

Ecosystem Carbon Stocks of Micronesian Mangrove Forests

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Received: 16 August 2010 / Accepted: 5 January 2011 / Published online: 22 February 2011
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Abstract Among the least studied ecosystem services of mangroves is their value as global carbon (C) stocks. This is significant as mangroves are subject to rapid rates of deforestation and therefore could be significant sources of atmospheric emissions. Mangroves could be key ecosystems in strategies addressing the mitigation of climate change through reduced deforestation. We quantified ecosystem C stocks at the seaward, interior, and upland edges of mangroves in the Republic of Palau and Yap, Federated States of Micronesia. The relatively high aboveground biomass coupled with carbon-rich soils resulted in the presence of large ecosystem carbon stocks compared to other tropical forests. Ecosystem C storage at the Palau site ranged from 479 Mg/ha in the seaward zone to 1,068 Mg/ha in the landward zone; in the Yap site C storage ranged from 853 to 1,385 Mg/ha along this gradient. Soils contained ~70% of

the ecosystem C stocks. The elevation range of mangroves was <146 cm, suggesting that projected sea-level rise can influence a large portion of existing stands. Declines in ecosystem carbon stocks will be pronounced if mangroves are replaced by communities adapted to greater inundation such as seagrass communities, where C pools were $\leq 7\%$ of that of mangroves (48 Mg C/ha).

Keywords Climate change · Ecosystem carbon pools · Peat soils · Sea-level rise · Tropical Wetlands

Introduction

Mangroves are important ecosystems of tropical coastal zones, providing a variety of ecosystem services such as sources of food (fishes, crabs, etc.), wood, and protection from extreme events such as cyclones and tsunamis (Giesen et al. 2007, Mitsch and Gosselink 2007; Alongi 2008, 2009). Ironically, mangrove forests are threatened by land use/land cover change as well as global climate change. Rates of deforestation/conversion are among the highest of all tropical forests, far exceeding rates in upland forests (Valiela et al. 2001; Langner et al. 2007). Land conversion related to aquaculture, urban, and agricultural development has resulted in the loss of over 35% of mangroves between 1980 and 2000 (Valiela et al. 2001; Giesen et al. 2007). Global climate change impacts that may exacerbate losses include sea-level rise, changes in tropical storm (cyclone) intensity, and changes in stream flows that discharge into mangroves (Gilman et al. 2008).

Among the most important, but poorly quantified, functional attributes of mangroves is that of ecosystem carbon storage, and its implications and vulnerability to both land use and global climate change. Many studies

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have measured aboveground biomass and composition of mangroves (Saenger 2002; Komiyama et al. 2008; Kauffman and Cole 2010). Total aboveground biomass of mangroves varies enormously but those of a forest stature are similar to that of tropical forests located on uplands (Alongi 2009). However, to quantify carbon emissions resulting from deforestation and conversely their values as carbon reservoirs, it is important to quantify the total ecosystem C stock (aboveground and belowground pools). Few studies have quantified total ecosystem C pools. Recent reviews of coastal C dynamics and energetics contained little or incomplete data on the total ecosystem C storage of mangroves (Bouillon et al. 2008; Alongi 2009; Laffoley and Grimsditch 2009). Information is particularly lacking in belowground C pools in mangroves and these pools are expected to be high due to deep, organic-rich soils (e.g., Golley et al. 1962; Fujimoto et al. 1999). As such, these forests may be of high value in terms of C storage, which is particularly relevant to climate change mitigation strategies focusing on reducing carbon emissions through reduction of deforestation. On the islands comprising Micronesia, losses of even relatively small patches of mangrove forests through either climate change or land cover change would represent a significant loss of terrestrial C stocks.

Rapid rates of sea-level rise as a consequence of global climate change have been identified as a primary threat to mangroves (Gilman et al. 2008), but how this change will affect ecosystem carbon storage is almost completely unknown. Mangroves in many regions are zoned compositionally with distance from the seaward edge (ecotonal to seagrass) due to different species' tolerances to different levels of tidal inundation, wave action, and salinity (Giesen et al. 2007). As sea-level rises, landward migration of the conditions creating these zones would be expected (Alongi 2008; Gilman et al. 2008), meaning that seaward-zone communities may replace landward-zone communities. In some cases, seagrass communities (which are suited to greater tidal inundation) may replace seaward-edge mangroves, yet the degree to which C stocks would vary among these zones, and the potential consequences of their movements under climate change, has received little study.

We hypothesized Micronesian mangroves would be among the most C-dense of tropical ecosystems due to relatively large belowground C pools coupled with an aboveground structure of high tree volume and density. The objectives of this study were to quantify the composition, structure, and C stocks of mangrove forests; and how these vary among zones of differing distance from the seaward edge. These ecosystem attributes are important for predicting how mangrove forests and their ecosystem services will be affected by global climate change as well as land cover change. The relevance of this study is underscored by their location on tidal flats over coral sands fringing high islands

of the western Pacific. These areas are considered among the most vulnerable to influences of global climate change—particularly sea-level rise, increased storm surges, and increased typhoon severities (IPCC 2007; Gilman et al. 2008). In addition, as financial mechanisms become available for the payment of ecological services or mitigation of climate change, measured baseline information on mangrove ecosystem carbon stocks, structure, and function will be required to calculate potential credits under mechanisms such as Reduced Emissions from Degradation and Deforestation (REDD+) and other C marketing systems.

Methods

Study Areas

Ecosystem C pools, composition, and structure were intensively sampled in two mangrove forests of Micronesia in the western Pacific Ocean. The first was located on the island of Babeldaob, Airai State, Republic of Palau (7° 21' 8.09" N, 134° 32' 21.57" E). The second was located near the northwest corner of the island of Yap, the westernmost state of the Federated States of Micronesia (FSM; 9° 35' 16.31" N, 138° 07' 39.69" E). Both islands were surrounded by barrier reefs, and both mangrove forests were growing over former reef flats and coral sands fringing the island. Most of the mangrove forests on both islands are located on this topography, but mangroves in estuaries are also present, especially at Palau. The sediments of both sites were classified as an *Illachetomel* Peat (Euic, isohyperthermic, Typic Sulphhemists) by Smith (1983a) and Smith (1983b). These soils are typical of Micronesian mangrove ecosystems and cover 11.6% of Yap and 9.4% of Palau by area.

Field Methods

The relative elevation gradient of each mangrove site was determined using a laser surveying level with 0 cm in elevation occurring at the seagrass/mangrove transition from which relative changes in surface elevation (± 1 cm) were measured. We measured elevation changes at ~ 1 – 2 m intervals from the adjacent sea grass communities to the landward edge of the mangroves.

At each mangrove site we sampled aboveground forest structure, composition, and ecosystem C pools at three positions along the hydrological/elevational gradient from the seaward to the upland edge. A 125-m transect parallel to the marine shore was established in the seaward zone of the mangrove (near the ecotone with seagrass), in the interior of the mangrove (mid-slope), and near the landward edge of the mangrove forest. The seaward zone transect was established approximately 13 m from the seagrass ecotone

while the landward transect was located a similar distance below the mangrove ecotone with the uplands. Each transect was composed of six 7-m radius (0.0154 ha) circular plots established every 25 m. Species composition and structure were determined through identification of the species and measurement of the diameter at 1.3 m height (dbh) of all trees rooted in the circular plots (or for *Rhizophora* spp. at the point directly above stilt roots). All trees greater than 1.3 m in height were measured. From these data we calculated basal area, stand density, and tree biomass. Aboveground tree biomass was determined using species-specific allometric equations with dbh as the independent variable (Appendix). Equations used to calculate tree volume and mass were developed for Micronesian mangroves by Cole et al. (1999) and Kauffman and Cole (2010). Prop root biomass for *Rhizophora* spp. and leaf biomass for all species were calculated from published equations in Clough and Scott (1989) as reported in Kauffman and Cole (2010). Below-ground tree mass was calculated using a general allometric equation developed for mangroves by Komiyama et al. (2005).

Biomass of dead and downed wood was non-destructively sampled using the planar intercept technique (Brown and Roussopoulos 1974; Kauffman et al. 1998; Van Wagner 1968). In each of the six plots along each of the three major transects, we established four subtransects in directions 45° off the main transect line ($n=24$ downed wood subtransects per main transect). Downed wood was partitioned into classes based on particle diameter. Diameter classes and equations used to partition woody debris were the same as those of Kauffman et al. (1995) and Guild et al. (1998) for determination of woody debris in upland tropical forests: 0–0.64 cm diameter, 0.65–2.54 cm diameter, 2.55–7.5 cm diameter and ≥ 7.6 cm diameter. For wood particles ≥ 7.6 cm diameter, we further separated particles into sound and rotten classes. Lengths of each sampling plane (subtransect) were similar to previous studies in Micronesian mangrove (Kauffman and Cole 2010): 2 m for wood particles ≤ 0.64 cm diameter, 5 m for particles 0.65 to 2.54 cm diameter, 10 m for particles 2.55 to 7.5 cm diameter, and 12 m for coarse wood (i.e. logs ≥ 7.6 cm diameter). Data to parameterize equations for calculating wood debris mass in mangroves were reported in Kauffman and Cole (2010; Appendix).

At the Palau site we also quantified the ecosystem C pool of the seagrass community adjacent to the seaward edge of the mangrove. A transect similar to those in mangroves was established parallel to the mangrove edge approximately 50 m from the mangrove ecotone. In each of five plots we determined total aboveground biomass by harvesting all above-sediment vegetation within four 50×50 cm microplots ($N=20$). All aboveground vegetation was clipped and placed in a plastic bag, thoroughly washed in the laboratory, placed in paper bags, and dried at 60°C to constant mass.

Soil C pools were sampled at each of the six plots in each transect (18 per site). Near the center of each plot, we measured organic soil depth by forcing a bamboo rod or soil auger downward through the organic horizons to the comparatively impenetrable underlying coral sand surface. Soil cores were extracted with a sampler constructed of 5.14-cm diameter PVC pipe, minimizing soil disturbance during the extraction process. We collected samples for determination of sediment bulk density and C concentration at the following depths: 0–15 cm, 15–30 cm, 30–50 cm, and 50–100 cm. Where soils were deeper than 100 cm (generally <200 cm), values from 50 to 100 cm were applied to deeper layers, as subsequent sampling from our related studies have shown bulk density and C concentration to be fairly uniform over that depth range. In the Palau seagrass community, sediment depths were measured every 2 m along the transect ($N=40$). As the mean sediment depth of the seagrass community was 14 cm, only one sample was collected at each of six locations. Samples were transported from the field and immediately placed in an oven at 60°C and dried to constant mass. Carbon and nitrogen concentrations of plant and sediment samples were analyzed via the induction furnace method using a Costech EA Carbon-Nitrogen Analyzer at the University of Hawaii-Hilo analytical laboratory. Carbon mass was determined as the product of the C concentration multiplied by the corresponding bulk density of each sample. Carbon pools of live and dead components were calculated as the product of biomass multiplied by carbon concentration. Carbon concentration was determined through analysis of five wood samples of the three dominant tree species and five leaf samples of the dominant seagrass species.

Due to diurnal inundation of the entire mangrove forests during high tides, the sampling was necessarily limited to the low tide periods of the day. Given mangroves' lack of understory vegetation (Snedaker and Lahmann 1988) or leaf litter (due to intensive harvesting by crabs), these negligible pools were not included in our sampling, nor was algal, epiphyte, or seedling biomass.

Mangrove structure, density, biomass, and C pool differences between zones within sites were tested using a one-way analysis of variance. If main effects were significant, differences among zones were compared using Tukey's HSD multiple comparison tests (Ramsey and Schafer 2002).

Results

Elevational Gradients of the Mangrove Forests

At the seagrass mangrove ecotone at both sites there was an abrupt increase in elevation of ~30 cm. The distance from

seagrass to the upland edge at the Palau mangrove was 328 m, with a corresponding rise in relative elevation of 146 cm (Fig. 1). The elevation of the seaward, interior, and landward zone transects were 4, 52, and 134 cm above the elevation at the mangrove/seagrass ecotone. At the Yap site, the distance from the seaward edge to the upland edge was 252 m. There was a narrow nypa palm (*Nypa fruticans* Wurmb) community present at the upland edge that was not sampled. The soil surface elevation gain over this distance was 106 cm (Fig. 1). Elevations of the seaward, interior, and landward zone transects were 31, 85, and 104 cm above the elevation at the mangrove/seagrass ecotone, respectively.

Composition, Aboveground Biomass, and Aboveground C pools

Both the Palau and the Yap mangroves were largely composed of three tree species: *Sonneratia alba* J.E. Smith, *Rhizophora apiculata* Bl, and *Bruguiera gymnorrhiza* (L.) Lamk. The exception to this was the seaward zone of the Palau site, where *Rhizophora mucronata* Lam was abundant. Even though the species present at both sites were similar, there were substantial differences in forest structure (Fig. 2). The Palau site was a very dense stand dominated by *Rhizophora* spp. while the Yap site was dominated by fewer

and larger *S. alba* and *B. gymnorrhiza*. Mean tree density of the Palau site was 2,421 trees/ha, compared to 780 trees/ha at the Yap site. While there was a three-fold greater tree density at the Palau site, basal area and wood volume of the Yap site were 60% and 51% greater due to dominance by larger trees. Mean total tree biomass at the Yap site was 363 Mg/ha, compared to 225 Mg/ha at the Palau site (Table 1).

Along the gradient from the seaward edge to the landward edge, we found shifts in composition and structure between the three zones at the Palau site. The seaward-zone mangrove was dominated by *S. alba* and *R. mucronata*, but interior and landward zones were dominated by *R. apiculata*. Tree density in the seaward zone was twice that of the landward zone (3,326 trees/ha compared to 1,507 trees/ha; $P=0.002$). While tree density was higher in the seaward zone, the larger-statured trees dominated the landward zone, resulting in higher basal area and aboveground biomass (Figs. 2a and c, Table 1). Total aboveground biomass (TAGB) of the Palau mangroves ranged from 204 Mg/ha in the seaward zone to 323 Mg/ha in the landward zone. In contrast, TAGB of the adjacent seagrass community was just 0.39 Mg/ha.

Shifts in composition and structure at the Yap site were not as pronounced as the Palau site (Fig. 2). Based upon basal area, *S. alba* and *B. gymnorrhiza* co-dominated this mangrove (Fig. 2d). Unlike the Palau site, tree density was lowest in the seaward zone and highest in the landward zone (650 trees/ha compared to 1,083 trees/ha; $P=0.05$; Fig. 2). Similar to the Palau site, tree biomass was lower in the seaward zone (251 Mg/ha) compared to interior (456 Mg/ha) and landward (383 Mg/ha) zones. Downed wood biomass averaged 29.6 Mg/ha (10–15% of TAGB) at the Palau site and was relatively constant among zones; while at the Yap site downed wood biomass averaged 43.1 Mg/ha (6–16% of TAGB), with the lowest value in the landward zone. While standing tree mass was lower in the seaward zone, downed wood mass was two-fold greater (48 Mg/ha) than that of the interior zone (24 Mg/ha) at the site possibly reflecting greater disturbance at the mangrove/ocean edge. Overall, the mean TAGB of the *Sonneratia*-dominated Yap site (406 Mg/ha) was somewhat higher than that of the *Rhizophora*-dominated Palau site (254 Mg/ha; $P=0.10$).

Belowground Pools

Belowground roots represented a large proportion of the total plant biomass. Mean total belowground biomass was 171 Mg/ha at Palau and 312 Mg/ha at Yap ($P=0.07$; Table 1). Mean root:shoot ratios (belowground to aboveground tree biomass) were 0.67 and 0.77 for Palau and Yap, respectively.

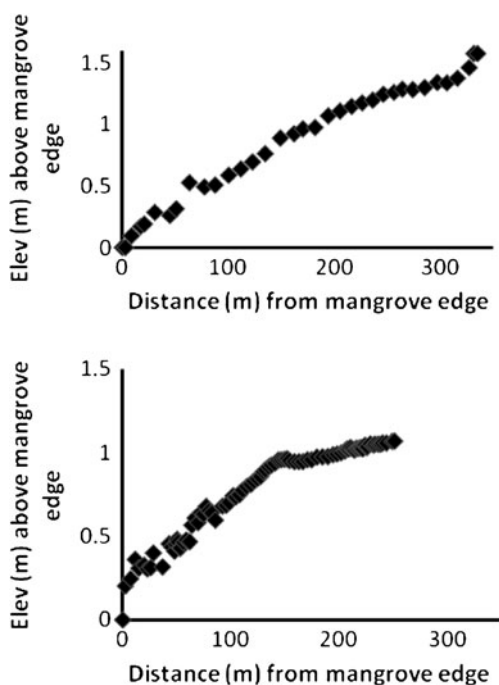


Fig. 1 Surface elevation (m) of mangrove forests in the Republic of Palau (*top*) and Yap, Federated States of Micronesia (*bottom*). Data represent elevational rise where 0 is the elevation at the seagrass/mangrove ecotone

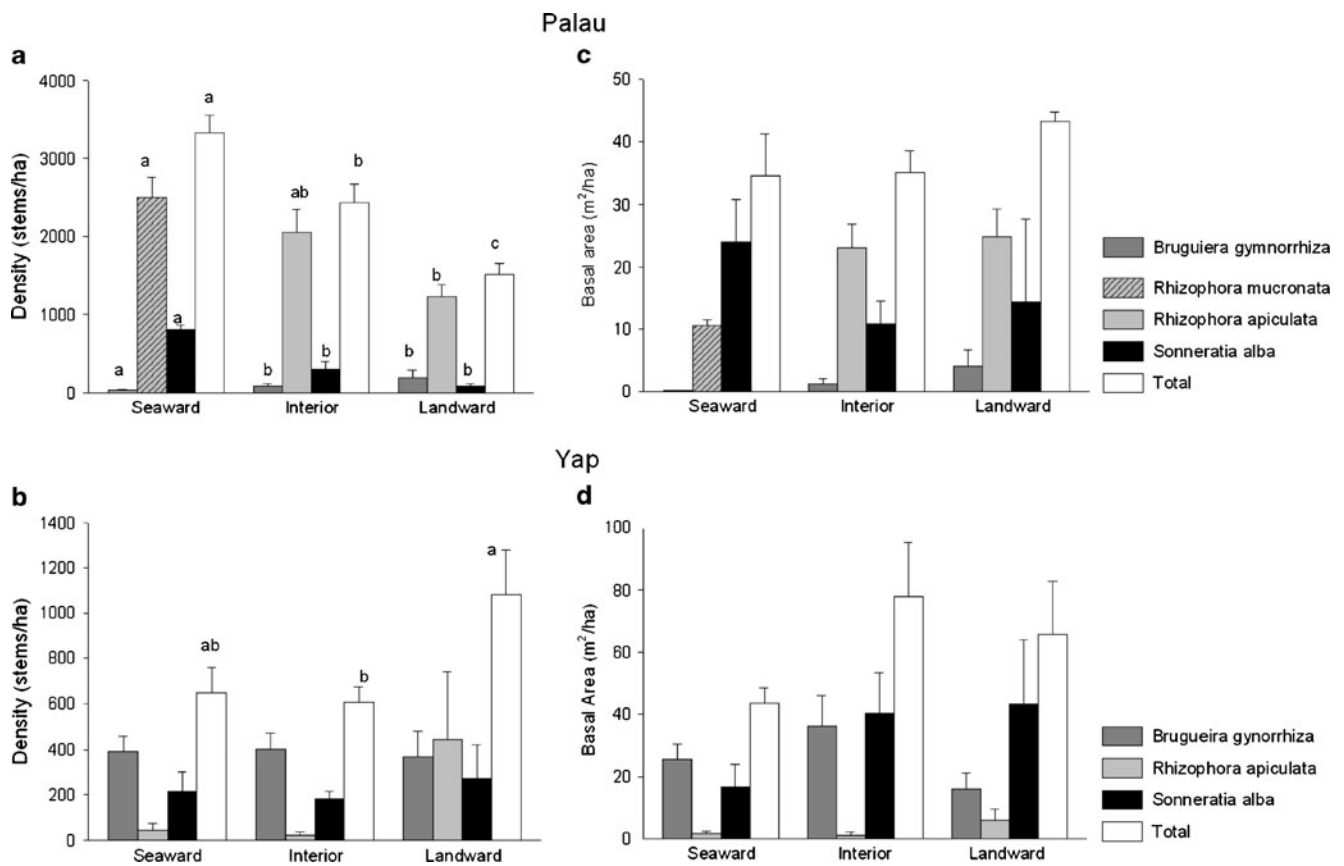


Fig. 2 Tree density (stems/ha; Figs. A and B) and basal area (m²/ha, Figs C and D) of sampled mangroves in Airai State, Republic of Palau and Yap, Federated States of Micronesia. Error bars represent one

standard error of the mean. Different letters above bars denote a significant difference ($P \leq 0.05$) when testing for individual species and total differences between zones within locations

Table 1 Tree volume and plant biomass pools of mangrove forests of Airai, Republic of Palau and Yap, Federated States of Micronesia. Data are means and standard errors in parenthesis

Zone	Tree wood volume (m ³ /ha)	Aboveground tree biomass (Mg/ha)	Aboveground tree Carbon ^a (Mg/ha)	Dead downed wood (Mg/ha)	Total aboveground biomass (Mg/ha)	Belowground tree biomass (Mg/ha)	Belowground tree Carbon ^a (Mg/ha)
Airai, Palau							
Seagrass	0.0	0.39 (0.03)	0.12 (0.01)	0.0	0.39 (0.03)	—	—
Seaward	199 (47)	174 (37)	81.4 (17.6)	29.7 (8.1)	204 (38)	150(37)	70 (17)
Interior	195 (22)	212 (24)	98.0 (11.1)	24.7 (6.2)	237 (22)	151 (16)	70 (8)
Landward	279 (87)	289 (66)	133.7 (31.1)	34.4 (8.5)	323 (73)	216 (61)	100 (29)
<i>Mangrove mean</i>	225 (27)	225 (34)	104.4 (12.9)	29.6 (2.8)	254 (36)	171 (17)	80 (8)
Ruunuw, Yap, FSM							
Seaward	297 (44)	251 (34)	116.7 (16.2)	48.2 (9.3)	299 (27)	215 (28)	100 (13)
Interior	550 (131)	456 (105)	212.9 (49.2)	57.5 (11.9)	514 (118)	392 (94)	178 (42)
Landward	453 (136)	383 (101)	179.1 (47.9)	23.6 (1.8)	407 (102)	333 (93)	154 (45)
<i>Mangrove mean</i>	432 (74)	363 (60)	169.2 (28.2)	43.1 (10.1)	406 (62)	312 (52)	144 (23)

^a Carbon pools of trees were calculated as the product of tree biomass multiplied by wood carbon content: *B. gymnorrhiza*=46.3%; *R. apiculata*=45.9%; *S. alba*=47.1%, and an average of all species of 46.4%. For seagrass, aboveground C mass was calculated as the product of aboveground biomass multiplied by the C concentration of the dominant *Enhalus acoroides* tissues, which was 30.7%.

Table 2 Soil properties by sampling depth in the Airai mangrove forest and adjacent seagrass community, Republic of Palau. Data are mean and standard error in parenthesis

Zone	Sample Depth (cm)	Carbon (%)	Nitrogen (%)	C/N ratio	Bulk density (g/cm ³)	Carbon mass (Mg/ha)
Seagrass	0–14	16.7 (0.5)	0.58 (0.01)	28.8 (0.5)	0.20 (0.01)	48.0 (4.3)
Seaward	0–15	21.5 (0.9)	0.67 (0.05)	32.5 (1.8)	0.20 (0.01)	65.3 (5.0)
	15–30	19.9 (0.5)	0.63 (0.02)	31.6 (0.8)	0.20 (0.01)	59.9 (3.3)
	30–50	18.5 (1.2)	0.56 (0.04)	33.5 (2.3)	0.18 (0.02)	67.1 (7.8)
	50–89	17.2 (1.2)	0.49 (0.02)	34.8 (1.5)	0.18 (0.02)	122.6 (16.6)
	Total					314.9 (19.1)
Interior	0–15	17.7 (1.7)	0.53 (0.05)	33.3 (0.8)	0.22 (0.01)	59.4 (6.7)
	15–30	20.4 (1.4)	0.58 (0.03)	35.4 (1.1)	0.23 (0.01)	69.8 (4.1)
	30–50	21.1 (0.7)	0.61 (0.02)	34.7 (0.6)	0.20 (0.02)	84.5 (6.0)
	50–101	18.7 (1.3)	0.49 (0.03)	38.0 (0.9)	0.25 (0.03)	214.7 (17.3)
	Total					428.4 (11.5)
Landward	0–15	12.0 (0.6)	0.39 (0.05)	32.1 (2.2)	0.36 (0.03)	63.4 (4.4)
	15–30	17.3 (2.7)	0.43 (0.06)	39.6 (0.7)	0.27 (0.02)	66.4 (6.3)
	30–50	19.1 (2.9)	0.42 (0.04)	44.6 (3.4)	0.32 (0.04)	111.3 (5.9)
	50–100	17.0 (1.2)	0.38 (0.03)	44.6 (1.9)	0.31 (0.04)	262.4 (22.2)
	100–160	17.0 (1.2)	0.38 (0.03)	44.6 (1.9)	0.31 (0.04)	315.0 (26.6)
	Total					818.4 (45.6)

At both sites, soil depth increased with distance from the seaward edge (Tables 2 and 3). Soil depth (to coral sands and rubble) was 14 cm in the seagrass community at Palau. At the seagrass/mangrove ecotone there was an abrupt increase in soil depth (Fig. 1). The mean soil depth of

seaward zone plots was 89 cm at Palau, increasing to 101 cm in the interior zone and 160 cm in the landward zone. At the Yap site, mean depth of the soil profile was 148, 159, and 231 cm in the seaward, interior, and landward zones, respectively.

Table 3 Soil properties by sampling depth in the Ruunuw mangrove forest, Yap, Federated States of Micronesia. Data are mean and standard error in parenthesis

Zone	Sample Depth (cm)	Carbon (%)	Nitrogen (%)	C/N ratio	Bulk density (g/cm ³)	Carbon mass (Mg/ha)
Seaward	0–15	12.2 (1.6)	0.47 (0.05)	25.8 (0.7)	0.27 (0.02)	48.7 (4.8)
	15–30	12.1 (1.5)	0.40 (0.04)	29.7 (1.5)	0.32 (0.02)	57.8 (7.6)
	30–50	10.8 (1.0)	0.39 (0.03)	27.6 (1.1)	0.34 (0.03)	73.5 (10.7)
	50–100	13.7 (1.7)	0.42 (0.03)	32.5 (2.3)	0.34 (0.03)	236.4 (39.1)
	100–148	13.7 (1.7)	0.42 (0.03)	32.5 (2.3)	0.34 (0.03)	237.2 (44.6)
	Total					614.0 (63.1)
Interior	0–15	7.3 (1.1)	0.25 (0.03)	28.9 (1.5)	0.51 (0.05)	55.1 (9.9)
	15–30	8.4 (1.5)	0.29 (0.05)	29.0 (0.9)	0.48 (0.04)	62.0 (13.0)
	30–50	9.6 (1.0)	0.29 (0.03)	33.4 (1.8)	0.37 (0.01)	70.0 (6.5)
	50–100	7.5 (1.2)	0.24 (0.04)	30.5 (1.2)	0.41 (0.04)	150.7 (25.2)
	100–159	7.5 (1.2)	0.24 (0.04)	30.5 (1.2)	0.41 (0.04)	192.5 (67.9)
	Total					530.4 (89.2)
Landward	0–15	10.7 (1.9)	0.35 (0.05)	29.9 (1.3)	0.41 (0.07)	56.5 (4.3)
	15–30	12.5 (2.2)	0.35 (0.02)	34.9 (4.1)	0.44 (0.03)	78.4 (10.4)
	30–50	11.6 (1.1)	0.35 (0.02)	33.4 (1.5)	0.50 (0.07)	112.9 (15.2)
	50–100	9.4 (1.1)	0.27 (0.03)	35.3 (0.5)	0.50 (0.02)	232.4 (24.5)
	100–231	9.4 (1.1)	0.27 (0.03)	35.3 (0.5)	0.50 (0.02)	561.8 (72.3)
	Total					1,041.9 (59.3)

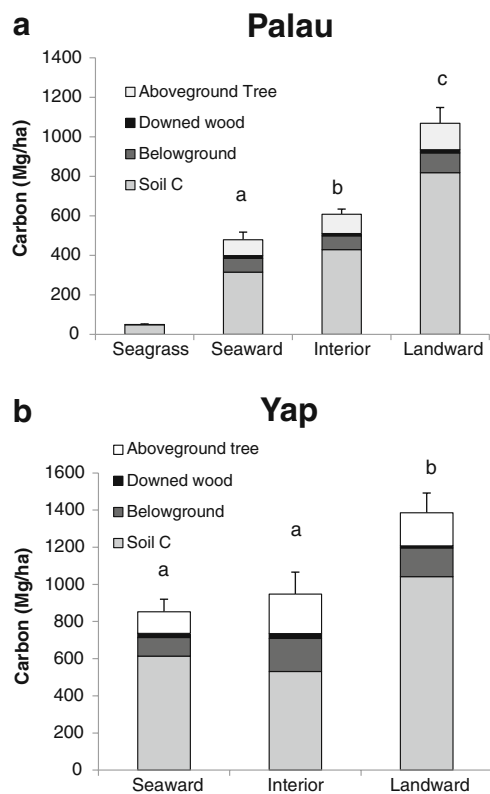


Fig. 3 Ecosystem C stocks of seagrass and mangroves at the Palau site and for mangroves at the Yap site. Error bars represent one standard error of the mean of the total ecosystem pool. Different letters above bars denote a significant difference ($P \leq 0.05$) in ecosystem pools between different zones within the mangrove stands

Few changes were detected in either chemical or physical properties with soil depth. Carbon, nitrogen, and soil bulk density remained relatively uniform throughout the soil depth profile. The greatest variation in C concentration at the Palau site was at the sediment surface where C concentration of the 0–15 cm depth was 22% in the seaward zone and 12% in the landward zone (Table 2). At the greatest depths we found that C concentration exceeded 17%. Belowground C pools of the seagrass community at the Palau site was 48 Mg/ha (Table 2). The belowground C pools of the mangrove forest transects were dramatically greater at 315, 428, and 818 Mg/ha for the seaward, interior, and landward zones, respectively.

Comparing the two mangrove forests, soil depths were greater at the Yap sites, while C concentrations were lower. Mean C concentrations of all depths ranged from 12% to 22%, at the Palau site and from 7% to 14% at the Yap site. The combination of higher bulk densities, greater sediment depths, and still-high C concentrations resulted in belowground C pools of 614, 530, and 1,042 Mg/ha for the seaward, interior, and landward zones, respectively at the Yap site (Table 3).

Ecosystem C Stocks

The total ecosystem C stock in the Palau seagrass community was 48 Mg/ha. Moving landward, the total ecosystem C stock of the seaward-zone mangrove was 479 Mg/ha (Fig. 3). Ecosystem C stocks increased toward the landward edge at both sites ($P \leq 0.01$ at both sites). Ecosystem C stocks in the landward zone were 136% and 64% greater than that of the seaward zone for the Palau and Yap sites, respectively. The mean ecosystem C stock for the Palau and Yap sites was 718 and 1,062 Mg/ha, respectively.

The combination of high aboveground biomass and deep, organic-rich soils resulted in large ecosystem C stocks for these mangroves (Fig. 3). Although aboveground tree components were large, they were relatively minor compared to the belowground pools and accounted for only 13–22% of total ecosystem C. Increasing ecosystem C storage from the seaward to the landward zones is largely a function of increasing soil C pools, which are reflective of the increasing depth to coral sands. For example, at the ends of the elevational gradient at the Palau mangrove, soil C pools were 315 and 818 Mg/ha. Soils composed 66% of total ecosystem C pool in the seaward zone and 77% at the landward zone (Fig. 3).

Discussion

The mean aboveground biomass for these sites is at the higher end of aboveground biomass for mangroves of Asia and the Pacific. Komiyama et al. (2008) reported mangrove biomass to range from 41 to 460 Mg/ha in the region. Our

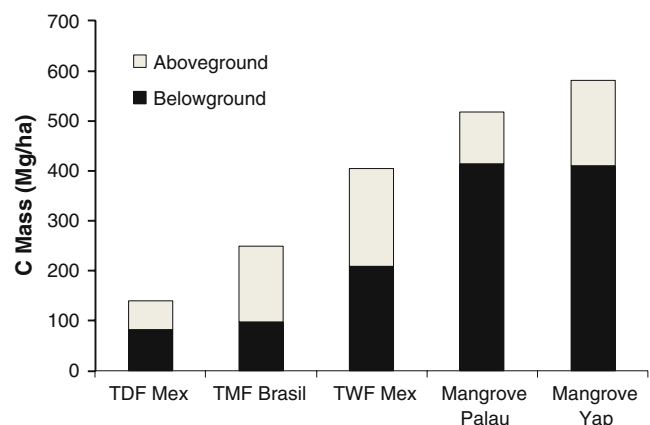


Fig. 4 Ecosystem C stocks of selected upland tropical forests and the mangroves sampled in this study. All belowground C pools are to 1 m depth. The data presented are from tropical dry forest, Jalisco, Mexico (TDF Mex, Jaramillo et al. 2003); tropical moist forest, Rondonia, Brazil (TMF Brazil; Kauffman et al. (1995); and tropical wet forest, Veracruz, Mexico (TWF Mex, Hughes et al. 2000)

estimate of 514 Mg/ha for the Yap interior zone exceeds that of sites reported in their study. Kauffman and Cole (2010) reported that TAGB for six Micronesian mangrove forests ranged from 169 to 517 Mg/ha. The TAGB of the Yap site sampled here, but immediately following typhoon Sudal, was 517 ± 179 Mg/ha (Kauffman and Cole 2010), compared to an aboveground biomass of 406 ± 62 Mg/ha four years later (Table 1). The differences may be due to differences in sampling methods as well as continued mortality, decomposition, and biomass decline of the stand following the typhoon.

Although there were compositional and structural differences, the combination of relatively high aboveground forest biomass over deep organic soils resulted in high ecosystem C stocks for both mangrove forests in this study. Ecosystem C storage in these mangroves is among the largest that have been reported in the literature for any tropical forest (IPCC 2007; Kauffman et al. 2009, Fig. 4). However, comparisons of ecosystem C stocks are notoriously difficult due to natural variation as well as differences in sampling approaches. We made comparisons of ecosystem C stocks with some of the most common tropical forests types where belowground data at least 1 m in depth existed (Fig. 4). Note that the mangrove numbers we utilize in this comparison are much lower than reported elsewhere in this paper because for consistent comparisons we did not include root biomass or soil C below 1 m in depth. Ecosystem C pools (aboveground and soil C pools to 1 m) were 148 Mg/ha in Mexican tropical dry forest (Jaramillo et al. 2003) and 249 Mg/ha in moist forests typical of eastern and southern Amazonia (Cummings et al. 2002; Kauffman et al. 1995; Kauffman et al. 2009). The ecosystem stocks of these widespread forests were less than half of that of the mangroves sampled in this study. The ecosystem C stocks of Mexican tropical wet forests on productive volcanic soils (Hughes et al. 2000) were well below those of the mangroves (Fig. 4), underscoring the value of mangroves as global C stocks.

Root biomass, which was excluded in analysis for Fig. 4, is quite high in mangroves relative to upland forests. Root:shoot ratios in these sites were 0.67 and 0.77, which is similar to that reported for mangroves by Komiyama et al. (2008). Nevertheless, root mass of mangroves is reported with caution due to well known difficulties in measuring root mass and in developing robust allometric equations. The mass of roots in this study was estimated to range from 148 to 392 Mg/ha, much higher than root masses reported for upland tropical forests. For example, Jaramillo et al. (2003) reported root mass of a Mexican tropical evergreen forest on fertile soils to 1 m ranged from 19 to 27 Mg/ha. Aboveground biomass of these forests was 403 ± 50 Mg/ha (Hughes et al. 2000), with a root:shoot ratio of 0.06.

The most significant differences in ecosystem C stocks between mangroves and upland forests were the belowground pools consisting of organic, in contrast to mineral soils. The mean belowground pools of upland forests reported in Fig. 2 range from 83 Mg/ha in dry forest to 210 Mg/ha in tropical wet forest. In contrast, the mean soil C pools (to 1 m depth) in mangroves of this study were 414 and 411 Mg/ha in the Palau and Yap sites, respectively. These substantial differences can largely be explained by the continuously high concentration of C throughout the soil profile in the mangroves. For example, Hughes et al. (2000) reported the soil C concentrations of Mexican wet forests reported in Fig. 4 were 5.0–7.8% at depths of 0–15 cm and decreased to 1.9% at the 50–100 cm depth. In contrast, C concentration at lower depths in mangrove were 7.5–18.7% (Tables 2 and 3) and in some areas this high concentration of C was present at depths considerably below 1 m.

The high C pools coupled with the other important ecological services provided by mangroves underscore their values and potential benefits from conservation and/or restoration. Rates of deforestation are quite high for mangroves, likely far exceeding that of upland forests (Valiela et al. 2001; Giesen et al. 2007). For example, Langner et al. (2007) reported rates of deforestation of mangroves were 8%/yr in Indonesia between 2002 and 2005, compared to 1.7% for upland forests. Assuming C pools of deforested mangroves were similar (prior to clearing) to those reported here, this suggests land cover change in mangroves is a significant source of atmospheric C emissions. A number of incentives to reduce deforestation and land cover change (e.g., REDD+) have been discussed as a viable means of mitigating climate change (Kanninen et al. 2007). High rates of land cover change in mangroves, coupled with large quantities of C susceptible to loss, underscore mangroves' exceptional relevance to strategies aimed at mitigating C emissions from land use activities.

Climate Change, Sea-Level Rise, and the Loss of Mangroves

Rising sea-level related to climate change is expected to have among the greatest impacts on mangroves and other coastal wetlands if surface elevations cannot keep pace with accelerating rates of sea-level rise (Gilman et al. 2008). Mangroves on coral reef flats such as those sampled here developed with a sea-level rise of 1–2 mm y^{-1} (Fujimoto et al. 1999) compared to a predicted average rate of sea level rise of 3–4 mm y^{-1} in the next century (IPCC 2007). Recent global projections suggest that sea-levels are likely to rise in excess of one meter by 2100 (Bindoff et al. 2007; Hansen 2007; Rahmstorf 2007; Pfeffer et al. 2008).

The low elevation and gradients of mangroves coupled with increases in sea-level rise and other predicted climate change influences place mangroves in oceanic-fringe settings, such as those sampled here, at risk. We found that the ecosystem C pool at elevations too low for mangrove persistence (seagrass communities) were only about 7% of that of mangroves (Fig. 3). Further, within the elevational boundaries of mangroves there was an increase in ecosystem C pools with increasing elevation. Given the relatively steep elevational rises on the landward edge, particularly at the Palau site, little new suitable habitat would be created for mangrove colonization. Thus, the elevation band where mangroves currently exist would be greatly reduced by a 1 m sea-level rise on these islands. This is significant, as the mangroves in this study occurred in elevation bands of 144 cm at the Palau site and 106 cm at the Yap site and mangroves currently compose 9.4% and 11.7% of the land area of these islands, respectively.

The rates of mangrove loss associated with sea-level rise could be ameliorated to some extent by both allocthonous and autochthonous processes affecting mangrove surface elevation (Gilman et al. 2008). On Pohnpei Island, FSM, Fujimoto et al. (1999) calculated sediment accumulation rates of 0.82–1.98 mm year⁻¹ over the last 3,000 years. Elevation rises in mangroves associated with belowground primary productivity and organic matter accumulation rates exceeding decomposition and erosion could slow mangrove disappearance associated with sea-level rise. However, the synergistic effects of climate change components that may affect mangroves such as increased typhoon severity, storm surges, changes in ocean circulation patterns, ocean acidification, upland hydrological/sedimentation influences (Gilman et al. 2008; IPCC 2007), and how humans respond to climate change could result in lowered productivity and/or increased mangrove mortality, thereby reducing the ability of mangrove surfaces to keep pace with rising sea-levels. Thus, both deforestation and the synergistic effects of climate change may result in significant C emissions arising from mangrove loss, resulting in positive climate feedbacks. Additional studies are needed to determine how climate change and dynamics within mangrove communities interact to affect persistence of these important coastal forests.

Acknowledgments Margie Falanruw, Francis Ruegorong, Larry Mamit, and Cimarron Kauffman provided valuable assistance in the field and with logistics. We are grateful to the Yap Division of Agriculture, the Palau Agriculture and Forest Agency, and the people of Yap and Palau for their cooperation and assistance in allowing us to work in their mangroves. We thank the Patrick Colin and the Coral Reef Research Foundation for generously allowing us the use of their laboratory in Palau. The study was funded by the USDA Forest

Service, PSW Research Station and the USDA Forest Service International Programs.

Appendix

Table 4 Equations to determine biomass of mangrove forests

Species and plant part	Equation
Live wood volume (m ³) ^a	
<i>Bruguiera gymnorhiza</i>	$V_{\text{wood}} = 0.0000754(D)^{2.50} (R^2 = 0.84)$
<i>Sonneratia alba</i>	$V_{\text{wood}} = 0.0003841(D)^{2.10} (R^2 = 0.78)$
<i>Rhizophora</i> spp.	$V_{\text{wood}} = 0.0000695(D)^{2.64} (R^2 = 0.96)$
Live wood biomass (kg)	$AGB_{\text{wood}} = 1000(V_{\text{wood}} \times Sg)^b$
Leaf biomass (kg) ^c	
<i>Bruguiera gymnorhiza</i> ^d	$AGB_{\text{leaf}} = 10^{(-1.1679 + 1.4914 \times \log(D))}$
<i>Rhizophora</i> spp.	$AGB_{\text{leaf}} = 10^{(-1.8571 + 2.1072 \times \log(D))}$
Prop root biomass (kg) ^e	
$D \leq 5.0$ cm	$AGB_{\text{p.root}} = AGB_{\text{wood}} * 0.101$
$D > 5.0 \leq 10$ cm	$AGB_{\text{p.root}} = AGB_{\text{wood}} * 0.204$
$D > 10 \leq 15.0$ cm	$AGB_{\text{p.root}} = AGB_{\text{wood}} * 0.356$
$D > 15 \leq 20.0$ cm	$AGB_{\text{p.root}} = AGB_{\text{wood}} * 0.273$
$D > 20$ cm	$AGB_{\text{p.root}} = AGB_{\text{wood}} * 0.210$
Belowground tree biomass(Kg) ^f	$W_R = 0.196\rho^{0.899}(D)^{1.11}$
Wood debris biomass (Mg)	
≥ 7.6 cm diameter	$Sg * 100((\pi^2 \sum D^2)/(8L));$ where $Sg = 0.69^g$
$> 2.55\text{--}7.5$ cm diameter	$Sg * 100((\pi^2 NQMD^2)/(8L));$ where $Sg = 0.0.71$ and $QMD = 4.52^g$
$> 0.65\text{--}2.54$ cm diameter	$Sg * 100((\pi^2 NQMD^2)/(8L));$ where $Sg = 0.64$ and $QMD = 1.33^g$
≤ 0.64 cm diameter	$Sg * 100((\pi^2 NQMD^2)/(8L));$ where $Sg = 0.48$ and $QMD = 0.43^g$

Definitions for symbols used in the equations are: V_{wood} = live wood volume (m³), AGB = aboveground biomass, Sg = specific gravity (g/cm³), D = diameter of downed wood particles (cm), N = number of pieces of wood present along the transect, QMD = quadratic mean diameter of downed wood particle size class (cm), and L = the transect length (cm).

^a Wood volume equations for this study are from Kauffman and Cole (2010).

^b Specific gravities to convert volume to wood biomass are from Hidayat and Simpson (1994); Simpson (1996). Sg (g/cm³) by species are: *Bruguiera*=0.84, *Sonneratia*=0.78, and *Rhizophora*=0.96.

^c Equations are from Clough and Scott (1989).

^d Equation also used for *Sonneratia*.

^e *Rhizophora* prop root biomass ($AGB_{\text{p.root}}$) as a percentage of AGB_{wood} , were derived from Clough and Scott (1989).

^f Belowground tree biomass is from Komiyama et al. (2005).

^g Data on specific gravity and quadratic mean diameters of downed wood for Micronesian mangroves are from Kauffman and Cole (2010).

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