6–27.9 (2.01)	2.1	Mineral-sand	*A.marina*	<2 m	8	July 2006	Undisturbed	NA
Twin Cays, Belize	16°50′ N, 88°06′ W	25.4–28.8 (~2.5)	0.5	Organic-peat	*R.mangle*	5–7 m	9	January 2004	Undisturbed	Feller and others unpublished data
				Organic-peat	*R.mangle*	2 m	9			Feller and others unpublished data
				Organic-peat	*R.mangle*	< 1.5 m	9			Feller and others unpublished data
Hinchinbrook Channel, Queensland	18°20′S, 146° 10′ E	18.8–28.8 (2.12)	2.3	Organic-peat	*R. lamarkii*	5–7 m	9	July 2006	Undisturbed	NA
				Mineral–sand	*C. tagal*	<1.5 m	9			NA
Cape Cleveland, Queensland, Australia	19°16′ S, 147° 01′ E	21.7–27.4 (1.17)	2.3	Mineral-sand	*A.marina*/ *C. tagal*	< 1.5 m	6	July 2006	Undisturbed	NA
Giralia, Western Australia	21°44′ S, 114° 35′ E	17.7–31.7 (0.26)	1.6	Mineral-silt	*A.marina*	<1.5 m	9	April 2006	Undisturbed	Estimated from Arreola-Lizarraga and others 2004, an equivalently arid setting
				Mineral-silt	*A.marina*	3–5 m	9			Estimated from Bunt 1995
Exmouth, Western Australia	21°58′ S, 113° 57′ E	17.7–31.7 (0.26)	1.7	Mineral-sand	*A.marina*	<1.5	6	April 2004	Undisturbed	Estimated from Arreola-Lizarraga and others 2004, an equivalently arid setting

Table 1. continued

Site	Lat. Long.	Average annual min. and max. air temp in °C and rainfall (m)	Tidal range (m)	Soil	Species	Tree stature	Number of trees or samples	Month and year of soil respiration measurements	Human influences identified at the site	Source of litterfall data
Fort Pierce, Florida	27°33′N, 80°20′W	18.0–27.9 (1.37)	0.5	Mineral-silt	*R. mangle*	5–7 m	9	May 2004	Urban and agricultural development in the catchment	Raulerson unpublished data
				Mineral-sand	*A. germinans*	2–4 m	9			NA
				Mineral-sand	*A. germinans*	< 1.5 m	9			Raulerson unpublished data
Moreton Bay, Queensland	27°52′ S, 153° 20′ E	15.7–25.5 (1.15)	1.8	Mineral-sand	*A.marina*, *R. stylosa*	7–13 m	14	October 2005	Undisturbed	Davie 1984
Whangapoua, New Zealand	36°45′S, 175°30′E	11.4–19.6 (2.0)	1.6	Mineral-sand	*A.marina*	2–3 m	8	January 2004 and 2005	Forestry in the catchment	NA
				Mineral-sand	*A.marina*	<1.5	8			NA
Waikopua, New Zealand	36° 55′ S 174° 30′E	11.3–18.9 (2.5)	2.4	Mineral-silt	*A.marina*	2–3 m	8	January 2004 and 2005	Urban and agricultural development in the catchment	Estimated from May 1999
				Mineral-silt	*A.marina*	< 1.5 m	8			Estimated from May 1999

Delta-T Devices Ltd., Cambridge, United Kingdom). Tree height was measured with a telescoping pole.

Total belowground carbon allocation was calculated using the mass balance approach of Raich and Nadelhoffer (1989) which was tested by Giardina and Ryan (2002), where TBCA $= F_S - F_A + F_E + F_{STOR}$, where F_s is soil efflux, F_A is aboveground litter production, F_E is losses (export) and F_{STOR} is carbon stored in soils per unit time. Assuming that C storage and export is low compared to litter inputs and respiration then: TBCA $= F_s - F_A$. F_s was estimated by extrapolating soil respiration measured in μmol m^{-2} s^{-1} to g C m^{-2} y^{-1} assuming CO_2 efflux is constant diurnally but varies seasonally. The simplification of constant rates throughout the day was adopted because no significant temporal variation in soil respiration was observed between 9 a.m. and 3 p.m. at the Florida site (data not shown) and daily variation in other tropical forests was also low (for example, Davidson and others 2000). In periodically flooded mangroves soil respiration may also be influenced by daily tidal inundation. Comparison of CO_2 flux under submerged conditions and in air (similar to our measurements) have been made on soil cores at two sites, southern Thailand and Exmouth (Alongi and others 2000; Alongi and others 2001). Fine roots within the cores were detached and thus the root respiration component of CO_2 flux may have been underestimated; however, analysis of these data show respiration rates under submerged conditions are correlated with respiration rates measured in air, although the relationship was variable: Log (CO_2 flux in air) = 0.855 + 0.371 Log(CO_2 flux submerged), $R^2 = 0.319$, $P < 0.0026$. Respiration measured in air was slightly lower than that measured when cores were submerged, thus the scaled-up data presented may be underestimated, particularly in forests that are submerged for extended periods in each tidal cycle (for example, seaward fringing forests in microtidal settings).

CO_2 efflux was integrated annually in two ways, first by assuming there was no seasonal variation in soil respiration, and second by scaling soil respiration with annual variation in air temperature at each site. Soil respiration is sensitive to annual variation in temperature and also to phenological patterns, but these factors tend to co-vary (for example, Curiel Yuste and others 2004). I assumed maximum soil respiration occurred in the summer and minimum in the winter. Using each sites' annual temperature variation in conjunction with proportional changes in soil respiration calculated from the curve in Figure 3 (for example, a 5°C reduction in temperature from the maximum value

resulted in soil respiration that was 80% of maximum summer value) I estimated maximum and minimum rates for each site. I then integrated annually assuming a linear increase from minimum winter values to maximum summer values. Annual rates of CO_2 efflux estimated in this way were similar to the values estimated using the ''no seasonality'' calculations except at sites with large variations in annual temperature (approx. 10°C) that had been measured in summer, that is, New Zealand and Florida. Overall, seasonally integrated values were significantly different from the ''no seasonality'' values (paired t test: $t = -2.76$, 15 df, $P = 0.0141$) but they did not alter the overall conclusions of the study, which were similar using either the ''no seasonality'' or seasonally adjusted values.

In contrast to many terrestrial forests, export of litter and dissolved C exports (F_E) could be substantial (Twilley 1985; Twilley and others 1986; Robertson and others 1992; Dittmar and others 2006), particularly at sites with high tidal ranges (Twilley and others 1992). Estimates of F_E for mangroves are between 10 and 50% of litterfall (Twilley 1985) and range from 2 to 420 gC m^{-2} y^{-1} (Twilley and others 1992). In the mangrove study sites used in the current study it would be expected that taller, fringing forests will have higher rates of export compared to dwarf forests which are exposed to less frequent tidal flushing. The effect of potential C exports was calculated by adding 10 and 50% of litterfall to TBCA. This potential variation in TBCA due to export has been indicated graphically.

Litterfall had been directly measured in previous studies at some sites (for example, Belize, Florida and Bocas del Toro) and was estimated for other sites using values from the literature. In Waikopua and Whangapoua, litterfall was estimated from tree height using the regression provided by May (1999) who measured litterfall of mangroves within the Waikopua estuarine system. In Exmouth, litterfall of the *A. marina* dwarf trees was assumed to be similar to that of dwarf *A. germinans* in a similarly arid region of Mexico (Arreola-Lizarraga and others 2004), and for fringing sites in Giralia Bay was taken from Bunt (1995). Litterfall for Moreton Bay was taken from Davie (1984) for a similar stature forest.

Data Analysis

Multiple regression analysis was used to test for significant relationships between soil respiration and LAI, and soil temperature. Due to the shape of the soil respiration-temperature curve we included a temperature squared term in the model. Linear regression was used to test for a significant relationship between ANPP estimated from litterfall and soil respiration for a subset of the sites, and also used to test for significant relationships between ANPP and TBCA. Q_{10} for soil respiration was assessed as the ratio of respiration at 26°C to respiration at 16°C after Fang and Moncrieff (2001), where $Q_{10} = (R_{T2}/R_{T1})^{10/(T2-T1)}$, where R is respiration and T1 and T2 are temperature expressed in °K. ANOVA was used to test for effects of microbial mat removal on soil respiration, where mat removal was fixed effect in the model and site was a random effect.

Results

Mean soil respiration over the sites ranged from approximately −0.25 to 2.97 μmol C m^{-2} s^{-1} (Figure 1). Dwarf forests had a similar range of respiration rates as taller forests. Although the more human modified sites, Hutchinson Island and Waikopua close to the city of Auckland had the highest respiration rates. Respiration rates were also high at the undisturbed sites at Cape Cleveland and Whangapoua. Mangrove soil respiration rates were generally in the lower range of that observed in terrestrial ecosystems (hatched bar provided for comparison), but were comparable to rates observed in terrestrial forested ecosystems. Soil respiration at the two New Zealand sites was measured over two consecutive years. Although respiration rates differed between years, soil respiration at Waikopua was consistently greater than that at Whangapoua.

Soil respiration varied with both forest LAI and soil temperature ($R^2 = 0.332$, $F_{3155} = 25.7$; LAI $P < 0.0001$, soil temperature $P < 0.0001$ and soil temperature^2 $P = 0.0003$). Over all sites soil respiration increased with increasing forest LAI (Figure 2, $R^2 = 0.177$), although there was a high level of variation about this relationship. Variation in soil temperature also explained a significant but small proportion of the variation in soil respiration over the sites ($R^2 = 0.20$), but the temperature response was not linear (Figure 3). Soil respiration increased to a maximum at approximately 25–27°C and then declined with further increases in temperature. Between 16° and 26°C, the Q_{10} of soil respiration was 2.6. At low LAI light penetrates the canopy enhancing soil surface temperatures and also stimulating growth of photosynthetic biofilms or microbial mats (for example, Lee and Joye 2006). To test whether the decline in soil respiration at higher temperatures in dwarf forests could be due to carbon fixation by the photosynthetic biofilm on

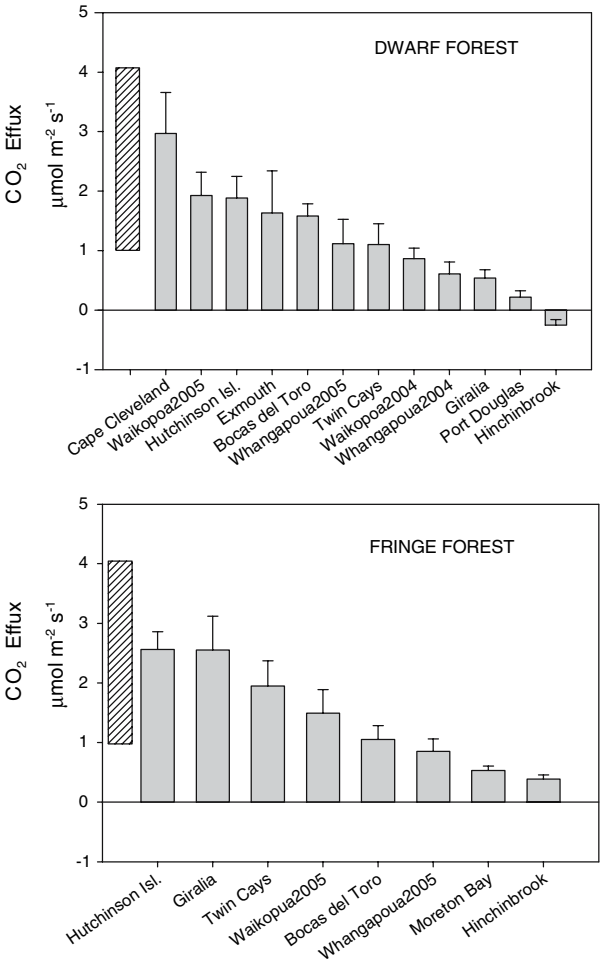

Figure 1. Variation in soil respiration over all mangrove sites. Upper panel shows values for dwarf forests smaller than 2 m tall. Lower panel is taller forests that fringe channels or open water. For comparison the range of terrestrial soil respiration of forested sites from Raich and Nadelhoffer (1989) appears as a hatched bar. Negative CO_2 efflux indicates CO_2 uptake by the soil.

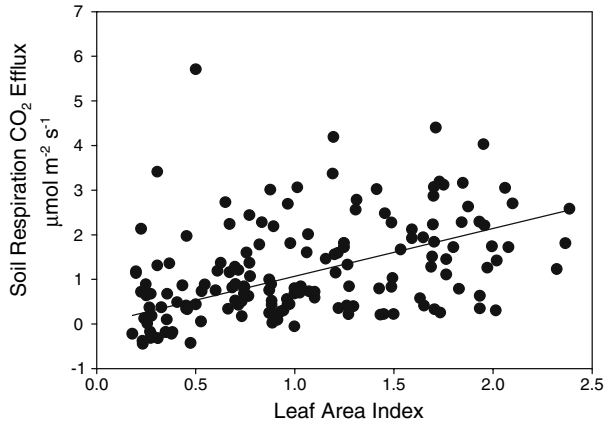

Figure 2. Relationship between leaf area index (LAI) and soil respiration (CO_2 Efflux) for ten mangrove sites. Equation of the line is: CO_2 Efflux = 0.366 + 0.800 × LAI, R^2 = 0.177, $P < 0.05$.

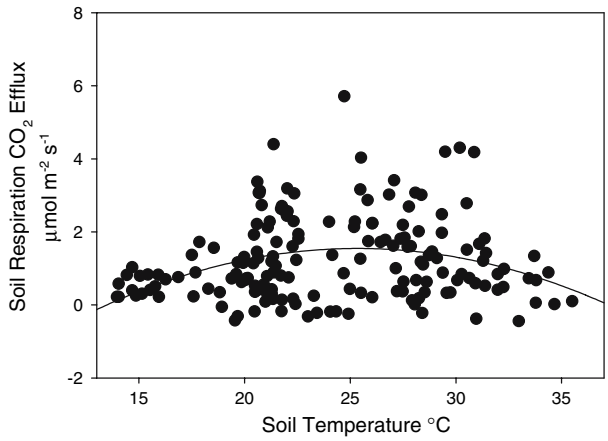

Figure 3. Response of mangrove soil respiration to soil temperature for ten mangrove forests. Equation of the line of best fit is: Soil CO_2 Efflux = −5.509 + 0.557 × T–0.011 × T^2, where T is soil temperature in °C, R^2 = 0.20, $P < 0.05$.

the soil surface, I removed the top 0.5 cm of the soil profile at four sites and immediately re-measured soil respiration. Soil respiration rates where the biofilm was removed were significantly higher than for intact soil (Figure 4, Main effect of mat removal $F_{1,3}$ = 409.4, P = 0.0003). Although soil respiration rates over the sites varied (main effect of site $F_{3,62}$ = 27.132, $P < 0.0001$) the removal of the surface biofilm had a similar effect at all sites.

Total belowground carbon allocation was estimated using soil respiration and ANPP from a subset of sites where litterfall has been measured or could be estimated. Soil respiration and litterfall were significantly correlated (Figure 5, R^2 = 0.35, P = 0.024), but had a shallower slope than the relationship between soil respiration and litterfall of terrestrial forests (compare with the dashed line of Raich and Nadelhoffer 1989). Annual soil respiration that was not adjusted for seasonal variation in temperature had a higher correlation with litterfall (R^2 = 0.53, data not shown). TBCA ranged from 151 to 634 gC m^{-2} y^{-1} (mean 410 ± 45 gC m^{-2} y^{-1}). In mangrove forests there was no significant linear relationship between TBCA and ANPP (Figure 6). TBCA as a proportion of ANPP for dwarf forest was significantly greater than that for taller forests (Dwarf 15.3 ± 5.9 versus Tall forest 3.2 ± 0.9: $F_{1,12}$ = 6.93, P = 0.0219); thus per unit ANPP dwarf mangroves allocate relatively more C belowground than do taller mangrove forests.

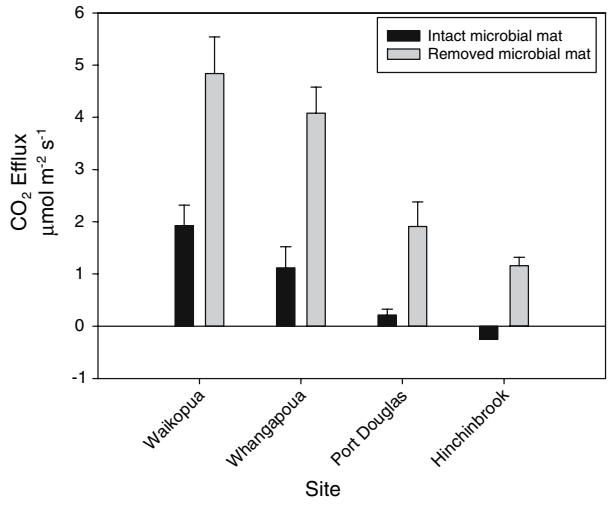

Figure 4. Mean soil respiration in dwarf mangrove forests with an intact surface microbial community (*black bars*) and where the microbial community had been removed (*grey bars*) (N = 6–8). Removing the surface microbial community had a significant effect on soil respiration: $F_{1,3}$ = 409.4, P = 0.0003.

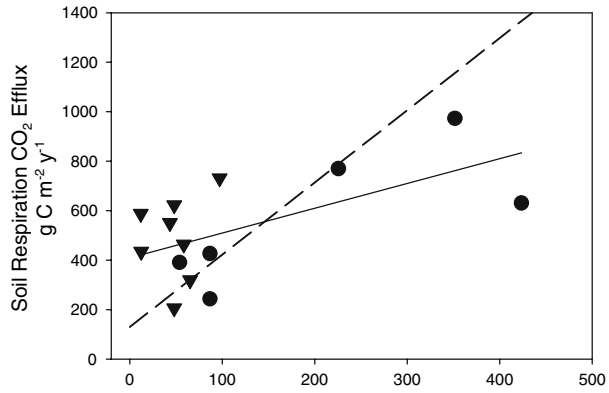

Figure 5. Relationship between soil efflux and litterfall over seven mangrove sites. Sites include dwarf forests (<2 m height, *downward triangles*) and tall forests (*circles*). The dashed line is the relationship for terrestrial forests from Raich and Nadelhoffer (1989, slope = 2.92). The regression line is the least squares line of best fit for dwarf forests (<2 m height, *downward triangles*) and tall forests (*circles*), and is of the form: Efflux = 409 + 1.00 × Litterfall, R^2 = 0.356, P = 0.024.

Discussion

Discovering direct links between above- and belowground processes facilitates scaling measurements of CO_2 exchange over landscapes. Mangroves are important autotrophic ecosystems in the tropical and subtropical coastal zone, providing important ecosystem services, one of which is carbon sequestration (Ewel and others 1998; Alongi 2002; Chmura and others 2003). This study aimed to discover links between soil respiration and aboveground primary productivity over a wide range of mangrove sites. Due to the potential importance of the temperature sensitivity of soil respiration to C sequestration in forest soils (Raich and Schelsinger 1994; Boone and others 1998; Grace and Rayment 2000), we also assessed the sensitivity of mangrove soil respiration to temperature by using natural temperature variation over our sites that spanned a wide range of latitudes.

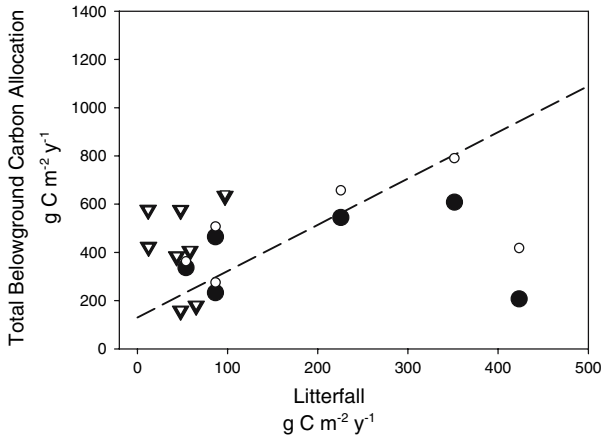

Figure 6. Relationship between total belowground carbon allocation and litterfall over seven mangrove sites. There was no significant correlation. Sites include dwarf forests (<2 m height, *downward triangles*) and tall forests (*circles*). Small open symbols are values of TBCA calculated assuming carbon export of 10% of litterfall in dwarf forest and 50% of litterfall in taller forests. The dashed line is the relationship for terrestrial forests from Raich and Nadelhoffer (1989).

Links Between Aboveground Productivity and Soil Respiration

Mangrove soil respiration across the 11 mangrove sites was highly variable, but similar to that observed in terrestrial ecosystems (Figure 1, Raich and Nadelhoffer 1989; Raich and Schesinger 1994) and other wetland soils (Howes and others 1985; Amador and Jones 1993). Soil respiration rates were generally higher than those reported from mangrove soil cores (Alongi and others 2000, 2001, 2005a, b), but were similar to those measured in undisturbed soils using closed chambers (Middleburg and others 1996; Chimner 2004), probably reflecting the contribution by live roots to mangrove soil respiration, either directly through root tissue respiration or through bacterial respiration dependent on root exudates (Kuzyokov 2002).

Soil respiration was significantly correlated with LAI over all sites but the data were highly variable (Figure 2). Only a small portion of this variability could be attributed to variations in soil temperature (Figure 3). LAI is an indicator of aboveground biomass, which is often closely correlated to belowground biomass (Cannell and Dewer 1994). The highly variable relationship between LAI and soil respiration observed over our study sites could reflect wide variation in allocation to fine roots (Ruess and others 2003), or variation in the heterotrophic component of respiration both within and between sites (Bond-Lamberty and others 2004). Both of these factors may be strongly influenced by nutrient availability and redox of soils, which may vary widely within and among mangrove forest ecosystems (Alongi and others 2000, 2001, 2005a, b; Feller and others 2002; Lovelock and others 2007a, b). Errors in the gap fraction method used to estimate LAI over forests of differing structure may also contribute (Bréda 2003). As LAI can often be measured remotely (for example, Green and others 1998), the relationship between LAI and respiration may be a useful tool in estimating soil respiration over large spatial scales.

Across the sites mangrove forest soil respiration was correlated with litterfall (Figure 5) as has been observed in terrestrial forests (Raich and Nadelhoffer 1989; Davidson and others 2002). The slope of the mangrove soil respiration versus litterfall relationship was lower than that observed for terrestrial forests (1.00 compared to the terrestrial forest slope of 2.92, Raich and Nadelhoffer 1989). This lower sensitivity (shallower slope) of mangrove soil respiration to increasing ANPP is linked to higher TBCA per ANPP in low productivity, low stature mangrove forests, and possibly to lower TBCA in taller stature forests with higher ANPP (Figure 6). Fundamental differences in the environment for roots between wetland and terrestrial forest soils that are linked to tidal inundation, for example, wetlands have highly variable redox states and nutrient availability, may contribute to the differences observed between mangroves and terrestrial forests in their TBCA over gradients in ANPP. Data from more productive forests than those included in this study, for example, in Asia (for example, Alongi and others 2004), and Central America (for example, Golley and others 1975), would be needed to confirm a trend of lower TBCA in taller mangroves compared to terrestrial forests.

The high TBCA estimated in dwarf forests compared to taller forests may be linked to investment of C belowground needed to withstand adverse environmental conditions, particularly anaerobic conditions and low nutrient availability, which are common in dwarf or scrub forests (Alongi and others 2000, 2001, 2005a, b; Feller and others 2002, 2003; Lovelock and others 2004, 2007a, b. Relatively high rates of soil respiration and TBCA in dwarf forests compared to taller forests are unlikely to be due to respiration of live roots as live root densities, root growth rates and root respiration rates are low in dwarf mangrove forests (McKee 2001; Lovelock and others 2006; McKee and others 2007), but could be due to high rates of C exudatation from roots and high levels of heterotrophic respiration (for example, Vazquez and others 2000).

Higher proportional TBCA in dwarf mangroves compared to terrestrial forests could also be due to mineralization of C from other, non-mangrove tree sources, which would introduce errors when using the carbon balance model. Detrital inputs from adjacent seagrass and macroalgal beds, or from the microphytobenthic community and from delivery of sediments could enhance soil respiration and estimated TBCA. Delivery of sediments and detritus is lower in landward dwarf forests compared to seaward fringing mangrove stands (Furukawa and others 1997) making additional inputs from outside the mangrove a small source of error in the model for dwarf forests. In contrast in situ production by microbial mats can be substantial (for example, Lee and Joye 2006) and may contribute to the high TBCA in dwarf compared to taller fringing forests.

Problems with the carbon balance model's assumption of steady state conditions have been discussed in detail by Davidson and others (2002). Carbon imports and exports in tidal dominated ecosystems like mangroves are likely to give rise to errors in estimation of TBCA using the carbon balance method (Figure 6). Estimation of TBCA that included export of 10–50% of litterfall increased TBCA, but did not change the overall patterns evident in the data. More thorough assessment of C export is needed, particularly of dissolved organic C (Twilley and others 1992; Dittmar and others 2006). Errors associated with direct methods of estimating C allocation below ground are also very large (for example, Komiyama and others 1987; Robertson and Dixon 1993). The technical difficulties of making direct measurements of carbon allocation belowground in mangrove soils and the need to assess TBCA for carbon budgets over a wide range of representative forests make a first pass assessment using the carbon balance method useful, despite the potential flaws. A spatially detailed understanding of C imports and exports from mangrove soils would greatly improve

the confidence in using carbon balance models, as would longer term measurements of soil respiration that encompassed variation with tidal cycles and over seasons.

Influence of Temperature on Soil Respiration

Some of the variation in soil respiration over sites could be explained by variation in soil temperature (Figure 3). Temperature responses of intact mangrove soil respiration between 16° and 26°C (on the upward slope of the curve in Figure 3) was on average 2.6, close to the median Q_{10} measured over a range of terrestrial vegetation types and sites (Raich and Schelsinger 1994; Boone and others 1998) and that predicted by Lloyd and Taylor (1994) indicating that mangrove soil respiration is not less sensitive to temperature as might be surmised from their tropical and subtropical distribution. The high variability in Figure 3 also indicates that Q_{10} is variable. Q_{10} has been observed to vary seasonally, due to variation in temperature, water content of soils and also with phenology (for example, Xu and Qi 2001; Janssens and Pilkegaard 2003; Curiel Yuste and others 2004). Additionally, soil respiration did not increased with temperature over the whole temperature range but showed a decline at higher temperatures (Figure 3). Across the sites, higher temperatures in mangrove soils were often associated with sparse canopies of dwarf forests, where greater levels of direct sunlight penetrate through mangrove canopies illuminating and warming the soil surface. High light levels at the soil surface stimulate growth of microbial communities, which are comprised of cyanobacteria, diatoms, and other microalgae (Potts 1979; Joye and Lee 2004; Underwood and others 2005). These communities are capable of high rates of carbon fixation (Schories and Muhlig 2000; Lee and Joye 2006). Experimental removal of the surface biofilm in New Zealand and the cyanobacterial mat in North Queensland sites (Port Douglas and Hinchinbrook Channel) confirmed that photosynthetic organisms on soil surfaces significantly decreased the efflux of respired C from deeper in the soil (Figure 4). Flux of CO_2 into mangrove soils has been previously observed, along with increases in respiration with soil depth (Alongi and others 2001).

Mangroves are highly efficient at conserving nutrients within individual trees (Feller 1995; Feller and others 2003; Alongi and others 2005a, b; Lovelock and others 2007a, b, and also at the ecosystem level (Alongi and others 1992). The results presented here suggest that in additional to efficient nutrient conservation, C losses from soils are also low in mangrove ecosystems, and are influenced by the activity of photosynthetic microbial communities, particularly in dwarf forests. They also suggest that the effects of global warming on soil respiration in mangrove forests is likely to be complex, depending not only on the effects of increases in temperature on photosynthesis, root respiration and the activity of bacterial communities, but also on the temperature response of benthic photosynthetic microorganisms. Additional interactions are likely with other factors that influence mangrove canopy development and thus light levels reaching the soil surface, including sea level rise (Ellison and Farnsworth 1996), levels of nutrient enrichment (Lovelock and others 2006), and storm damage (Cahoon and others 2003) and underscore the importance of understanding the roles of benthic microbial communities in carbon and nutrient cycling in estuaries (An and Joye 2001) and other ecosystems with photosynthetic microbial crusts (for example, Cable and Huxman 2004).

Conclusions

Mangroves have similar rates of soil respiration as terrestrial forests, but they may achieve this at lower ANPP, giving support to the hypothesis that mangrove forests allocate more carbon belowground than do terrestrial forests. This was particularly evident in dwarf forests which can be extensive (Lugo 1997). Over all sites, soil respiration correlated with LAI and litterfall, which may provide tools to scale up CO_2 flux from mangrove ecosystems from currently available data sets. The response of mangrove soil respiration to increasing temperature was similar to that of terrestrial forested ecosystems, with a Q_{10} of approximately 2.6 for the lower temperature range (to 26°C). At higher soil temperature, often in dwarf forests, soil respiration declined with increasing temperature due to the activity of benthic photosynthetic microbial communities which are important in retaining respired C within the ecosystem.

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