

Article

Spatiotemporal Heterogeneity of Mangrove Root Sphere under a Tropical Monsoon Climate in Eastern Thailand

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Abstract: Mangrove ecosystems under tropical monsoon climates experience changes in environmental factors, especially seasonal variations in salinity. These changes might have direct influences on the mangrove root sphere, which plays an important role in carbon dynamics and supports mangrove growth. We aimed to elucidate how the soil properties including salinity and nutrient budget affect the mangrove roots in the wet and dry seasons across the mangrove zonation (*Avicennia*, *Rhizophora*, and *Xylocarpus* zones). This area is in a secondary forest at the Trat River estuary, eastern Thailand. Root mass was observed at 0–10 and 10–20 cm depths across all zones and the living roots were separated into diameter classes. The soil water salinity was measured at a 10 cm depth. We analyzed the nitrogen, phosphorus, and carbon contents in the roots and soil. Spatiotemporal changes occurred due to the vegetation zonation and the variations in salinity and the content of soil available phosphorus that caused different root sphere conditions along the distance from the river. The highest root biomass was found in the riverward *Avicennia* zone, which was 4.8 times higher than that of the inland *Xylocarpus* zone in the wet season. The root necromass distribution along the zonation showed an opposite trend to that of biomass. Among seasons, the root size-class proportion differed, with high fine roots observed during the wet season. We confirmed that the root sphere showed both spatial and temporal heterogeneity. Mangrove roots, especially fine roots, interacted with changing salinity, inundation regime, and biological processes evoked by microtopographic gradients as a consequence of mangrove zonation and seasonal rainfall. Our findings indicate how the root sphere differed by specific vegetation structure in this mangrove forest. Therefore, these might provide an ecological perspective for the mangrove rehabilitation plans to facilitate below-ground carbon stock.

Keywords: root biomass; necromass; salinity; seasonality; zonation; tropical mangrove; secondary mangrove

1. Introduction

Mangrove ecosystems have been considered to be carbon-rich ecosystems with the capacity for potentially long-term carbon storage based on their high productivity [1–3]. A considerable amount of carbon is allocated in mangrove root systems [4,5], which is known as the ‘bottom-heavy tree form’ [6], with a high ratio of root to shoot biomass [7–9]. A large amount of root biomass functions to support overall plant growth mechanically and physiologically in muddy and waterlogged soil conditions [10], maximizing water uptake [1], and increasing nutrient acquisition under saline and low-nutrient conditions [11–13]. Mangrove roots are an important source of organic matter in soils [14], with approximately 7% of the total organic carbon within 1 m-deep soil contributed by mangrove root biomass and necromass, as reported by Alongi [2]. A large fraction of root necromass and organic matter exists

in the soil because of low decomposition and waterlogged conditions [15,16]. However, mangrove forests have been threatened by climate change (i.e., sea level rise, changing salinity regimes) [17], meaning that the ecological processes and nutrient cycling in mangrove forests may be disrupted. Under climate change, the mangrove forests showed resilience to changing environments, especially the response of below-ground components [18,19].

Mangrove vegetation has a heterogeneous forest structure called zonation due to various environmental gradients [20–24]. Secondary mangrove forests also present mangrove zonation under the influences of environmental gradients [25,26]; however, the development of distinct zonation in the rehabilitated mangrove forests may take several decades [27]. The topography and elevation of the forest floor affect mangrove zonation, which is related to variations in inundation and salinity regimes [28]. The different inundation periods cause variations in the salinity regimes in the intertidal zone [29,30]. Therefore, salinity regimes must be profoundly considered at spatial and temporal scales since they directly influence the root sphere in mangrove ecosystems. However, few studies have examined the relationship between the quantitative traits of roots and changes in the environment, including changes in salinity regimes, across mangrove zonation.

During the last two decades, a series of mangrove studies, in particular on productivity and carbon dynamics, have been conducted by our research team in a secondary mangrove forest in eastern Thailand under a tropical monsoon climate. At this study site, distinct vegetation zones have been reported, with the dominant tree species being *Avicennia alba*, *Rhizophora* spp., and *Xylocarpus granatum* located from the riverside of the Trat River towards inland areas [31–33]. Several research projects have been simultaneously conducted, including those on overall forest productivity [34,35], inundation period [33], and salinity regimes [30,36]. Besides these studies, Bukoski et al. [37] recently estimated the carbon stock of mangrove forest in eastern Thailand by using the predictive models. These findings have revealed that productivity and carbon fluxes in each compartment of this mangrove forest (i.e., above-ground biomass, coarse woody debris, fine root production, and soil respiration) vary among vegetation zones, possibly because of differentiated salinity regimes across the zones from the riverside to inland areas. The spatiotemporal patterns of root quantitative traits at this site have not been studied in association with changes in environmental regimes. This information will be important supportive data for improving the mangrove rehabilitation approaches in such a sustainable way that mangrove afforestation can function as a carbon stock, similar to the natural mangrove forests.

Under tropical monsoon climates, mangrove productivity has been studied in regard to environmental factors, for example, seasonal patterns of precipitation and salinity [38], low salinity conditions during the wet season [39,40], and the contents of nitrogen (N) or phosphorus (P) [41,42]. Regarding seasonal variation, large nutrient fluxes usually occur during the wet season in tropical estuarine areas [43]. The roles of P have shown that soil with relatively low P concentration increases fine root biomass in Florida mangroves [8] and in Micronesian mangroves [44]. Lovelock et al. [45] suggested that soil P increases hydraulic conductivity under high salinity conditions, supporting mangrove growth. However, nutrient limitation in mangrove forests is too complex to assess according to both spatial and temporal variations [22,46].

The objectives of this study are: (1) to examine the root biomass and necromass distribution across three vegetation zones in a mangrove forest with distinct dry and wet seasons, and (2) to investigate the spatiotemporal heterogeneity occurring in the root sphere including salinity and nutrient conditions and nutrient contents in mangrove root tissues. We discussed the relationship between heterogeneity and root distribution in each mangrove forest zone based on variations in environmental regimes. In addition, we recommended the implications for mangrove rehabilitation based on our findings.

2. Materials and Methods

2.1. Study Site

This study was conducted in an estuarine mangrove forest in Trat Province, eastern Thailand (12°12' N, 102°33' E, Figure 1a); this mangrove forest is fed by the Trat River, which flows into the Gulf of Thailand. The local community utilized this forest for selective logging until the government prohibited it in the late 1980s. As a result, the forest has been naturally rehabilitated over 30 years and transformed into a secondary mangrove forest providing local fisheries for the local community [32]. This site has a single daily tide with an average range from 0.5 to 2.6 m (recorded in 2018, Hydrographic Department of the Royal Thai Navy). The study site has a tropical monsoon climate with a mean air temperature of 27.6 °C and a mean annual rainfall of 4880 mm. Five months during the wet season (May to October during 2008–2017) received 87.2% of annual rainfall (at the Klong Yai Weather Station, Meteorological Department of Thailand, located approximately 50 km from the study site).

A permanent study plot was established in 2004 with an area of 50 × 120 m². The forest structure consists of various mangrove species that shows zonation in regard to the dominant tree species. This zonation occurs from the riverside to inland areas and includes the *Avicennia*, *Rhizophora*, and *Xylocarpus* zones [30,32] as shown in Figure 1b. The dominant tree species in each zone contributed the highest proportion of basal area (BA) to the total BA of all trees recorded in that zone. The riverside *Avicennia* zone (0–40 m) was dominated mainly by *Avicennia alba*, accounting for 63.4% of the total BA. For the *Rhizophora* zone (40–100 m), *Rhizophora apiculata* and *R. mucronata* were the dominant species accounting for 76.0% of the total BA. The inland *Xylocarpus* zone (100–120 m) was mainly composed of *Xylocarpus granatum*, accounting for 59.5% of the total BA (unpublished data). Above-ground biomass was estimated using a common allometric equation as 169.9, 259.2, and 227.0 ton·ha^{−1} in the *Avicennia*, *Rhizophora*, and *Xylocarpus* zones, respectively [32].

The relative elevation of the forest floor was reported by Umnouysin et al. [33], who noted that in regard to the topographic gradient, relative elevation increases towards the inland zone (Figure 1b). The average elevation compared with the datum point is 33 ± 8 cm in the riverside *Avicennia* zone, 48 ± 12 cm in the *Rhizophora* zone, and 65 ± 12 cm in the most inland *Xylocarpus* zone [33]. As a result of the elevational gradient, the inundation period is longer in the riverside area, with average inundation periods of 12.8, 9.3, and 2.3 h in the *Avicennia*, *Rhizophora*, and *Xylocarpus* zones, respectively [32].

2.2. Root and Soil Sampling

The two transect lines were established from the river to inland areas along a 120 m distance (Figure 1b) and showed a gradual increase in landward surface elevation [30,33]. In total, 18 sampling points were selected on the two transect lines, consisting of six in the *Avicennia* zone, eight in the *Rhizophora* zone, and four in the *Xylocarpus* zone. At each point, two connected soil blocks (10 × 10 cm² in area and 0–10 and 10–20 cm in depth) were collected for root and soil analysis. Simultaneously, approximately 20 mL of soil water was collected at a 10 cm depth using a syringe with a porous cup, and the salinity was measured by using a salinometer (YK-31SA, SatoTech, Kawasaki, Japan). Root and soil sampling was conducted during the dry season (25 March 2018) and wet season (18–19 July 2018). All samples were stored in a refrigerator (7 °C) and subsequently roots were separated in the laboratory at Chulalongkorn University.

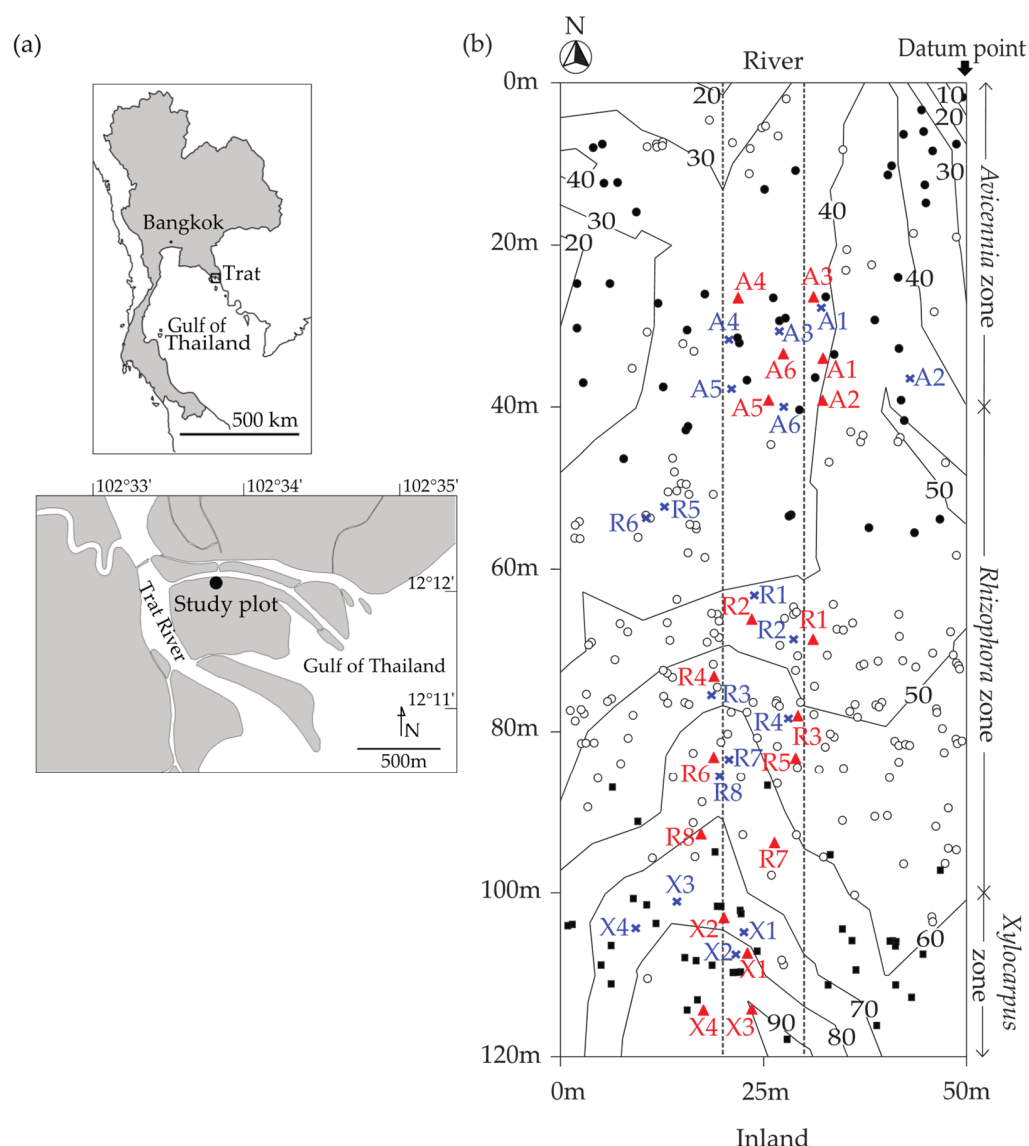


Figure 1. Trat River Estuary in eastern Thailand; (a) study plot location and (b) sampling locations in the study plot with a 10 cm contour interval and presence of trees with diameter at breast height (DBH) > 15 cm that includes *Avicennia alba* (closed circle symbols), *Rhizophora* spp. (open circle symbols), and *Xylocarpus granatum* (closed square symbols); dotted lines represent line transects with sampling points during the dry season (red symbols) and wet season (blue symbols).

2.3. Root and Soil Analysis

The roots from each soil block were washed with tap water through a 0.5 mm meshed sieve and manually sorted into live (biomass) and dead (necromass) roots using visual criteria, in which live roots were firm with intact tissues while dead roots were dark, discolored, and had lost elasticity [47]. Then, the living roots were classified into diameter-size classes: fine roots (0–2 mm), small roots (2–5 mm), medium roots (5–10 mm) and large roots (>10 mm). Above-ground roots such as pneumatophores were separated from below-ground roots. All root samples were oven-dried at 60 °C until a constant weight was obtained and then weighed. The soil blocks (0–20 cm depth) were air-dried then removed coarse plant debris and sieved through 2 mm and 0.5 mm meshes for further soil nutrient analysis.

For root and soil nutrient analysis, the dried root samples ($n = 18$ each season) and the soil samples ($n = 18$ each season) were analyzed with three replications at the Soil Science Laboratory, Department of Silviculture, Faculty of Forestry, Kasetsart University,

Thailand. The total carbon (TC) and nitrogen (TN) contents were determined using the dry combustion method with a CHNS/O analyzer (2400 Series II, Perkin Elmer, Waltham, MA, USA); total phosphorus (TP) in root tissues was determined using the Vanadomolybdate yellow color method, and soil available P was determined by using the Bray II method (UV-VIS spectrophotometer, UV mini 1240 Shimadzu, Kyoto, Japan).

2.4. Data Analysis

All statistical analyses were performed using SPSS version 22 software (IBM Corp., New York City, NY, USA). The data were tested for normality of distribution and equality of variance using the Kolmogorov-Smirnov test and Levene's test, respectively. The differences among vegetation zones (for root biomass, necromass, and root and soil nutrients) were analyzed using one-way analysis of variance (ANOVA), and the non-parametric test (Kruskal–Wallis test) was applied for the data with a non-normal distribution. The post hoc test was performed using Tukey's test (normally distributed data) and pairwise comparisons (non-parametric test) with the statistical results considered significantly different when the significance level was $p < 0.05$. The independent sample t -test or Mann–Whitney U test was used to determine seasonal differences. The proportion of root diameter classes was compared using the goodness-of-fit test (χ^2 test). The relationships of roots (root mass and nutrient concentrations) and soil nutrient contents were determined using linear regression analysis.

3. Results

3.1. Proportion of Roots Among Root Size Classes

The respective diameter classes of living roots (0–20 cm depth) showed different proportions among the vegetation zones (Figure 2). In the *Rhizophora* zone, the fine roots contributed the highest percentage of total root biomass, which accounted for 62% and 73% during the dry and wet seasons, respectively (Figure 2). In the *Avicennia* and *Xylocarpus* zones, the medium and large roots contributed the highest percentages, accounting for 71%–74% and 69% during the dry and wet seasons, respectively. The proportion of small roots was not significantly different among the zones (ANOVA, $F = 2.20$, $p = 0.127$).

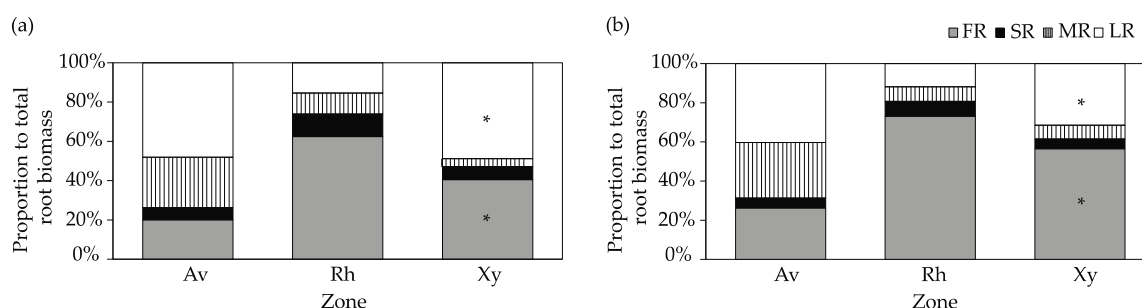


Figure 2. Proportion of root biomass in the *Avicennia* (Av), *Rhizophora* (Rh), and *Xylocarpus* (Xy) zones categorized into diameter classes, including fine roots (FR), small roots (SR), medium roots (MR), and large roots (LR), during the dry (a) and wet (b) seasons. The symbols indicate significant differences from a goodness-of-fit test with χ^2 ($p < 0.05$) between seasons (*).

In most cases for the small to large root categories, the proportion of each root diameter class was not significantly different between the dry and wet seasons. Although the proportion of fine roots seemingly increased during the wet season in all vegetation zones (Figure 2), statistical significance was only detected in the *Xylocarpus* zone (goodness-of-fit, $\chi^2 = 12.04$, $p = 0.001$).

3.2. Spatial Variation in the Root Mass

Among the vegetation zones, the total biomass in the 0–20 cm depth showed a significant difference (ANOVA, $F = 7.66$, $p = 0.002$). The total root biomass was highest in the *Avicennia* zone, followed by the *Rhizophora* and *Xylocarpus* zones (Figure 3a).

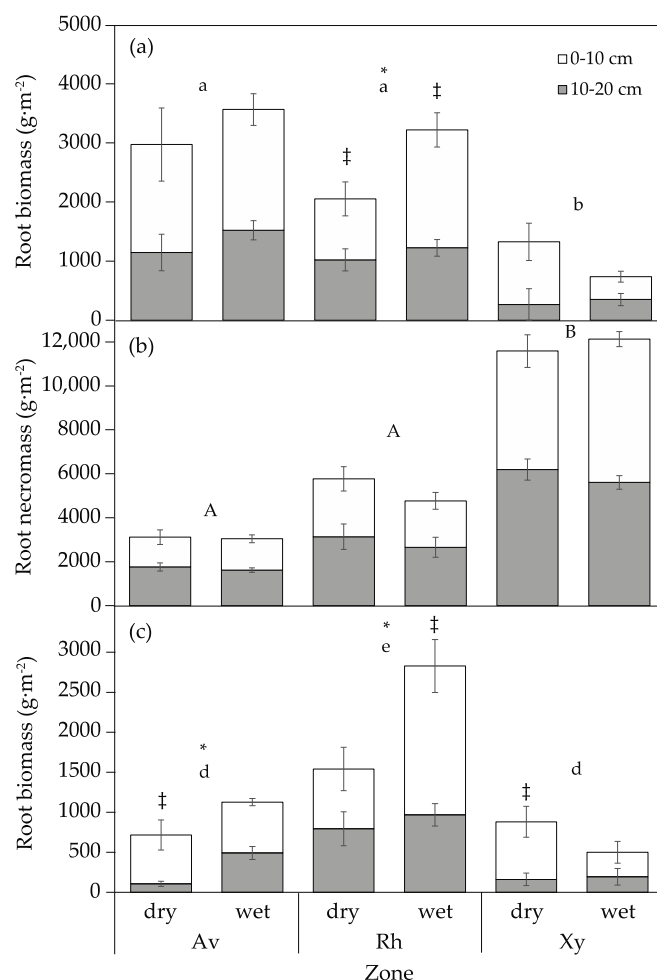


Figure 3. Total root biomass (a), necromass (b), and fine-root biomass (c) represented as the mean \pm SE in the *Avicennia* (Av), *Rhizophora* (Rh), and *Xylocarpus* (Xy) zones during the dry and wet seasons in the separated soil depths. The symbols indicate significant differences from the independent t -test ($p < 0.05$) between seasons (*) and soil depth (†). The letters show significant differences among zones ($p < 0.05$) using Tukey's post hoc test and pairwise comparisons.

The root necromass in the 0–20 cm depth also varied across the vegetation zones (Kruskal–Wallis, $H = 21.618$, $p < 0.0001$). The highest necromass was found in the *Xylocarpus* zone, followed by the *Rhizophora* and *Avicennia* zones (Figure 3b).

3.3. Temporal Variation in the Root Biomass between Dry and Wet Seasons

The total root biomass in the 0–20 cm depth during the wet season was seemingly high compared with that during the dry season in the *Avicennia* and *Rhizophora* zones (Figure 3a). However, significance was detected only in the root biomass in the *Rhizophora* zone (ANOVA, $F = 6.72$, $p < 0.05$, Figure 3a). Additionally, fine root biomass in the 0–20 cm depth was higher during the wet season in the *Avicennia* and *Rhizophora* zones (Figure 3c), in which fine root biomass increased to 157.1% and 183.6% during the wet season, respectively. Moreover, significance was detected in the above-ground pneumatophore biomass in the *Avicennia* zone (t -test, $t = 3.47$, $p = 0.012$), with averages of 1087 ± 239 g·m⁻² and

$202 \pm 47 \text{ g} \cdot \text{m}^{-2}$ during the dry and wet seasons, respectively. For root necromass, the temporal differences between dry and wet seasons were not significant (Figure 3b).

Between the two layers, root biomass in the 0–10 cm depth was obviously higher than that in the 10–20 cm depth in most cases (Figure 3a). In the *Rhizophora* zone, both total root biomass in the 0–10 cm depth were higher than that in the 10–20 cm depth during both the dry and wet seasons (ANOVA, $p < 0.05$, Figure 3a). For fine roots, the top 0–10 cm layer had the highest mass during the wet season, especially in the *Rhizophora* zone (Figure 3c). This tendency was also noticeable during the dry season in the *Avicennia* and *Xylocarpus* zones. For root necromass, the vertical differences were all non-significant.

3.4. Comparison between Root Biomass and Necromass

The distribution of root biomass showed an inverse trend to that of the root necromass distribution (Figure 4a). The total root biomass in the 0–20 cm depth showed a decreasing tendency towards the inland areas (linear regression, $R^2 = 0.269$, $p = 0.001$, Figure 4a). However, root necromass in the 0–20 cm depth showed an increasing tendency towards the inland areas (linear regression, $R^2 = 0.705$, $p < 0.001$, Figure 4a). Total root biomass and necromass in the 0–20 cm depth had negative relationships (linear regression, $F = 10.08$, $p = 0.003$) with distance from the river (Figure 4a). Relatively high root biomass was found in the *Avicennia* zone in the riverside area, while relatively high root necromass was found in the *Xylocarpus* zone in the inland area, regardless of season.

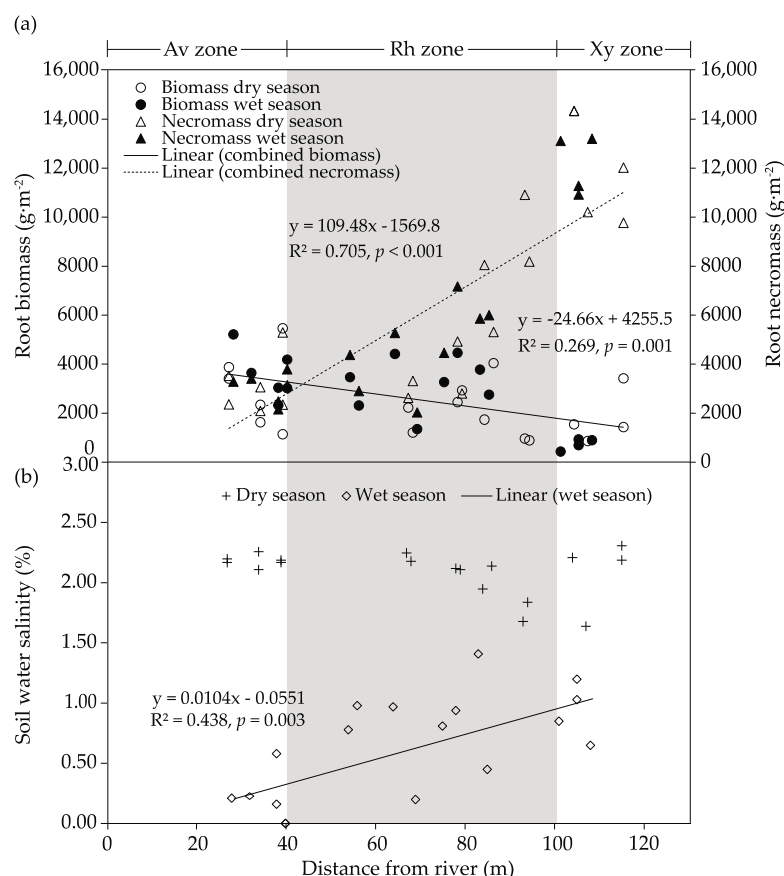


Figure 4. The linear relationships between total root mass (biomass and necromass) (a) and soil water salinity (b) along distance from the river across the zonation: *Avicennia* (Av), *Rhizophora* (Rh), and *Xylocarpus* (Xy) zones. The regression lines show the significant regression models.

3.5. Salinity Differences

Soil water salinity measured at a 10 cm depth showed noticeable seasonal differences (Figure 4b). During the dry season, the mean salinity in the *Avicennia* zone ($2.18 \pm 0.02\%$)

was slightly higher (not significant) than the mean values of $2.03 \pm 0.07\%$ and $2.09 \pm 0.15\%$ in the *Rhizophora* and *Xylocarpus* zones, respectively. During the wet season, the overall soil water salinity decreased and varied within a range from 0.00 to 1.41%. The salinity during the wet season showed a tendency to increase towards the inland areas (linear regression, $R^2 = 0.438$, $p = 0.003$, Figure 4b).

3.6. Variations in Nutrient Concentrations

Between the dry and wet seasons, both TC and TN contents in root tissues were not significantly different (Table 1). A slight increase during the wet season was recognized in the *Avicennia* zone. However, among the vegetation zones, root TC and TN concentrations showed significant differences (ANOVA, $F = 52.95$, $p < 0.001$, Table 1). In the *Avicennia* zone, root C and N contents in both seasons were the highest. The C:N ratio of root tissues in the *Avicennia* zone was the lowest in both seasons. The N:P ratios were not significantly different between the dry and wet seasons, with an average of 5.52 across all zones. The N:P ratios had a tendency to be relatively high in the *Avicennia* zone in both seasons, but we could not find significant zonal variations (Table 1).

Table 1. The values of nutrient concentrations of root and soil samples (mean \pm SE) across the vegetation zones during the dry and wet seasons with the results of statistical analysis showing the effects of zonation. The P contents in root tissues and soil were TP (%) and available P ($\text{mg} \cdot \text{kg}^{-1}$), respectively.

Element	Season	Root			Soil		
		<i>Avicennia</i>	<i>Rhizophora</i>	<i>Xylocarpus</i>	<i>Avicennia</i>	<i>Rhizophora</i>	<i>Xylocarpus</i>
TC (%)	Dry	$47.70 \pm 0.30^{\text{ns}}$	$46.23 \pm 0.81^{\text{ns}}$	$47.70 \pm 0.41^{\text{ns}}$	$5.74 \pm 0.12^{\text{ns}}$	$7.70 \pm 0.87^{\text{ns}}$	$8.23 \pm 0.80^{\text{ns}}$
	Wet	$48.38 \pm 0.45^{\text{a}}$	$46.11 \pm 0.21^{\text{b}}$	$44.06 \pm 1.47^{\text{ab}}$	$5.92 \pm 0.06^{\text{ns}}$	$6.32 \pm 0.20^{\text{ns}}$	$6.07 \pm 0.76^{\text{ns}}$
TN (%)	Dry	$1.13 \pm 0.03^{\text{a}}$	$0.83 \pm 0.03^{\text{b}}$	$0.95 \pm 0.03^{\text{c}}$	$0.37 \pm 0.01^{\text{ns}}$	$0.36 \pm 0.04^{\text{ns}}$	$0.36 \pm 0.03^{\text{ns}}$
	Wet	$1.22 \pm 0.02^{\text{a}}$	$0.88 \pm 0.03^{\text{b}}$	$0.99 \pm 0.04^{\text{b}}$	$0.41 \pm 0.004^{\text{a}}$	$0.34 \pm 0.01^{\text{b}}$	$0.29 \pm 0.03^{\text{b}}$
P	Dry	$0.19 \pm 0.06^{\text{ns}}$	$0.22 \pm 0.02^{\text{ns}}$	$0.22 \pm 0.02^{\text{ns}}$	$47.09 \pm 1.22^{\text{a}}$	$13.83 \pm 0.88^{\text{b}}$	$5.96 \pm 0.28^{\text{c}}$
	Wet	$0.26 \pm 0.06^{\text{ns}}$	$0.20 \pm 0.05^{\text{ns}}$	$0.23 \pm 0.02^{\text{ns}}$	$41.96 \pm 1.04^{\text{a}}$	$19.53 \pm 2.96^{\text{b}}$	$2.48 \pm 0.21^{\text{c}}$
C:N	Dry	$42.43 \pm 0.94^{\text{a}}$	$56.39 \pm 2.05^{\text{b}}$	$50.90 \pm 2.07^{\text{b}}$	$15.53 \pm 0.32^{\text{a}}$	$21.65 \pm 0.36^{\text{b}}$	$22.92 \pm 0.50^{\text{b}}$
	Wet	$39.61 \pm 0.61^{\text{a}}$	$53.23 \pm 2.11^{\text{b}}$	$44.82 \pm 1.69^{\text{ab}}$	$14.59 \pm 0.11^{\text{a}}$	$18.82 \pm 0.34^{\text{b}}$	$20.95 \pm 0.37^{\text{b}}$
N:P	Dry	$6.32 \pm 1.25^{\text{ns}}$	$3.76 \pm 0.40^{\text{ns}}$	$4.39 \pm 0.39^{\text{ns}}$	-	-	-
	Wet	$6.54 \pm 2.09^{\text{ns}}$	$7.76 \pm 4.35^{\text{ns}}$	$4.36 \pm 0.40^{\text{ns}}$	-	-	-

Remark: Significant differences are shown with different letters ($p < 0.05$) by Tukey's post hoc tests (ANOVA) and pairwise comparisons (non-parametric test). The letter 'ns' indicates a non-significant difference among vegetation zones.

For soil nutrient concentrations, seasonal variation was not significant in all cases (Table 1). However, it is noteworthy that soil C and N concentrations in the *Avicennia* zone tended to increase during the wet season (Table 1). Concentrations of available soil P were negatively related to distance from the river in both seasons (Figure 5). They showed significant differences in the vegetation zones (Kruskal–Wallis, $H = 47.13$, $p < 0.001$, Table 1). However, the soil C:N ratios were positively related to distance from the river, which indicated increased inland C:N ratios (Figure 5) and thus the lowest ratio in the *Avicennia* zone (Kruskal–Wallis, $H = 38.33$, $p < 0.001$, Table 1).

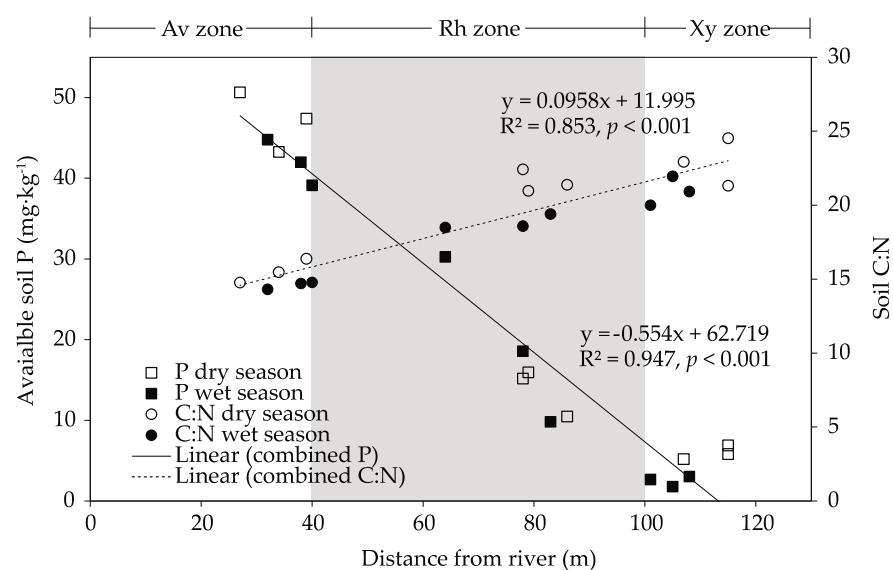


Figure 5. The relationships between soil nutrient parameters (available P and C:N ratio) and distance from the river across the zonation: *Avicennia* (Av), *Rhizophora* (Rh), and *Xylocarpus* (Xy) zones.

4. Discussion

4.1. Seasonal and Zonal Variation in Root Biomass

Mangroves often show a seasonal growth pattern under a tropical monsoon climate. During the wet season, mangroves generally increase their growth in trunk basal area [30,39,48–50], leaf production [51,52] and root production [32,53–55]. In this study, we analyzed the root mass existing in the top 20 cm of soil, which is referred to as a tide-sensitive layer [36]; the soil profile was divided into two layers, including the tide-sensitive layer in the top ca. 20 cm depth that experiences daily inundation, and an underlying aquifer layer where inundated water penetrates slowly from above. Thus, the examined total root biomass in the 0–20 cm depth was influenced mostly by the inundated water that caused higher root biomass in the riverward zone during the wet season (Figure 3a).

The tropical monsoon climate causes temporal heterogeneity in the root spheres of mangrove forests. In the studied plot, the inundated water from the Trat River during the wet season was nearly freshwater, and during the dry season, it was saline water [36]. The low salinity conditions during the wet season creates a favorable condition for the growth of mangrove roots, based on evidence that Pongpam et al. [32] reported a high production of fine roots during the wet season (May to July) in the same study plot. Their study relates to the present results, which showed high fine root biomass and its proportion to total root biomass during the wet season (Figures 2 and 3c). Regardless of season, total root biomass in the 0–20 cm depth was higher in the *Avicennia* zone than in the more inland zones (Figure 4a). This resulted from the inundation process of freshwater from the Trat River that caused relatively high trunk growth rates [30] and leaf emergence rates [56] in *A. alba* trees during the wet season under low salinity at the same study site. This was also a result of the characteristics of *A. alba*, which is a dominant tree and is considered a fast-growing species [57,58] with a dense cable-root system concentrated in the topsoil [59].

4.2. Effects of Salinity Variation on Root Distribution

The salinity regimes along the 120 m transect line have been previously studied at this study plot by Komiyama et al. [30], which were consistent with our results as shown in Figure 4b. During the wet season, the *Avicennia* zone on the river edge had relatively low salinity levels compared with those in the inland *Xylocarpus* zone. On the other hand, salinity distribution during the dry season showed a reverse trend due to the inundation regimes (period and frequency) of saline water in the riverside areas. Therefore, the high root biomass in the *Xylocarpus* zone during the dry season (Figure 3a) was explained by

the seasonal changes in salinity distribution along the transect line. Thus, the spatial heterogeneity in the root sphere of mangrove forests was influenced not only by the specific characteristics of the trees but also by the interactions of the microtopography and inundation regimes.

The vertical distribution of roots between the 0–10 cm and 10–20 cm layers was significantly different in the *Rhizophora* zone in both seasons. However, the difference in root biomass in the *Rhizophora* zone between the two layers was large during the wet season but small during the dry season (Figure 3a,c). In the *Xylocarpus* zone, the high fine root biomass distributed in the 0–10 cm layer during the dry season (Figure 3c) suggests that fine roots increased under the lower saline conditions in the surface soil layer. Fine roots are sensitive to changing environments since they function in water and nutrient absorption. Therefore, fine roots can respond to changing environments in a short period of time based on optimal saline conditions. Pongparn et al. [32] reported high root production during the wet season, especially fine roots in the 0–30 cm depth at the same study site. This probably indicates a strategy of mangrove trees in which they optimize their growth by allocating roots, especially fine roots, into the soil layers with favorable saline environments. Nevertheless, further investigation with consecutive root production data is necessary to support this inference.

The spatiotemporal heterogeneity of root biomass was affected by different distribution of mangrove species due to different salt-tolerance mechanisms. *Avicennia* can cope with the wide range in salinity levels by using three physiological mechanisms related to salt stress including salt exclusion, salt accumulation, and salt excretion [60]. The *Avicennia* roots have apoplastic barrier that excludes salt ions from entering the vascular tissues [61,62] and the salt can be accumulated in root cortex [63]. Moreover, the salt can be excreted through the glands on the foliar of *Avicennia* [60]. This might explain how the *Avicennia* trees could maintain high root biomass under high salinity level in the dry season. While the *Rhizophora* trees have been reported for two mechanisms—salt exclusion and accumulation—however, in the *Xylocarpus* trees, only the salt accumulation mechanism was found [60]. This reflects the lower ability to deal with high salinity levels for *Rhizophora* and *Xylocarpus* trees.

4.3. Effects of Nutrients on Root Distribution

In the root sphere of mangrove forests, both temporal and spatial heterogeneity are closely related to nutrient conditions. For example, root biomass distribution is influenced by the nutrient conditions in mangrove forests [55,64]. Generally, the budgets of nutrients in estuarine mangrove forests are determined chiefly by the nutrient loads from the river. At our study site, the Trat River transported large amounts of nutrient fluxes (NO_3^- , NH_4^+ , and PO_4^{4-}) from upstream during the wet season [65]. We found that the nutrient contents in the riverside area were relatively higher than those in the inland zones. In particular, the soil available P contents in the *Avicennia* zone were approximately fivefold higher than those in the *Xylocarpus* zone (Table 1).

Nutrient availability is a major factor affecting mangrove growth, as reported for N and P limitations [13]. Several authors have reported that mangrove forests are P-limited (i.e., [42,45,66,67]), but some mangroves are likely to be N-limited (i.e., [46,67,68]), even though ammonia nitrogen is abundant in mangrove soil [13]. The soil TN contents tended to increase in the *Avicennia* zone during the wet season (Table 1), although there was no statistical significance among zones. However, the TN concentrations in root tissues in the *Avicennia* zone were significantly higher than those in other zones (Table 1). It is considered that nutrient fluxes accelerated by a large river flow during the wet season enhanced root N concentrations and then increased the root biomass in the riverward *Avicennia* zone. We also found high contents of available P in soil but not total P in roots (Table 1). Feller et al. [67] reported that mangrove roots did not acquire additional P from phosphate-saturated soil.

The N:P ratio in plant tissues can indicate a limitation of nutrients in the ecosystem related to soil nutrient availability and plant nutrient uptake, which has been generally examined in leaf tissues [13,69–71]. Koerselman and Meuleman [70] reported indicative N:P ratios in plant tissue that determine whether the forest ecosystem is N-limited (<14), P-limited (>16), or co-limited in both N and P ($14 < \text{N:P ratio} < 16$). In our study, the average N:P ratio in root tissues was 5.52, regardless of season or zone, which suggests that this estuarine mangrove forest may be considered to be N-limited.

4.4. Root Necromass Distribution

Plant necromass partly regulates nutrient budgets in forest soil via a decay process. We found an interesting relationship between the trends of root biomass and necromass along the line that transects with spatial heterogeneity. The distribution of root biomass showed zonal variation with inverse trends in the distribution of root necromass (Figure 4a). Relatively high root biomass was found in the *Avicennia* zone in the riverside area, while relatively high root necromass was found in the *Xylocarpus* zone in the inland area regardless of season.

The magnitude of root necromass accumulation is determined by root litter production and decay processes in the soil. The decay process in mangrove forests is usually regulated by biological factors, i.e., root chemical contents [72,73] and root sizes [8,72], and physical factors, i.e., tidal regimes [72]. At the same study site, the ratio of fine root necromass to total fine root mass was the highest in the *Xylocarpus* zone (0–30 cm depth), followed by the *Rhizophora* and *Avicennia* zones [15]. For *Xylocarpus* trees, the roots contain high contents of suberin and tannins [74], which might slow the decay rate of the root necromass. At the same study site as the present study, Pongparn et al. [31] found low rates of soil respiration in the *Xylocarpus* zone, which received less frequent inundation. Moreover, the soil C:N ratio is usually related to the decay process. In this study plot, the soil C:N ratios were high in the *Xylocarpus* zone (Table 1, Figure 5). This also suggests that the decay process occurs relatively slowly in the *Xylocarpus* zone in the inland area. Consequently, the root necromass accumulation was high in an inland direction (Figure 4a), indicating the spatial heterogeneity of the root sphere in this mangrove forest.

4.5. Implications for Mangrove Rehabilitation

The ecological considerations improve the initial success of mangrove restoration [75]. However, the fundamental ecological knowledge for mangrove restoration and management is insufficient [76], in particular the below-ground study. Our study provides evidence that the root distribution and root sphere in the mangrove forest showed spatiotemporal variations across the zonation in response to different inundation period, salinity, and nutrient conditions. Nevertheless, climate change might alter the salinity regimes [17,77] and nutrient budgets [78] in mangrove ecosystems. Sea level rise also impacts mangrove forests, but it has been reported that the mangrove forests resisted the increasing sea levels by enhancing soil accretion through soil organic matter accumulation as a result of high root production [18,19]. These processes were referred to as increasing ‘vertical accommodation space’ for carbon and organic material stocks in mangrove forests [79]. Therefore, a better understanding of the mangrove root ecology in relation to changing environments (salinity and nutrient regimes) obtained from our study will increase the success of mangrove rehabilitation plans. Based on this ecological viewpoint, the appropriated species can be selected for mangrove restoration and consequently will benefit from a long-term carbon conservation, especially the below-ground carbon stock.

5. Conclusions

We found that different inundation, salinization, and decay processes according to the topographic gradient in the study site caused spatial heterogeneity in the root sphere in the mangrove forest with a distinct zonation. In addition, the variations in the root sphere along the distance from the river were influenced by the available phosphorus content

in the soil. As a result, the spatiotemporal heterogeneity of root distribution occurred in relation to environmental changes across the zonation and specific characters of mangrove trees. The highest root biomass was found in the riverside *Avicennia* zone regarding the characters of *Avicennia alba* trees as a fast-growing species and physiological adaptation to the high salinity. The highest root necromass was reported in the inland *Xylocarpus* zone, in contrast to root biomass distribution, due to relatively low root decomposition. Simultaneously, temporal heterogeneity, particularly with regard to soil salinity and fine root biomass, occurred under the tropical monsoon climate. The high fine root biomass in all zones during the wet season was attributed to optimal conditions with low salinity and sufficient nutrient supply. The combination of spatiotemporal heterogeneity was confirmed to regulate the root dynamics in this mangrove forest. We suggest that such heterogeneity of the root sphere may produce the existence of mangrove zonation, which should be considered in the below-ground carbon dynamics. Therefore, the heterogeneity of root sphere and mangrove zonation regarding environmental gradients provides an ecological perspective of mangrove ecosystems, which can be applied for mangrove rehabilitation to facilitate long-term below-ground carbon stock under climate change.

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