A tropical freshwater wetland: II. Production, decomposition, and peat formation

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Abstract

As much as 10% of the total carbon stored in peatlands occurs in the tropics. Although tropical peatlands are poorly understood scientifically, they are increasingly exploited for a variety of human uses. Our objective was to measure baseline carbon cycling data in one type of tropical peatland in order to understand better how peat accumulates in these ecosystems. Average plant production for two study sites on the island of Kosrae in the Federated States of Micronesia over 2 year was 1122 g C m^{-2} year^{-1}, of which 1058 g C m^{-2} year^{-1} was aboveground plant production (bole, buttress and litterfall). Although leaves contributed a high proportion of total plant productivity, their rapid decomposition left little carbon for peat accumulation. In contrast, fine roots only contributed ~10% to plant productivity, but their slow decomposition allowed them to accumulate as peat. Wood (branches and stems) probably contributed the most carbon to the formation of peat. Despite being on the soil surface, small branches decomposed more slowly than leaves because of their high C:N and lignin:N ratios. In summary, we suggest that tropical peatlands in Micronesia accumulate peat not because of high plant production but rather because of slow decomposition of roots and wood under anaerobic conditions that result from nearly constant high water levels.

Introduction

Tropical peatlands represent as much as 10% of the total carbon stored in peatlands (Immirzi et al. 1992), which cover roughly 4 million km^2 or 3% of the Earth's land surface (Maltby and Proctor 1996). They can be up to 10 m deep, and accumulation rates can be rapid, averaging 4–5 mm/year, with some sites as fast as 5–10 mm/year (Maas 1996). These rates are significantly faster than in most temperate and boreal peatlands, which accumulate less than 1 mm/year, often slower than 0.5 mm/year (Gorham 1991; Gorham et al. 2003). Although tropical peatlands are poorly understood scientifically, they are increasingly exploited for peat extraction, fisheries, fossil fuels, minerals, forestry, and agriculture (De la Cruz 1986; Rieley et al. 1996; Junk 2002). Tropical peatlands are at greater risk than remote temperate and boreal peatlands (such as in Canada and Russia), because they are often situated in densely populated low-lying coastal areas (Rieley et al. 1996). With

high population growth in many tropical countries, tropical peatlands are facing increasing rates of alteration and destruction (Vijarnsorn 1996).

In order to understand and manage peatlands it is imperative to understand the processes that regulate carbon cycling and the rate of peat accumulation. Peatlands accumulate carbon because plant production is faster than decomposition, allowing the build up of peat, which is partially decomposed plant material. Peat accumulates in subarctic and boreal peatlands because of low decomposition rates rather than high net annual primary production (Malmer 1986; Francez and Vasander 1995). However, tropical peatlands occur in consistently hot and often humid conditions, which are normally associated with both high production rates and rapid decomposition rates.

Several explanations are possible for how peat accumulates in the tropics. Tropical peatlands may function similarly to peatlands in other regions because higher temperatures in the tropics increase both plant production and decomposition rates similarly. Alternatively, hot and humid tropical conditions might cause key changes to the carbon cycling in peatlands.

Aboveground plant production is believed to be the primary source of peat (Clymo 1983). This paradigm was developed for *Sphagnum* moss peatlands, which is the dominant peat-producing plant in many regions and has no roots. However, tropical peatlands are predominantly forested with no moss cover (Rieley and Ahmad-Shah 1996). The high temperatures and more aerobic conditions on the surface of tropical peatlands may speed up the decomposition of leaves and wood, suggesting that roots could be more important to peat accumulation in the tropics. Although roots only contribute 10–30% of the total plant biomass in northern forested wetlands (Trettin et al. 1995), they occur below the soil surface in almost continually anaerobic conditions. The few documented root decomposition studies have shown that roots normally decompose slower than aboveground components (e.g.. Day et al. 1989; Thormann et al. 2001). Recent models also predict that peat could be composed of predominantly root material, with leaves contributing little to carbon storage (Chen and Twilley 1999; Chimner et al. 2002).

The future is uncertain for tropical peatlands, and the rate of disturbance and destruction is very high, yet there is little scientific information to help with management, sustainable use, or protection. Understanding how peat accumulates and how carbon cycles in the tropics will not only provide information for management of tropical peatlands, but it also will help in elucidating how carbon accumulates in all peatland types. The objective of this study was to obtain baseline carbon cycling data for one type of tropical forested peatland in order to understand better how peat accumulates in these wetlands.

Study sites

This study was conducted on the island of Kosrae (109 km^2), a high volcanic island in the Federated States of Micronesia in the western Pacific Ocean (Figure 1: 5°19′ N, 163°00′ E). Kosrae is 1.4 million years old and has a rugged, forested interior, a narrow coastal plain lined by mangroves around most of the island, and a fringing reef. Rainfall and temperature are aseasonal. Average daily temperatures during our study (May 2001–May 2003) ranged between 25 and 30 °C, with an average of 27 °C. Total rainfall during our study was 5900 mm/year during May 2001–May 2002, and 4900 mm/year during May 2002–May 2003. The long-term mean (1954–2001) for Kosrae is 5050 mm/year (NOAA Cooperative Weather Station 914395). September 2001 was the driest month with 250 mm, whereas December 2001 was the wettest with 1080 mm.

Peatlands are not usually associated with tropical islands. However, freshwater peatlands are estimated to cover 807 ha, or 1.2% of total land area, in the Federated States of Micronesia (USDA Soil Surveys 1983). Mangrove peatlands represent another 2446 ha, or 3.7% of total land area. Freshwater peatlands are often located directly behind mangrove forests or beach strands (Merlin et al. 1993). In Kosrae, they are dominated by *Terminalia carolinensis* Kanehira (hereafter called *Terminalia*), which is a large tree (up to 35 m tall) with a distinctive pagoda-shaped crown and large buttresses (Maxwell 1982). Endemic to Micronesia, this species is common only on the island of Kosrae, where it occupies about 300 ha (Miller 1984). On the neighboring island of
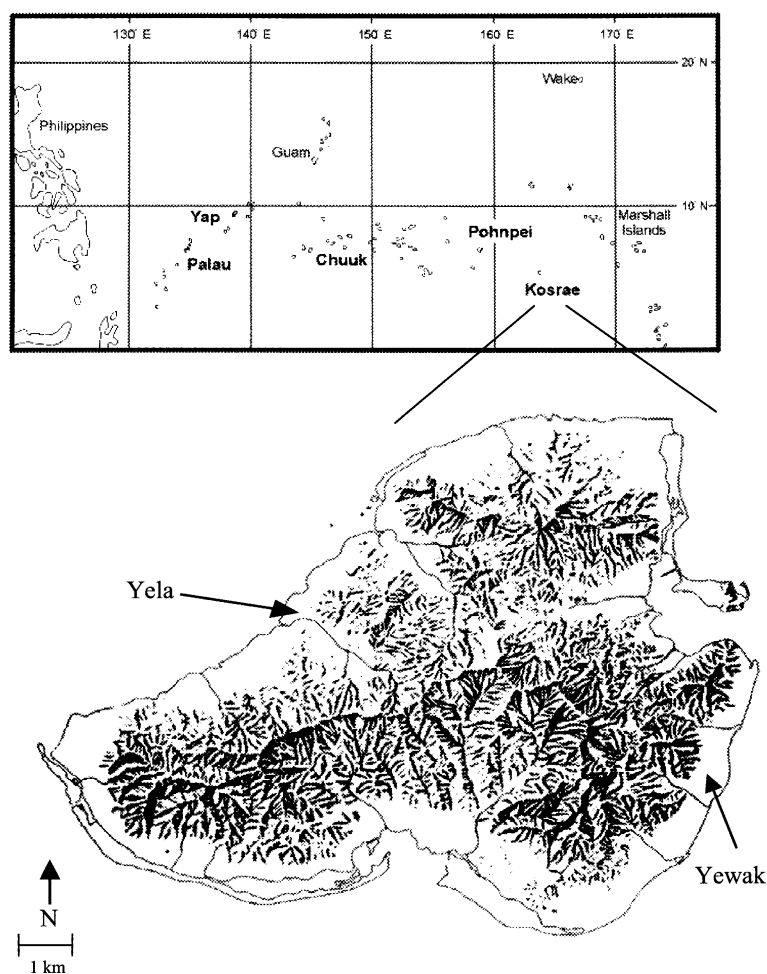
Figure 1. Location of the island of Kosrae, Federated States of Micronesia, in the western Pacific Ocean. Study sites are located in the Yewak region on the east side and the Yela region on the northwest side of Kosrae.

Pohnpei, it is much less common due to widespread conversion of wetlands to agriculture (Merlin et al. 1992).

We established two study sites. The first was located in the Yela basin (5°19.560′ N, 162°56.88′ E) in the municipality of Tafunsak on the north-west side of Kosrae (Figure 1), in one of the largest (68 ha) and most pristine forested wetlands in Micronesia. There are currently no roads into the area, although a road across the basin or around the rim has been proposed.

The second study site was located in an 18-ha forested peatland in the Yewak region (5°17.615′ N, 163°01.564′ E) in the municipality of Malem on the east side of Kosrae (Figure 1). Aerial photos from 1944 indicate that the western side of the peatland was intensively farmed until the end of

World War II. Subsequent aerial photos show that part of the agricultural portion of the peatland was converted to agroforestry and part was left to regenerate naturally. The eastern side of the peatland was not farmed intensively, but many large *Terminalia* trees have been harvested from it over the past 50 years.

Methods

Stand dynamics and plant production

Circular 0.04-ha plots were established in the center of each study site. Within each plot, each tree > 2.5 cm in diameter was identified, and its diameter was measured at 50 or 130 cm above the

highest buttress. Height of each tree was measured using a relaskop. Tree bands were installed (at the same height where diameter was measured) on five trees at each site: at Yela we used tree band data from five of the *Terminalia* trees being measured as part of another study (Allen et al. unpublished MS); at Yewak, we installed bands on five *Terminalia* trees and five trees of another common species, *Horsfieldianunu* Kanehira.

To translate diameter growth into wood production, we used previously developed outside-bark stem volume equations for a third tree species, *Barringtonia racemosa* (L.) Spreng. (Ewel et al. 2003), but no stem volume equations were available for *Terminalia* or *H. nunu*. We therefore derived regression equations to estimate outside-bark total tree volume (m^3) from stand inventory data collected in Kosrae (MacLean et al. 1988; Ewel et al. 2003).

Volume equations were derived by regressing volume against diameter. The final equations used to calculate stem volume are:

Terminalia (m^3/tree)
$$= 0.25 * \exp(dbh * 0.044474) : (R^2 = 0.66)$$

H. nunu (m^3/tree)
$$= 0.000128 * (dbh^{2.363}) : (R^2 = 0.89)$$

B. racemosa (m^3/tree)
$$= -0.03134 + (0.000446 * dbh^2) : (R^2 = 0.98)$$
$$(\text{Ewel et al. 2003})$$

Terminalia trees have large buttresses that were not measured in the stand inventory and are consequently not incorporated into the stem volume equations. To correct for this, we developed separate buttress volume equations. We measured the height, width, and length of all buttress segments on seven trees from both sites that ranged in size from 29.3 to 84.5 cm dbh. The volume of each buttress segment was calculated using the formula for a right triangle. Total buttress volume for each tree was calculated as the sum of all buttress segment volumes. Buttress volume was significantly correlated to dbh and was described by an exponential growth function:

Buttress Volume (m^3/tree)
$$= 0.076 * \exp(dbh * 0.038) : (R^2 = 0.99)$$

This equation was used to calculate buttress volume on all *Terminalia* trees.

Initial wood biomass was calculated using the allometric equations described above. Final wood biomass was calculated by using the new dbh after 1 year as determined for each tree species from the tree band data and recalculating volume using the allometric equations. Wood production was calculated by subtracting the final wood biomass from the initial wood biomass.

Litterfall was captured at each site in eight 1.0 m × 1.0 m litter traps constructed by attaching shade cloth to four 2.5 cm PVC pipes inserted into the soil. Litter was collected at monthly intervals for 2 year, sorted into components (leaves, reproductive parts, fine branches (< 10 cm), and miscellaneous), oven-dried for 3 days, and weighed.

To estimate large-branch fall (> 10 cm) we measured branches that fell into three replicate 5×5 m plots at each site. After all branches had been removed from the plots, we collected newly fallen branches at monthly intervals. They were dried and weighed.

Belowground fine root growth was calculated using in-growth root bags (Neill 1992; Weltzin et al. 2000; Chimner and Ewel 2004). Mesh bags 30 cm long and 10.1 cm in diameter made from fiberglass window screen (1.5 mm mesh) were filled with native root-free peat and inserted in an augered hole to a depth of 30 cm. Eight replicates were installed in each site. Roots were collected from the mesh bags, washed free of sediment, oven dried, weighed, and analyzed for carbon content using a CHN analyzer.

Decomposition bags

Decomposition bags were made for leaves, fine branches (< 10 mm), and fine roots (< 2 mm). Leaves were decomposed in 20 cm×20 cm mesh bags constructed from 1.5 mm fiberglass screen. Each mesh bag was filled with 6 g of air-dried leaves collected from freshly fallen litter. Fine branches were collected loose on the forest floor or from downed trees. After air-drying, 6 g were decomposed in 10 cm×20 cm mesh bags. Live fine roots were collected in the field, brought back to the lab, washed, and air-dried. Three grams of air-dried roots were inserted into 10 cm×10 cm 1.5 mm mesh fiberglass bags. Air-dried to

oven-dried conversion factors for leaves, fine branches, and fine roots were calculated from subsamples.

Decomposition bags for leaves and stems were placed on the soil surface, while root bags were buried at a depth of 5 cm. Five bags of each type were collected at 2, 4, 8, 12, 17, and 36 week. Upon collection, decomposition bags were stored at 4 °C in labeled Ziploc bags until processed. Each decomposition bag was washed in water to remove sediments, dried at 70 °C for 3 days, weighed, and ground for further chemical analysis.

The percent mass remaining for each plant type and site was calculated using the following equation:

$$M_R = [X_o - X)/X_o] \times 100,$$

where X_o represents initial dry mass and X = mass remaining. First-order and second-order exponential decay models were fitted to the decomposition data for each plant type and site using SYSTAT 10.0 non-linear regression (SPSS 2000). The first-order model was $M_R = 100*e^{-kt}$, where M_R = mass remaining at time t in years, and k was the decay constant (Olson 1963; Wieder and Lang 1982). The second-order model was $M_R = S * e^{-kt} + (1-S)* e^{-ht}$, where M_R = mass remaining at time t in years, S was the initial proportion of labile material, $(1-S)$ is the initial proportion of resistant material, k was the rate constant for the labile material, and h was the rate constant for the resistant material (Hunt 1977; Wieder and Lang 1982).

Substrate quality

Five replicate peat samples (0–5 cm) were collected from each site and analyzed for lignin, cellulose, and carbon and nitrogen contents. Plant material from the decomposition bags were also analyzed for lignin, cellulose, carbon, nitrogen, and $\delta^{13}C$ contents at every retrieval period. The five replicate decomposition bags at each site were pooled for analysis. Peat and plant samples were analyzed at the Agricultural Diagnostic Service Center, Sherman Laboratory, University of Hawaii. Lignin and cellulose concentrations were determined using the procedure of Goehring and Van Soest (1970). Total carbon and nitrogen were determined using dry combustion (LECO CHN-2000, LECO Corporation, St. Joseph, Michigan, USA). Carbon isotope measurements were conducted on a Caria Erba NC 2500 Elemental Analyzer with conflow II interface coupled to a Finnigan Delta-S mass spectrometer with a source upgrade.

Ancillary measurements

Groundwater levels were measured in monitoring wells constructed from 3.8-cm diameter slotted PVC pipes in each peatland. Wells were installed with a standard bucket auger of the same diameter as the well casing. Water tables were measured four times during the year. Water table levels were also continuously measured in Yewak with a YSI 600 XLM sonde (YSI, Inc., Yellow Springs, Ohio). Specific conductivity, pH, and redox potential were measured during each CO_2 sampling period. Redox was measured using referenced platinum electrodes inserted into the soil to a depth of 5 cm. Specific conductivity and pH were measured in the surface water using a portable meter.

Results

Environmental and soil parameters

There were few differences in pH, specific conductivity, or redox levels between sites (Table 1). Soil temperature varied only slightly during the study period, averaging 25 °C. Water table levels were maintained near the soil surface during the study period with fluctuations no greater than 10 cm. Bulk density was also similar between the sites, averaging 0.1 g/cm^3 (Table 1). Differences in peat chemistry that may reflect hydrogeomorphic differences between the sites were detected, however. The Yela site is located within a broad river valley that is flooded regularly during high rainfall events and consequently has a high amount of sediment deposited in the peatland. The peat there had an organic carbon content of only 20% (Table 2). This is in contrast to almost 50% organic carbon content for the peat at Yewak, which is not located in a river valley and has little sediment deposition. Nitrogen and lignin concentrations were also significantly lower in Yela. The C:N ratio was significantly lower in Yela, but lignin:N ratios were similar.

Table 1. Mean values of environmental parameters of the study sites.

	Yela	Yewak
PH	6.4	5.9
Redox (mv)	133	154
Specific conductivity (μS)	119	133
Soil temperature (C)	24.8	25.6
Water table (cm)	−0.1	3.4
Bulk density (g/cm^3)	0.11(0.01)	0.13 (0.03)

Surface water was used for determining pH and specific conductivity. Redox and soil temperature were measured at depths of 5 cm. Bulk densities are an average of five samples, whereas other values are averages of four measurements.

Forest structure and production

Three tree species were encountered in our study sites (Table 3). *Terminalia* and *H. nunu* were found at both sites, whereas *B. racemosa* was only encountered at Yela. The *Terminalia* in Yela were fewer in number but had twice the height, diameter, and basal area than in Yewak. *H. nunu* had similar heights and basal area at both sites but were much larger and fewer in number at Yela.

Many small *B. racemosa* were found in the understory at Yela.

Total wood volume was twice as high in Yela with 666 vs. 332 m^3/ha in Yewak (Table 3). The buttress volume of *Terminalia* averaged 88 and 49 m^3/ha, which accounted for 16 and 20% of the total stem volume in Yela and Yewak, respectively. Increment growth for *Terminalia* averaged 3.8 and 12.4 mm/year in Yela and Yewak, respectively. Despite having half the wood volume, Yewak had greater wood production due to higher increment growth, averaging 861 g m^{-2} year^{-1}, compared to 658 g m^{-2} year^{-1} for Yela.

Annual litterfall did not differ significantly ($p > 0.10$) between sites during either year (Figure 2). Annual litterfall rates for Yewak were not significantly different between years ($p = 0.4$); they totaled 1.33 and 1.65 kg m^{-2} year^{-1} for 2 years, with an average of 124 g m^{-2} month^{-1}. However, annual litterfall rates for Yela were significantly higher in the second year (2.04 kg m^{-2} year^{-1}) than the first (0.98 kg m^{-2} year^{-1}) ($p = 0.003$) for an average litterfall of 126 g m^{-2} month^{-1} for both years. Time of the year was a significant factor for litterfall ($p < 0.001$) with the highest rates

Table 2. Mean, standard deviation (s.d.), and *p*-values from *t*-tests of peat chemistry from Yela and Yewak.

	Yela		Yewak		p
	Mean	s.d.	Mean	s.d.	
Carbon (%)	19.9	2.62	47.0	0.99	< 0.001
Nitrogen (%)	1.20	0.17	2.34	0.23	< 0.001
Lignin (%)	23.5	4.41	47.9	3.54	< 0.001
C:N	16.6	1.44	20.3	2.54	0.029
Lignin:N	19.5	2.14	20.56	1.84	0.44

Table 3. Stand characteristic, above ground volume of stems and buttresses, and above ground growth of trees in Yela and Yewak.

	Yela			Combined	Yewak		Combined
	Terminalia carolinensis	*Barringtonia racemosa*	*Horsfieldia nunu*		*Terminalia carolinensis*	*Horsfieldia nunu*	
Mean height (m)	32	11	18	(16)	17	15	(16)
Mean dbh (cm)	59	17	54	(28)	23	15	(26)
Number of trees (ha)	100	400	50	550	250	200	450
Basal area (m^2/ha)	29	9	13	51	12	16	28
Butters volume (m^3/ha)	88			88	49		49
Stem volume(m^3/ha)	448	38	92	578	187	97	284
Total volume (m^3/ha)	536	38	92	666	235	97	332
Wood production[a] (kg C ha^{-2} year^{-1})	2014	490	326	2830	2907	795	3702

[a]Assuming carbon content of 43% and wood density of 522 kg/m^3 (*T. catappa*).
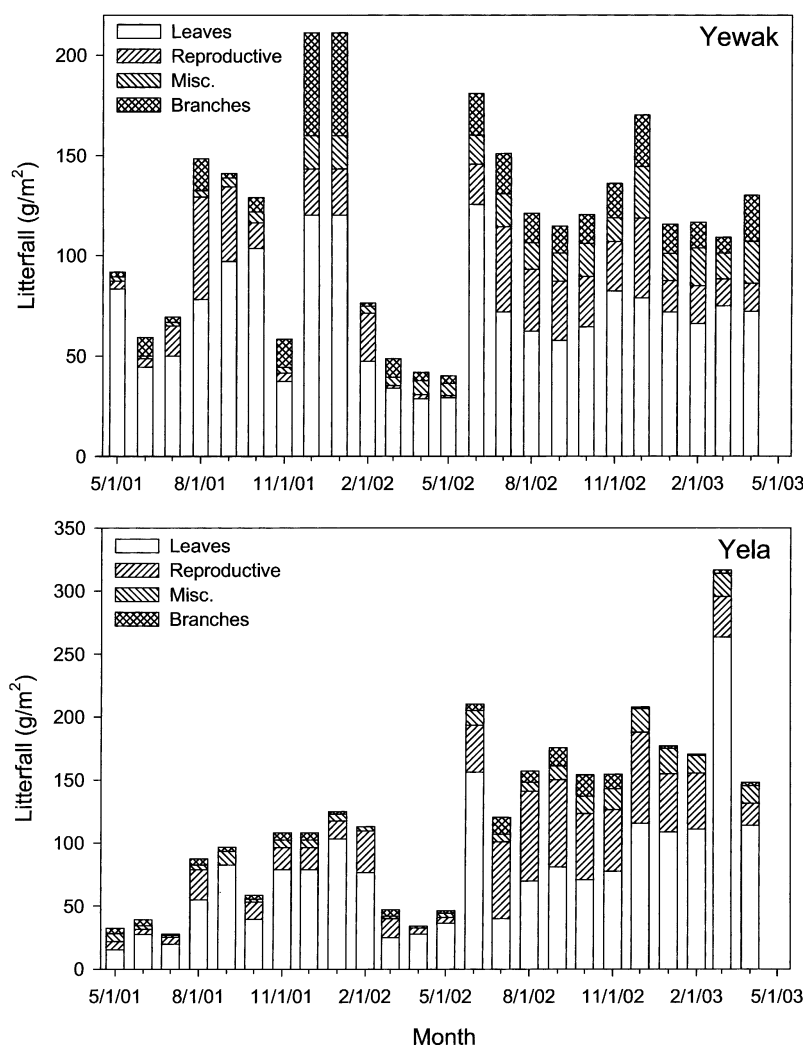
Figure 2. Litterfall patterns at Yewak and Yela sites for 2 year.

occurring during the winter months for both sites. For the two sites combined, litterfall consisted of 63% leaves, 21% reproductive material, 9% branches, and 7% miscellaneous material.

Fine root biomass did not differ significantly ($p = 0.08$) between Yela and Yewak, averaging 272 g/m^2. An average of 80% of the root biomass was found in the top 15 cm of the cores. Fine root production did not differ between the two sites ($p = 0.15$), averaging 300 g m^{-2} year^{-1}.

Plant production for this study was calculated as the sum of fine root production, litterfall,

branchfall, and wood production. We do not have data for coarse root production, but this is usually a small component of plant production. Annual plant production for Yewak totaled 1037 and 1175 g C m^{-2} year^{-1} for 2 years, averaging 1106 g C m^{-2} year^{-1} (Figure 3). Annual plant production for Yela totaled 864 and 1409 g C m^{-2} year^{-1} for 2 years, averaging 1137 g C m^{-2} year^{-1}. Overall, litter accounted for 36% and total wood production, including branches, accounted for roughly 30% and fine root production accounted for 12% of total production.
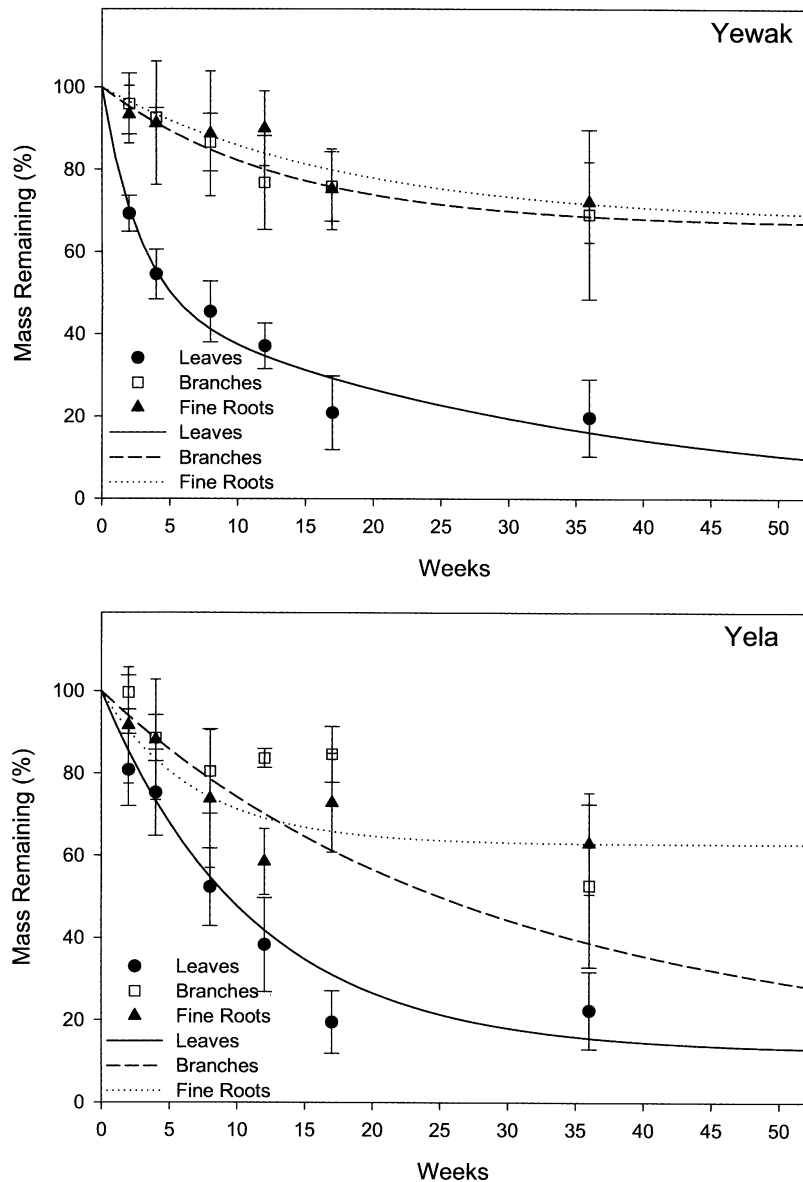
Figure 3. Mass remaining for leaves (solid line) and fine root (dashed line) decomposition bags over a 36-week period. Regression lines are the best fit double exponential regressions, and error bars are standard errors.

Decomposition

Decomposition rates were similar between sites with no significant differences for leaves, branches, or roots ($p > 0.05$). Decomposition of leaves occurred rapidly with an average of 50% remaining after 8 week and only 20% remaining after 17 week (Figure 4). Leaves had high k-values of 3.66 and 5.24 for the single exponential model at

Yela and Yewak, respectively (Table 3). However, after 17 week decomposition slowed dramatically with no significant difference between mass remaining after 17 and 36 week ($p > 0.05$).

Decomposition rates were slower for both roots and branches (Figure 4). Roughly 85% of branch mass remained after 8 week, and 60% remained after 37 week. This is similar to the roots, which had roughly 81% remaining after 8 week and 68%
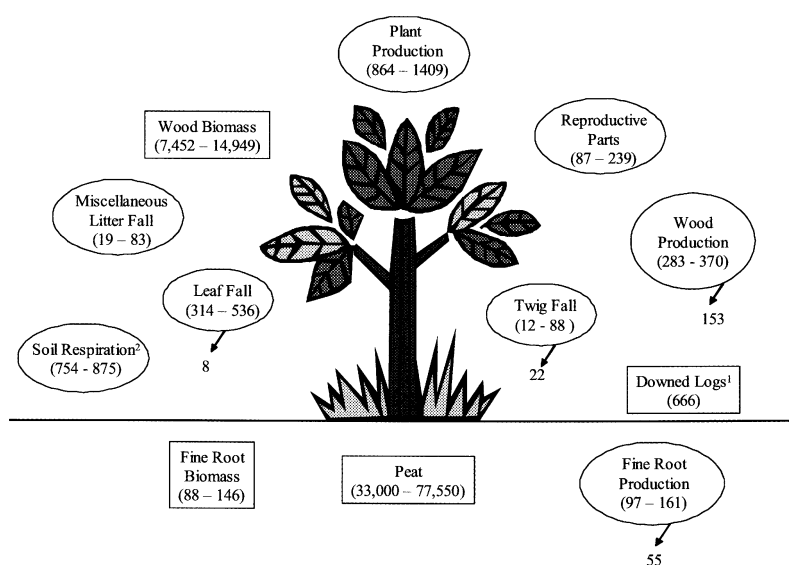
Figure 4. Tentative carbon budget for forested peatlands in Kosrae. Square boxes are pools, circles are fluxes, and arrows are residual carbon after 1 year of decomposition. Pools are in g C m^{-2} and fluxes and residual carbon are in g C m^{-2} year^{-1}. [1]Data from Allen et al. (unpublished MS), [2]Data from Chimner (2004).

remaining after 37 week. For the single exponential model, both branches and roots had *k*-values less than one. Branches had low *k*-values of 0.8 and 0.7 for the single exponential model; roots also had low *k*-values of 1.0 and 0.6 at Yela and Yewak, respectively (Table 4). The double exponential models fit as well as or better than the single exponential models for all components and sites (Table 4). They predicted that the leaves had more labile material than either the branches or roots.

The carbon concentrations of the different vegetation components were initially similar, averaging around 42% and changing little

throughout the decomposition process (Table 5). Initial nitrogen concentrations were lowest for the branches and highest for the roots. The nitrogen concentrations increased during decomposition in the leaves, but not for the fine roots and branches. Final lignin concentrations in the leaves stabilized at 8–12 week at about half of the initial concentration. Lignin concentrations remained the same or increased in the branches and fine roots during the decomposition process. The C:N and lignin:N ratios decreased in the leaves, but they increased or changed little in the branches and fine roots.

Table 4. Parameter estimates for single and double exponential decomposition models.

Parameter	Yela			Yewak		
	Leaves	Branches	Roots	Leaves	Branches	Roots
k	3.66	0.845	1.064	5.24	0.70	0.58
R^2	0.94	0.88	0.64	0.94	0.87	0.85
S	87.76	60.33	37.25	50.45	33.74	32.70
k	4.72	2.31	7.70	19.3	3.91	2.94
h	0.00	0.58	0.00	1.63	0.00	0.00
R^2	0.94	0.87	0.87	0.98	0.98	0.88

k is the decay constant for the first-order model. S is the initial proportion of labile material, k is the rate constant for the labile material, and h is the rate constant for the resistant material for the second-order model.

Discussion

Mechanisms of peat formation

Peatlands form when plant production exceeds decomposition, allowing organic matter to accumulate. Our plant production rates did not support the thesis that higher rates of plant productivity drive peat formation. Our average plant production for the two sites over 2 years was 1.12 kg C m^{-2} year^{-1}, of which 1.06 kg C m^{-2} year^{-1} was aboveground plant production (bole, buttress and litterfall) (Figure 5). In comparison, aboveground production rates of northern forested wetlands range from 0.100 to 1.01 kg C m^{-2} year^{-1} (Trettin et al. 1995). Stem production at Yewak and Yela averaged 327 g C m^{-2} year^{-1} compared to 48–541 g C m^{-2} year^{-1} from the same kinds of wetlands (Lugo et al. 1988, cited in Trettin et al. 1995).

Further evidence that high plant production is not important for tropical peat formation is apparent from the production rates of the dominant tree *Terminalia* in Kosrae. Tree growth rates of *Terminalia* in peat soils were significantly slower than in non-peat soils with depth to water table the most apparent environmental factor differentiating the two kinds of soil types (Allen et. al. unpublished MS). High water tables may have slowed not only plant production, but decomposition as well, allowing peat to form.

Decomposition and soil respiration generally increase with an increase in temperature (Hogg et al. 1992; Lloyd and Taylor 1994; Raich and Potter 1995; Fang and Moncrieff 2001; Silver and Miya 2001; Chimner 2004). Decomposition data for peatlands, excluding sphagnum bogs, reveal similar trends with increasing latitude (Figure 5). For example, leaves at higher latitudes lose between 20 and 40% of their mass within the first year, whereas leaves in our tropical site lost all their mass in the first year. Branches showed the same pattern as leaves. The temperature pattern for the limited data on fine roots was not as strong
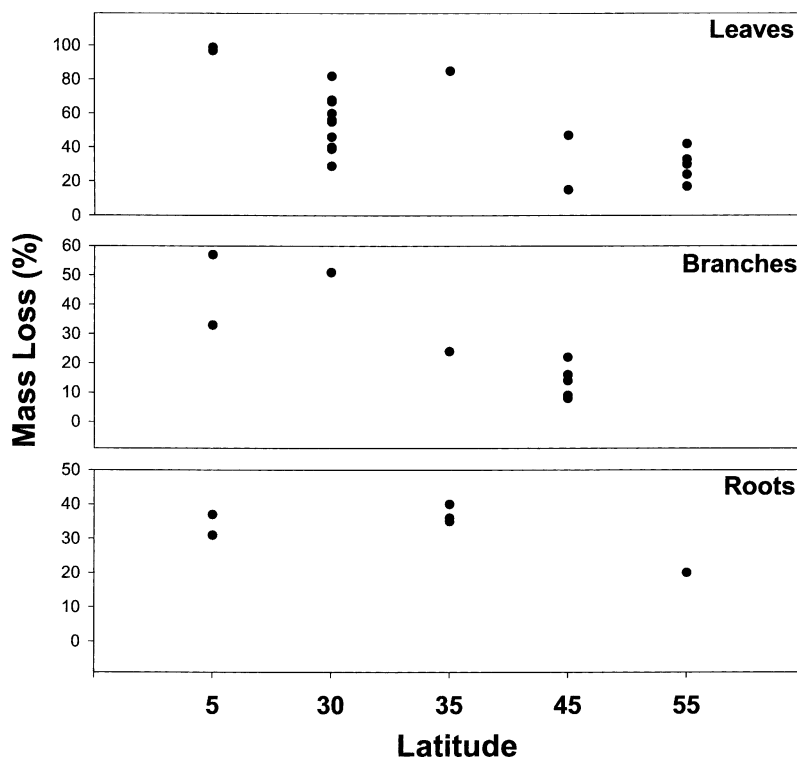

Figure 5. Pattern of mass loss from decomposition in forested peatlands (Reader and Stewart 1972; Heal and French 1974; Bums 1976; Duever et al. 1976; Brinson 1977; Chamie and Richardson 1978; Nessel 1978; Bartsch and Moore 1985; Tupacz and Day 1990; Conner and Day 1991; Thorman and Bayley 1997; Thorman et al. 2001; Chimner and Ewel this study).

(Figure 5). These differences indicate how peat can form in a tropical environment. Although leaves contributed a high proportion of total plant productivity, their rapid decomposition allowed little carbon to be available for peat accumulation. In contrast, fine roots only contributed ~10% to plant productivity, but their slow decomposition allowed them to accumulate as peat (Figure 5). Although we were not able to quantify coarse root dynamics, we believe that they would also have slow decomposition rates, probably slower than the fine roots due to poorer substrate quality, and would also contribute most of their biomass to peat formation, increasing the importance of roots to peat formation even more.

Wood (branches and stems) probably contributed the most carbon to the formation of peat (Figure 5). Despite being on the soil surface, small branches decomposed more slowly than leaves because of low substrate quality, as represented by their high C:N and lignin:N ratios (Table 5). If we assume that tree stems decomposed at the same rate as twigs, then stems would have added an additional 153 g C m^{-2} year^{-1} of carbon to the formation of peat (Figure 5).

We estimated a carbon balance for *Terminalia* wetlands by summing residual carbon amounts left over from the decomposition of plant production (Figure 5): we calculate that these sites had 235 g C m^{-2} year^{-1} of residual carbon. This does not include the 19–83 g C m^{-2} year^{-1} of miscellaneous litter fall for which we do not have decomposition rates. We assume that most of the miscellaneous litter fall was added to the peat profile as *Terminalia* seeds, which are large, very hard nuts that do not appear to decompose very fast. For instance, we found 380 g C m^{-2} of *Terminalia* nuts in the top 30 cm of soil in Yela while measuring fine root biomass.

Carbon gain can also be estimated by subtracting soil respiration from plant production (Trumbore et al. 1999; Chimner and Cooper 2003). If we assume that root respiration is half of total soil respiration, than we can estimate that these sites accumulated 407 g C m^{-2} year^{-1}. This does not account for losses due to dissolved organic carbon or CH_4 losses, which would lower the carbon gain. Combining these two indirect methods gives us an estimated accumulation of 300 g C m^{-2} year^{-1} for these systems. This is comparable to carbon accumulation rates in forested tropical peatlands in Thailand, which averaged 527 g C m^{-2} year^{-1} (Suzuki et al. 1999).

Peat is often thought of as a 'black box' with constant decay parameters or temperature-dependent rates. But organic matter is actually made up of a multitude of compounds, each with a different decay rate (Parton et al. 1987). The compounds can be roughly divided into three groups: non-structural carbohydrates, cellulose and

Table 5. Plant chemistry of leaves, branches, and fine roots from decomposition bags retrieved after progressive number of weeks.

	Yela						Yewak					
	2	4	8	12	17	36	2	4	8	12	17	36
Leaves												
Carbon %	42.2	41.4	41.3	38.5	36.7	38.9	42.7	42.1	41.8	43.0	43.2	43.7
Nitrogen %	0.6	0.7	1.4	1.3	1.2	1.6	0.8	1.1	1.3	2.0	1.8	2.1
Lignin %	39.7	37	39.4	33.9	34.1	35.4	30.8	39.3	41.1	23.3	44	39.1
C:N	69.2	59.2	29.9	30.6	30.6	24.9	56.2	38.2	31.9	21.8	24.4	20.5
Lignin:N	65.1	59.2	28.6	26.9	28.4	28.4	40.5	35.7	31.4	11.8	24.9	18.4
Branches												
Carbon %	42.3	44.1	43.1	43.8	42.3	46.0	45.1	43.7	43.9	44.7	44.9	47.6
Nitrogen %	0.4	0.4	0.3	0.2	0.4	0.4	0.3	0.3	0.3	0.4	0.4	0.3
Lignin %	29.8	25.9	30.1	30.8	30.2	33.5	31.9	29	31.3	34.7	38.8	36.2
C:N	109	116	166	183	108	132	173	137	151	115	121	153
Lignin:N	76	68	116	128	77	96	123	91	108	89	105	117
Roots												
Carbon %	43.0	42.6	43.4	44.6	44.3	44.8	42.8	42.6	42.5	44.3	43.4	44.9
Nitrogen %	1.2	1.1	1.2	1.1	1.1	1.3	1.3	1.3	1.4	1.5	1.6	1.6
Lignin %	34.5	39.3	32	39.9	38.4	43	35.2	40	34	37.3	34.9	44.9
C:N	36.7	38.0	36.2	40.6	39.9	34.5	34.0	33.0	30.0	29.5	26.6	27.9
Lignin:N	29.5	35.1	26.7	36.3	34.6	33.1	27.9	31.0	23.9	24.9	21.4	27.9

hemicellulose, and highly recalcitrant material like lignin (Verhoeven 1986). Tropical conditions should favor the rapid decomposition of all easily decomposable material, leaving behind mostly recalcitrant lignin as peat. Although there has been very little work in this area, there is some evidence that peat formed in warmer climates is more recalcitrant than peat formed in colder areas (Driessen and Rochimah 1976 as cited in Anderson 1983; Harden and Polak 1941 as cited in Andriesse 1988; Bridgham and Richardson 1992; Yavitt et al. 1997; Bridgham et al. 1998). Our data support this hypothesis: we also measured high concentrations of lignin in our peat samples.

Management implications

We found that Micronesian tropical peatlands accumulate peat not because of high plant production but rather because of slow decomposition of roots and wood. Their slow decomposition rates result from anaerobic conditions due to high water levels and poor drainage (Chimner and Ewel 2004; Allen et al. unpublished MS). Peatlands are the most widespread and numerous of all wetland types and can form under almost any climate regime if supplied with the proper hydrologic conditions. However, they are susceptible to changes in their hydrology (e.g., Chimner and Cooper 2003), and both human modification and climate change could affect hydrology in Micronesian peatlands. Farming and agroforestry are major land uses of peatlands in the tropics, with Kosrae being no exception, as about 97% of the households in Kosrae cultivate taro in wetlands (Drew et al. unpublished MS). However, we found that peat loss was likely to be slower in a Micronesian taro patch because natural hydrological conditions were maintained (Chimner and Ewel in press). The naturally high water tables in the taro patch maintained similar water chemistry, soil temperatures, decomposition rates, and soil respiration compared to an adjacent forested peatland (Yewak). In addition, any alterations to the peatlands caused by taro cultivation would probably not be permanent, because taro patches are periodically abandoned and left fallow for a few years. Thus we conclude that traditional taro cultivation is probably not a major threat to the peatlands.

Changes in climate could pose a threat to the sustainability of these wetlands. Temperature is not likely to be important, even if changes did occur at this tropical location, because decomposition was limited by anaerobic conditions and poor substrate quality, neither of which would be affected by increasing temperature. However, peat accumulation could be affected by changes in precipitation, which could alter the hydrologic regime of the peatlands. For example, water levels in Yela dropped up to 0.5 m for 6 month during the 1997–1998 ENSO-related drought (Drexler and Ewel 2001). Water table declines of this duration and magnitude could cause a significant loss of peat in these peatlands, suggesting that increased frequency of ENSO events could threaten the long-term integrity of these wetlands.

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