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The Relationships among Community Type, Peat Layer Thickness, Belowground Carbon Storage and Habitat Age of Mangrove Forests in Pohnpei Island, Micronesia

Kiyoshi Fujimoto[1*], Yukira Mochida[2], Takao Kikuchi[2], Ryuichi Tabuchi[3], Yasumasa Hirata[3], Saimon Lihpai[4]

[1]Faculty of Policy Studies, Nanzan University, Seto, Japan
[2]Graduate School of Environmental and Information Sciences, Yokohama National University, Yokohama, Japan
[3]Forestry and Forest Products Research Institute, Tsukuba, Japan
[4]Division of Forestry and Marine Enforcement, Department of Land & Natural Resources, Pohnpei State Government, Kolonia, The Federated States of Micronesia
Email: *kfuji@nanzan-u.ac.jp

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Abstract

This paper quantifies the relationships among community type, peat layer thickness and habitat age of the mangrove forests in Pohnpei Island, Micronesia and provides a discussion concerning the primary succession and the belowground carbon storage of the main mangrove community types. The ages of the habitat were estimated from a relationship between the thickness of the mangrove peat layer and the formative period, which was decided by calibrated radiocarbon ages. Mangrove communities in the coral reef type habitat were generally arranged in the following order, from seaward to landward: 1) the *Rhizophora stylosa* or *Sonneratia alba* community (I or II communities), 2) the typical subunit of the *S. alba* subcommunity of the *Rhizophora apiculata*—*Bruguiera gymnorrhiza* community (III(2)a subunit) and 3) the *Xylocarpus granatum* subunit of the same subcommunity of the same community (III(2)b subunit). Their habitat ages were estimated to be younger than 460 years, between 360 and 1070 years and between 860 and 2300 years, respectively. Based on these results and other evidences such as photosynthetic characteristics and pollen analysis derived from the previous studies, the primary succession was inferred to have progressed in the order mentioned above. Belowground stored carbon for the main community types in the coral reef type habitat were estimated to be less than 370 t C ha^{-1} for the I and the II communities, between 290 and 860 t C ha^{-1} for the III(2)a subunit and between 700 and

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[*]Corresponding author.

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1850 t C ha⁻¹ for the III(2)b subunit.

Keywords

Mangrove Forest, Community Type, Habitat Age, Belowground Carbon Storage, Primary Succession

1. Introduction

The mangrove forests on Pohnpei Island, in the Federated States of Micronesia, have not significantly suffered from human impact. This means that a clear zonation of mangrove communities can be found on the Island.

An overview of the mangrove forests in Pohnpei that describes their spatial distribution, total area and timber volume was provided by the USDA Forest Service (e.g. MacLean et al., 1986; Petteys et al., 1986). On the other hand, we have studied formative processes of mangrove habitats to predict the effects of anticipated rapid sea-level rise induced by global warming (e.g. Miyagi & Fujimoto, 1989; Kikuchi, 1995) and also elucidated forest structure, dynamics, biomass, productivity, and carbon storage abilities of mangrove forests across different habitat types on five permanent plots of 0.1 to 1 ha (e.g. Fujimoto et al., 1995b, 1999b, 2013; Tabuchi, 2006).

Through these studies, we have accumulated the phytosociological data necessary to classify community types, as well as the geomorphological data necessary to estimate the peat depth and habitat age. We also discussed the successional trends using the data obtained before 1993 to describe the relationship between community types and peat depth in relation to rise in sea-level (Kikuchi et al., 1999).

This paper clarifies the relationships among community type, thickness of the mangrove peat layer and habitat age using our recent data along with the data used in Kikuchi et al. (1999). In this paper "Habitat age" is defined as the number of years that have elapsed since pioneer mangrove species colonized a site. Although the relationship between mangrove vegetation and site environments such as geomorphological conditions and physiological adaptations to physico-chemical gradients has been discussed extensively (e.g. Thom, 1967; Ball, 1988), the ages of habitats with different community types is unknown.

The results of this study will contribute to the discussion on the successional series of mangrove forests in the Pacific region and estimate the spatial distribution of stored belowground carbon as well as aboveground. The relationship between belowground carbon storage and community type was not clarified in our previous study (Fujimoto et al., 1999b), though the general value of the coral reef type habitat was discussed. In this paper we also discuss primary succession and the stored belowground carbon per unit area for each main community type.

2. Study Area and Methods

Pohnpei is a high oceanic island of about 35,500 ha that consists of Tertiary volcanic rocks and is surrounded by barrier reefs. Annual rainfall is approximately 5000 to 6000 mm, with no apparent dry season. The annual mean temperature is 26.4˚C and the annual variation is not more than 1˚C from the mean temperature. Mean tidal range at Pohnpei Harbor is about 70 cm, and the maximum spring tidal range is approximately 150 cm.

Mangrove habitats develop mainly on the reef flats fringing the island, although some of them are situated in estuaries (**Figure 1**). This creates two main habitat types, with the former habitat referred to as the coral reef type and the latter as the estuary type. The substrata of these mangrove habitats mainly consist of peat (Miyagi & Fujimoto, 1989; Fujimoto et al., 1995a, 1995b). Based on phytosociological method, the mangrove forests in Pohnpei have been classified into three community types, along with six subcommunities and five subunits, by Mochida et al. (2006) as follows.

I. *Rhizophora stylosa* community
  (1) Typical subcommunity
  (2) *Enhalus acoroides* subcommunity
  (3) *Bruguiera gymnorrhiza* subcommunity
II. *Sonneratia alba* community

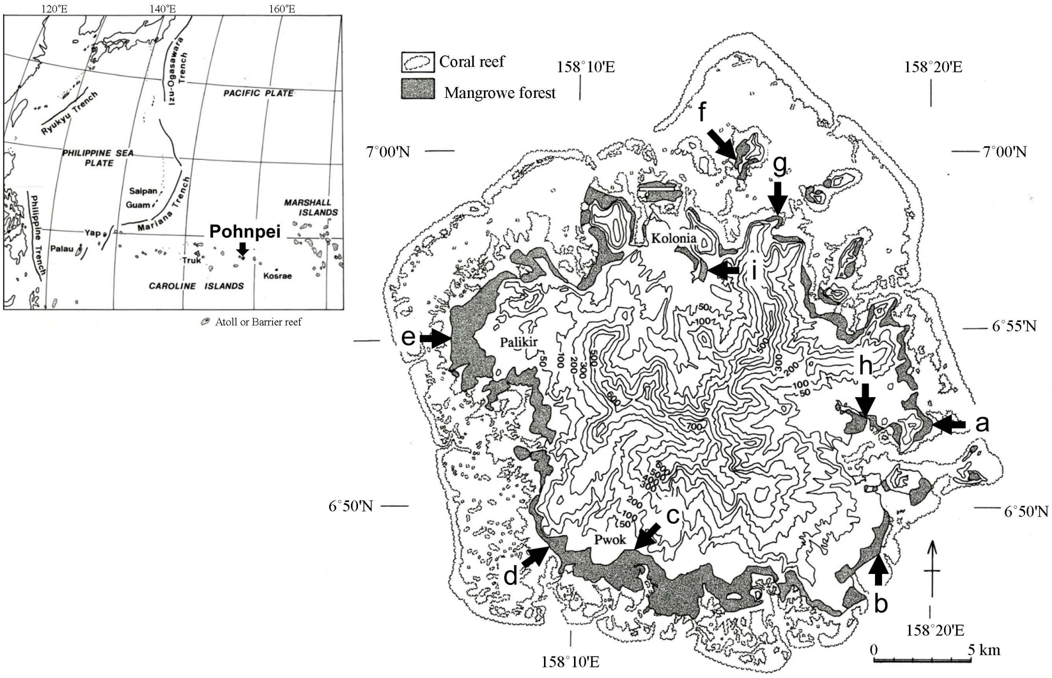

Figure 1. Map showing the study areas and location of transects.

III. *Rhizophora apiculate*—*Bruguiera gymnorrhiza* community
  (1) Typical subcommunity
  (2) *Sonneratia alba* subcommunity
    a) Typical subunit;
    b) *Xylocarpus granatum* subunit;
    c) *Lumnitzera littorea* subunit.
  (3) *Xylocarpus granatum*—*Heritiera littoraris* subcommunity
    a) Typical subunit;
    b) *Barringtonia racemosa* subunit.

In this paper we use a simple coding system to describe the community types, for example; I(1) describes the typical subcommunity of the *R. stylosa* community and III(2)a indicates the typical subunit of the *S. alba* subcommunity of the *Rhizophora apiculata*—*Bruguiera gymnorrhiza* community.

The relationship among vegetation, sediment and topography was examined for nine transects. Seven transects were situated in the coral reef type habitat and two were in the estuary type habitat (**Figure 1**). Four transects were along a line of permanent plots established in 1994, 2002 and 2003 (Fujimoto et al., 1995b; Tabuchi, 2006). Transects a to e, h and I, which were examined between 1988 and 1993, have been described in our previous publications (Fujimoto et al., 1995a, 1995b; Miyagi & Fujimoto, 1989; Miyagi et al., 1995). The topography along the transects was surveyed using a pocket compass with a level. A hiller-type peat sampler was used to examine sediments and to collect the samples for radiocarbon dating. The results were compiled in **Figure 2** and **Figure 3**.

Radiocarbon ages obtained from mangrove peat in our previous studies, as well as from lower tidal-flat deposits that were overlain by mangrove peat, were calibrated to calendar year using CALIB 7.0 (**Table 1**). A standard δ^{13}C value of mangrove plant bodies of −27‰ ± 3‰ (e.g. Fujimoto et al., 1999a, 1999b) was applied to calibrate for the samples that had not obtained a δ^{13}C value. The calibrated ages were obtained from a 50-year moving-average calibration curve.

The habitat age was then estimated from a resemble equation showing the relationship between the thickness of the mangrove peat and the formative period decided by the calibrated ages.

The stored belowground carbon for each main mangrove community was estimated using the data obtained from Fujimoto et al. (1999b), as well as the relationship between community type and the peat depth.

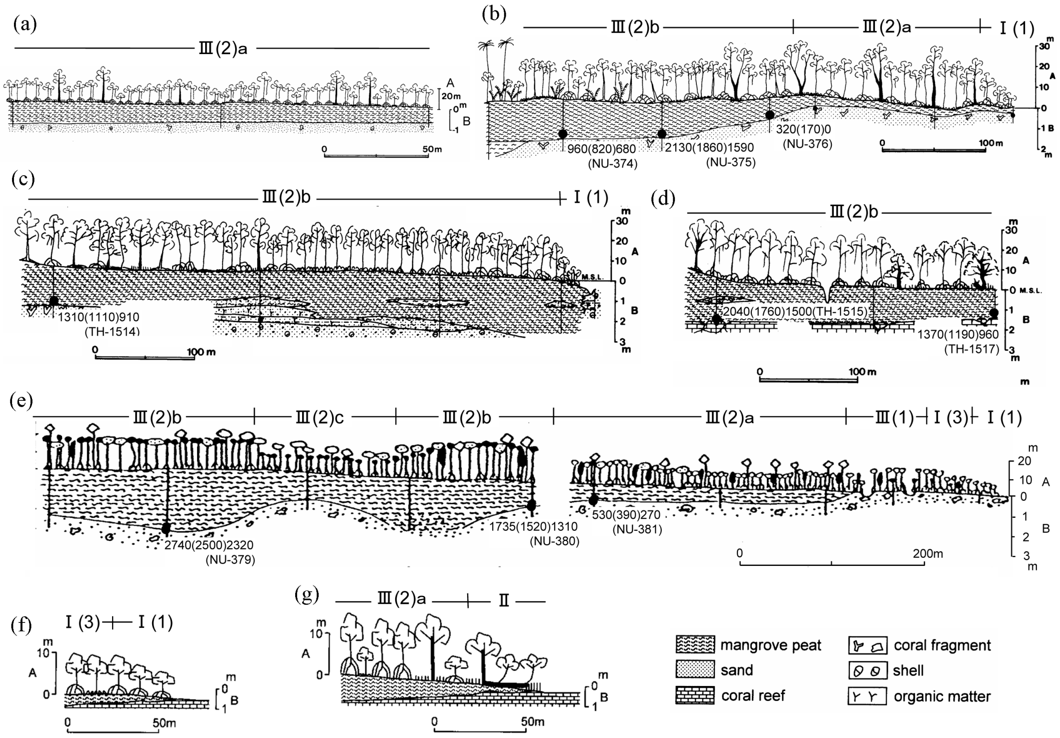

Figure 2. Community type, landform and sediments along transects in the coral reef type habitat. (a) Revised Fujimoto et al. (1995b); (b) Revised Fujimoto et al. (1995a); (c) (d) Revised Miyagi & Fujimoto (1989); (e) Revised Miyagi et al. (1995); (f) (g) This study. A: Scale for representing tree height, B: Vertical scale for to represent the topographic and geologic profile.

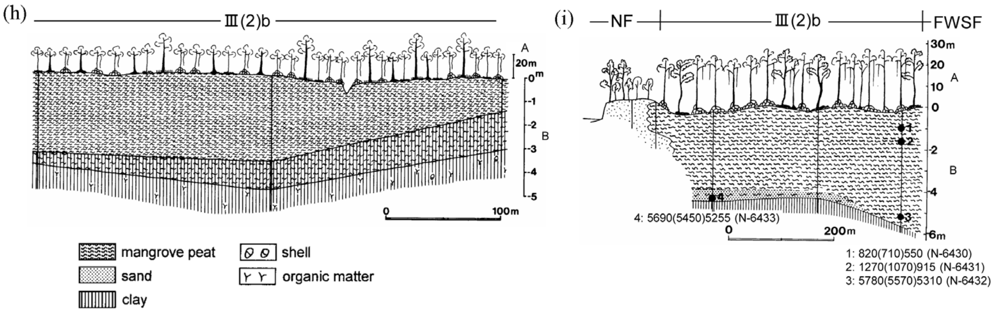

Figure 3. Community type, landform and sediments along transects in the estuary type habitat. (h) Revised Fujimoto et al. (1995b); (i) Revised Fujimoto et al. (1995a). A: Scale for representing tree height, B: vertical scale to represent the topographic and geologic profile, NF: Natural levee forest, FWSF: Freshwater swamp forest.

3. Results

3.1. Characteristics of Community Types along Transects

Of the community types described by Mochida et al. (2006), seven were found along the transects. These community types were:I(1) subcommunity, I(3) subcommunity, II community, III(1) subcommunity, III(2)a subunit, III(2)b subunit and III(2)c subunit (**Figure 2** & **Figure 3**).

The I(1) subcommunity developed along the seaward edge of the coral reef type habitat. It was 15 to 50 m in depth (**Figures 2(b)-(f)**) and was characterized by a tree height of less than 10 m and a high density of prop roots. The II community rarely appeared along the seaward edge of the coral reef type habitat, which was 10 to 20 m in depth (**Figure 2(g)**) and was characterized by prostrate trees and a high density of pneumatophores. The III(1) subcommunity appeared behind the I(3) subcommunity (**Figure 2(e)**). The III(2)a subunit usually

Table 1. Radiocarbon ages obtained from the mangrove peat and the lower tidal-flat deposit on Pohnpei, Micronesia.

Lob. Code	Depth (cm)	Measuredage (^{14}C BP, $\pm 1\sigma$)	Conventional age (^{14}C BP, $\pm 1\sigma$)	2σ calibrated age (cal BP)	Sampled year (AD)	Formative period (years)	Mean depth (cm)	Accumulation rate (mm/yr)
IAAA-102139[1]	80 - 85	350 ± 20	320 ± 30	460-(390)-310	2010	450	82.5	1.8
NU-374[2]	180 - 190	930 ± 80	900 ± 90	960-(820)-680	1990	860	185	2.2
NU-375[2]	170 - 180	1950 ± 100	1920 ± 110	2130-(1860)-1590	1990	1900	175	0.9
NU-376[2]	93 - 107	190 ± 70	160 ± 85	420-390, 320-(170)-0	1990	210	100	4.8
NU-379[3]	270 - 285	2450 ± 80	2420 ± 90	2740-(2500)-2320	1991	2541	277.5	1.1
NU-380[3]	130 - 140	1650 ± 90	1620 ± 100	1735-(1520)-1310	1991	1561	135	0.9
NU-381[3]	80 - 90	370 ± 70	340 ± 85	530-(390)-270, 200-150, 10-0	1991	431	85	2.0
NU-382[4]	90 - 100	270 ± 70	240 ± 85	480-(270)-70, 40-0	1991	311	95	3.1
NU-383[4]	155 - 170	1590 ± 120	1560 ± 130	1790-1770, 1765-(1470)-1260	1991	1511	162.5	1.1
NU-901[5]	110 - 125	1380 ± 95	1350 ± 110	1500-1450, 1440-(1260)-1030, 1020-1000	1997	1307	117.5	0.9
NU-902[5]	193 - 208	1800 ± 95	1770 ± 110	1920-(1690)-1420	1997	1737	200.5	1.2
TH-1514[6]	175 - 200	1210 ± 100	1180 ± 110	1310-(1110)-910	1988	1148	187.5	1.6
TH-1515[6]	204 - 219	1860 ± 110	1830 ± 120	2040-(1760)-1500, 1465-1430	1988	1798	211.5	1.2
TH-1517[6]	125 - 150	1310 ± 100	1280 ± 110	1370-(1190)-960	1988	1228	137.5	1.1
N-6428[7]	90 - 120	740 ± 80	710 ± 90	810-(660)-525	1992	702	105	1.5
N-6429[7]	150 - 180	720 ± 80	690 ± 90	780-(650)-520	1992	692	165	2.4
N-6430[2]	90 - 120	790 ± 80	760 ± 90	900-850, 840-830, 820-(710)-550	1992	752	105	1.4
N-6431[2]	150 - 180	1170 ± 80	1140 ± 90	1270-(1070)-915	1992	1112	165	1.5
*N-6432[2]	520 - 550	4870 ± 115	4840 ± 125	5890-5790, 5780-(5570)-5310	1992	-	-	-
*N-6433[2]	390 - 420	4760 ± 95	4730 ± 110	5690-(5450)-5255, 5180-5060	1992	-	-	-
**IAAA-120353[1]	310 - 320	2580 ± 30	2550 ± 30	2750-(2710)-2690, 2640-2510	2011	-	-	-
**Beta-98286[5]	330 - 360	2610 ± 60	2570 ± 60	2790-(2640)-2450	1997	-	-	-
**Beta-98287[5]	450 - 480	3240 ± 60	3200 ± 60	3575-(3430)-3320, 3290-3280	1997	-	-	-
**Beta-98288[5]	270 - 300	3090 ± 70	3050 ± 70	3410-(3260)-3045	1997	-	-	-

[1] This study, [2] After Fujimoto et al. (1995a), [3] After Miyagi et al. (1995), [4] After Omoto (1997), [5] After Fujimoto et al. (1999b), [6] After Miyagi & Fujimoto (1989), [7] Fujimoto et al. (unpublished). *Samples obtained from bottom horizon of a mangrove peat layer in an estuary type mangrove habitat, **Samples obtained from lower tidal-flat deposits. Value in parenthesis in the calibrated age shows a median probability.

appeared behind the I and II communities (**Figure 2(b)**, **Figure 2(e)** & **Figure 2(g)**). The III(2)b subunit, which occupied the widest area of the mangrove forests in Pohnpei, generally appeared behind the III(2)a subunit in coral reef type habitats (**Figures 2(b)-(e)**) and in estuary type habitats (**Figure 3**). The III(2)c subunit generally appeared on the inland side of mangrove forests (**Figure 2(e)**).

3.2. Relationships between Community Type and the Thickness of the Mangrove Peat Layer

Figure 4 shows the distribution of peat depth under the main community types obtained from the coral reef type habitat. The peat depth of the I(1) subcommunity and the II community was usually less than 50 cm (**Figure 2(b)**, **Figures 2(e)-(g)** & **Figure 4**). The I(3) subcommunity stood on about a 55 cm deep of mangrove peat layer, though only three points were measured (**Figure 4**). While the thickness of the peat layer under the III(2)a subunit was between 45 and 133 cm (**Figure 2(a)**, **Figure 2(b)**, **Figure 2(e)**, **Figure 2(g)** & **Figure 4**), under the III(2)b subunit it was between 107 and 285 cm (**Figures 2(b)-(e)** & **Figure 4**). The peat layer under the III(2)c subunit on Transect c was 138 cm, which was thinner than the III(2)b subunit along the same transect (**Figure 2(c)** & **Figure 4**). The peaty layer of the estuary type habitat, which was generally covered by the III(2)b subunit except on river banks, ranged from 300 to 500 cm deep (**Figure 3**).

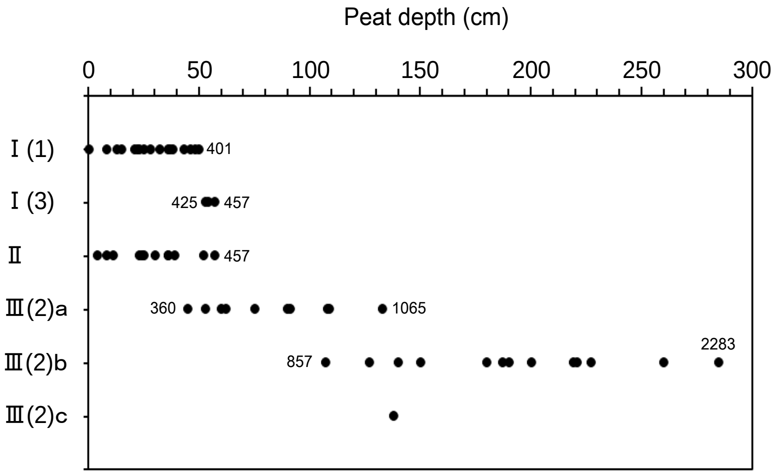

Figure 4. Range of peat depth under the main community types of the coral reef type habitat. Values in the figure show the minimum and maximum habitat ages (years) obtained from the equation in **Figure 5**.

4. Discussion

4.1. Relationship between the Thickness of Mangrove Peat and the Formative Period

In Kosrae Island, Micronesia, which is located about 550 km east of Pohnpei, mangrove forests inhabited estuaries only before 2100 ^{14}C BP (2100 cal BP) and retreated landward between 4100 and 3800 ^{14}C BP (between 4500 and 4200 cal BP) because of a rapid sea-level rise (Fujimoto et al., 1996). The sea level reached relatively high stand around 3700 ^{14}C BP (4100 cal BP) before the last lower sea-level phase around 2100 ^{14}C BP. Mangrove forests expanded on coral reefs by 2100 ^{14}C BP with the sea-level fall. Although the sea level has gradually risen over the past 2100 years, the habitats have been maintained by an accumulating of mangrove peat.

In Pohnpei, calibrated ages older than 2500 cal BP have not been obtained from mangrove peat in coral reef type habitats (**Table 1** & **Figure 2**). However, ages around 5500 cal BP and between 3400 and 2600 cal BP were obtained from the bottom horizon of mangrove peat and from the lower tidal-flat deposits overlain by mangrove peat in estuary type habitats (**Figure 3**), respectively. This evidence suggests that the pattern of sea-level changes and mangrove habitat dynamics on Pohnpei are the same as on Kosrae, and that coral reef type mangrove forests did not exist there before 2500 cal BP, although mangrove forests did inhabit estuaries. Therefore, on Pohnpei, the relationship between the thickness of the mangrove peat and the formative period can only be analyzed for the last 2500 years.

Previous studies have demonstrated that, despite a gradual sea-level rise of 1 to 2 mm yr^{-1}, most mangrove habitats with peat substrates in the Asia-Pacific region have been maintained during the last 2000 years by accumulating peat (Fujimoto et al., 1995a, 1996, 1999a). Therefore, mangrove peat accumulation rates indicating over 2 mm yr^{-1} are possibly contaminated by younger carbon through processes such as root penetration. **Figure 5** shows the relationship between the sampling depth of mangrove peat for radiocarbon dating and the calibrated age during the last 2500 years. The two outliers, NU-376 and NU-382, were rejected by a Smirnov-Grubbs test ($p < 0.05$) using EZR downloaded from the web site of Jichi Medical University (http://www.jichi.ac.jp/saitama-sct/SaitamaHP.files/download.html). The peat accumulation rate may have varied during the last 2500 years depending on the changes of the rate of relative sea-level rise. However, it is difficult to understand the changes using existing data. Thus, we approximated the relationship between the thickness of mangrove peat and the formative period by a linear expression to estimate habitat age.

4.2. Relationship between Community Type, Habitat Age and Succession

Mangrove communities in the coral reef type habitat in Pohnpei are generally arranged in the following order, from seaward to landward:1) the I or the II community, 2) the III(2)a subunit and 3) the III(2)b subunit. Using the equation in **Figure 5**, habitat ages of the I(1) subcommunity, the I(3) subcommunity, the II community,

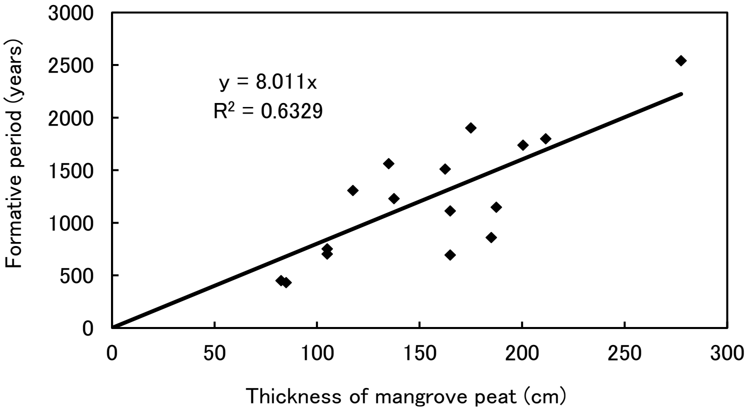

Figure 5. Relationship between the thickness of the mangrove peat layer and the formative period in Pohnpei, Micronesia.

the III(2)a subunit and the III(2)b subunit were estimated to be younger than 400 years, between 430 and 460 years, younger than 460 years, between 360 and 1070 years and between 860 and 2280 years, respectively (**Figure 4**).

These results suggest that the primary succession of mangrove forest in Pohnpei has progressed in the order mentioned above, along with a relative rise in the ground level as a result of peat accumulation. The results also suggest that it took about 400 years and 1000 years for the formation of the III(2)a subunit and the III(2)b subunit, respectively.

If the peat accumulation rate has equilibrated with the rate in the rise in sea level, the succession may not have proceeded even if enough time has elapsed. During the last 1000 years, the ground level has relatively risen as a result of peat accumulation; consequently allowing succession to progress, though succession is affected not only by changes in sea level but also various other factors such as seed supply and photo-environment.

Imanishi & Kira (1944) inferred almost the same primary successional series as mentioned above based on the arrangement of community types. However, they placed the *S. alba* dominant forest, which, judging from their description, seems to include the II community and the III(2)a subunit, between the *R. stylosa*-*R. apiculata* forest (corresponding to the I community) and the *X. granatum*-*S. alba*-*B. gymnorrhiza* forest (corresponding to the III(2)b subunit). Kikuchi et al. (1999) also described nearly the same successional trends as mentioned above, though the *S. alba* community was not recognized.

Studies analyzing different variables, such as forest dynamics, photosynthetic characteristics and pollen analysis, are needed to reinforce the discussion concerning the mangrove successional series. We established permanent plots in Pohnpei mangrove forests and have monitored forest dynamics since 1994 in order to ascertain the successional characteristics of these forests (Fujimoto et al., 1995b, 2013; Tabuchi, 2006). On the other hand, Kitao et al. (2003) found that the light-saturated electron transport rate was higher in *S. alba* and *R. stylosa* > *R. apiculata* and *B. gymnorrhiza* > *X. granatum*. Additionally, the tolerant capacity for photo-inhibition was higher in *S. alba* and *R. stylosa* > *R. apiculata* > *B. gymnorrhiza* and *X. granatum*. These results support the successional series mentioned above. Moreover, Yamanaka & Kikuchi (1995) reported that the pollen density of *Sonneratia* was relatively high throughout the peat layer except immediately at the surface and that the pollen density of Rhizophoraceae gradually increased toward the surface of the peat layer, with a final and rapid increase at the surface. This was found in a boring core obtained from the landward part of Transect i, although it was impossible to identify the pollen at genus or species level for Rhizophoraceae. Nevertheless, the results are consistent with this study's inference on succession.

The differences of formative initial conditions between the I and the II communities and the formative processes of the III(2)c subunit are not yet clear. Further studies are needed to fully understand these problems.

4.3. Belowground Carbon Storage for the Main Community Types

The clear relationship between community type and peat depth enables us to estimate the stored belowground carbon per unit area for each community type using the results of Fujimoto et al. (1999b), a value of 1300 t C ha^{-1} up to 2 m depth of mangrove peat in the coral reef type habitat in Pohnpei, and the known peat depth for each community type.

The peat depths are less than 57 cm for the Iand the II communities, 45 to 133 cm for the III(2)a subunit and 107 to 285 cm for the III(2)b subunit (**Figure 4**). A significant difference in stored carbon related to peat depth was not recognized up to a depth of 2 m (Fujimoto et al., 1999b). Therefore, assuming that there is a linear relation between peat depth and stored carbon, the belowground carbon of main community types in the coral reef type habitat are estimated to be less than 370 t C ha^{-1} for the I and the II communities, between 290 and 860 t C ha^{-1} for the III(2)a subunit and between 700 and 1850 t C ha^{-1} for the III(2)b subunit. The stored carbon in the estuary type habitat is estimated at about 2200 t C ha^{-1}. This was found by extrapolating and averaging the data obtained from two boring cores in Fujimoto et al. (1999b), which were 1771 t C ha^{-1} (365 cm deep) for a riverward site and 2116 t C ha^{-1} (347 cm deep) for a landward site. These calculations assume that the mean depth of the peaty layer is 4 m and that the lowest layer in these boring cores continues to a depth of 4 m.

5. Conclusion

This study clarified the relationship among community type, peat layer thickness, and habitat age of the mangrove forests in Pohnpei Island, Micronesia using the phytosociological and geomorphological data accumulated since 1988. This result enabled us to estimate the belowground carbon storage of the main mangrove community types and to discuss the primary succession and the approximate time required for the mangrove forests on Pacific islands in tropics. Analysis of the high-resolution satellite images such as QuickBird will enable us to estimate the spatial distribution of the main mangrove community types and, consequently, to quantify the belowground carbon storage using the results of this study as well as the aboveground.

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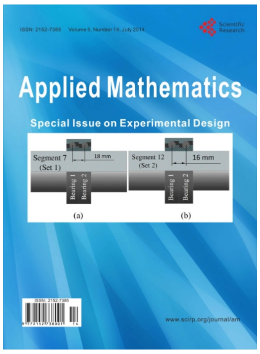
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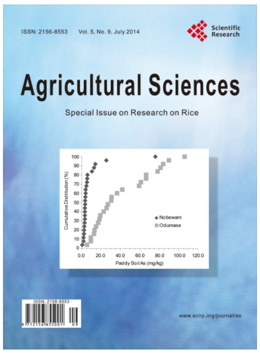
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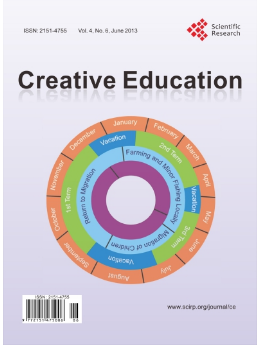
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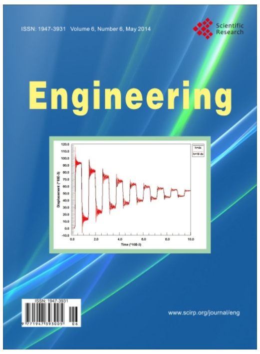
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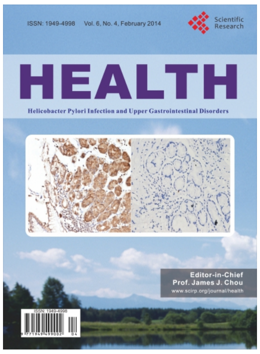
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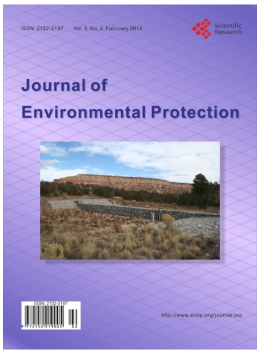
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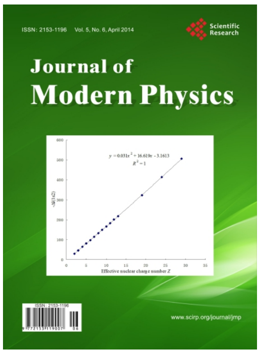
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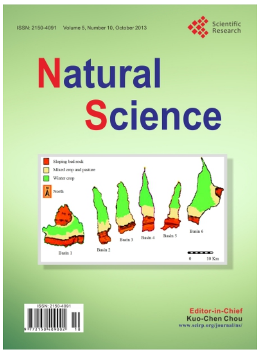
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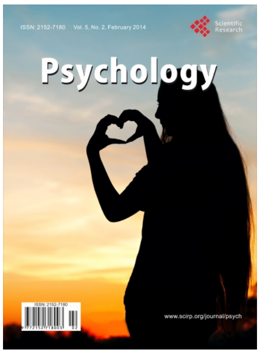
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