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Variations in litterfall dynamics, root biomass, and sediment accretion in restored and recolonized mangroves in Leyte, Philippines

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ABSTRACT

Litterfall production and decay, root biomass, and sediment accretion dynamics were investigated from restored 'planted' (R5, R8, R15, and R30 stands) and recolonized stands (C5, C12, and C20 stands) to investigate patterns in primary productivity, belowground biomass, and sediment accretion dynamics. Litterfall data was collected using litter traps over 12 months, while decay kinetics was investigated using a litterbag experiment. Root biomass and sediment accretion data were collected using makeshift acrylic corers. Litterfall production increased as stands aged, and tended to stabilize as it matured in restored (R8: 10.05 Mg/ha/yr; R30: 6.1 Mg/ha/yr) and recolonized stands (C5: 18.75 Mg/ha/yr; C20: 9.05 Mg/ha/yr). Leaf litter decay rates (K/d) showed no pattern with stand age, although the recolonized stands (range: 0.059–0.113 K/d) had lower decay rates compared to the restored (range: 0.073–0.123 K/d) and natural stands (range: 0.064–0.123 K/d). Root biomass declined with age in restored stands (R5: 67.16 Mg/ha, R30: 49.67 Mg/ha), but increased in recolonized stands (C5: 5.41 Mg/ha, C20: 19.50 Mg/ha). Very high rates of sediment accretion were found in younger restored (R5: 10.1 cm/yr) and recolonized stands (C5: 8.1 cm/yr) than mature stands (R30: 6.3 cm/yr; C20: 4.3 cm/yr). Our results showed disparities of patterns in mangrove vegetation growth in recolonized stands and huge potential contribution on mangrove productivity when these areas are effectively restored.

1. Introduction

Mangroves are among the most vital ecosystems in tropical and subtropical coasts delivering a wide variety of ecosystem services (Qin et al., 2024; Song et al., 2024; Duncan et al., 2022). The global total carbon export from mangroves is estimated to be 45 Tg C/yr (Bouillon et al., 2008), approximately 50 % as particulates (Jennerjahn, 2012). Global average litterfall in mangrove ecosystems was reported as 4.56 Mg C/ha/yr (Kristensen et al., 2008) contributing approximately 30–60 % of net primary production in forest ecosystems (Alongi, 2014a). Mangrove litterfall production and decay is a key ecological process in coastal ecosystems contributing to global carbon and nutrient cycling (Manzoni et al., 2008).

Litterfalls are a major contributor of organic matter (OM) and nutrients to mangrove sediments and adjacent ecosystems (Mamidala et al., 2023). The accumulation of OM in mangrove sediments can be affected by stand structure and age, litterfall production and decay, physico-chemical variables, and microbial activities (Cadiz et al., 2021; Pradisty et al., 2021; Wang'ondu et al., 2014). Young stands of planted mangroves have increasing litterfall with age in Gazi Bay, Kenya (Wang'ondu et al., 2014) and Tam Giang Lagoon, Vietnam (Nga et al., 2005). In Indonesia, restored stands composed of mixed species (~14–15 yrs; 13.96 Mg/ha/yr) have higher litterfall production compared to natural stands (10.18 Mg/ha/yr; Pradisty et al., 2022).

The intricate relationship between mangrove litterfall production and decay plays a crucial role in the overall dynamics of the mangrove ecosystem (Mamidala et al., 2023; Pradisty et al., 2021; Wang'ondu et al., 2014). As mangrove vegetation matures, the production of litter – composed of leaves, twigs, and reproductive parts increases with age (Wang'ondu et al., 2014; Nga et al., 2005). Belowground, the root biomass also increases with forest age (Tamooh et al., 2008; Alongi and Dixon, 2000) and is strongly dependent on nutrient gradients, salinity (Bassar et al., 2023), and hydroperiods (Chen et al., 2023). Root biomass influences a range of belowground processes, including carbon sequestration, sediment accretion, etc. (Salas-Rabaza et al., 2024; Bassar et al., 2023; Ahmed et al., 2022).

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0272-7714/© 2024 Elsevier Ltd. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

Sediment accretion is defined as the vertical accumulation of sediment deposited on the substrate surface over a specific time scale (Swales and Lovelock, 2020; Thomas and Ridd, 2004). Studies on short-term sediment accretion (i.e. minutes to months) have employed a range of methods, including the use of ruler, sediment traps, plates, and marker horizon (see review of Thomas and Ridd, 2004). In general, methods for short-term sediment accretion measurements are widely used and relatively of lower cost allowing numerous sites to sample and monitor. Despite the low-cost advantage, potential limitations include: (1) poor resolution (i.e. ruler method); (2) bias of trap measurements (i.e. sediment trap method); and (3) alteration of surficial sediment compaction (Swales and Lovelock, 2020). All of these issues potentially limit sediment accretion rate measurements and thus the use of alternative methods could provide supplemental information.

Specific stand management regimes (i.e. regulated exploitation, deforestation, afforestation, reforestation, natural regeneration in abandoned ponds, etc.) alter the physico-chemical conditions and influence the productivity of mangroves (Song et al., 2024; Bai et al., 2021; Ma et al., 2021). Intact mangroves have high primary productivity that result in high carbon stores (Alongi, 2014b). When disturbed, the changes in vegetation (Salmo et al., 2013; Kairo et al., 2008) and sediment (Stokes et al., 2023; Adame et al., 2018) may negatively affect the production and stabilization of litter (Ogawa et al., 2022). When restoration takes place in suitable sites and with appropriate methods, high rates of mangrove growth and gains in sediment accretion are observed, which are favorable for ecosystem provision and climate change mitigation (Song et al., 2024; Castillo et al., 2022; Sidik et al., 2019).

In countries where aquaculture is the major disturbance in mangrove ecosystems (including Philippines), abandoned ponds are potential areas for restoration (delos Santos et al., 2022). However, massive planting projects have been implemented in coastal fringes with site-species mismatch (Primavera et al., 2019) and even planting in seagrass beds (Samson and Rollon, 2008). Although some abandoned ponds have been included in planting projects, many were left unused resulting in patches of naturally recolonized stands (delos Santos et al., 2022; Luo et al., 2022). Differences in extractive pressures and pond management may affect how these abandoned ponds recover relative to reference stands (Sidik et al., 2019; Adame et al., 2018; Towatana et al., 2002). Knowledge on vegetation recovery and sediment dynamics in naturally recolonized abandoned ponds is important for adaptive management strategies to improve restoration outcomes.

Mangrove restoration studies worldwide are mostly focused on monitoring stand structure development (Azman et al., 2021), sediment recovery (Ma et al., 2021; Salmo et al., 2013), and fauna secondary succession (Barbanera et al., 2022) on planted versus intact forests. However, little is known in a chronosequence of restored 'planted' stands and naturally recolonized abandoned ponds. Yet, knowledge on the organic inputs, belowground biomass, and sediment dynamics in these varying mangrove stands is relevant to our understanding on changes in forest productivity and restoration process.

In this study, we investigated patterns in litterfall production, leaf litter decay, belowground root biomass, and sediment accretion across a chronosequence of restored 'planted' mangrove stands and naturally recolonized stands with intact mangrove forests as the reference (natural stands). Our study provides insights on the dynamics of mangrove forest change over time for adaptive management strategies to enhance restoration outcomes.

2. Materials and methods

2.1. Site information

The study was conducted in Ormoc Bay, mid-eastern Philippines between 10° 59′ 8.0880″ latitude, and 124° 32′ 51.5754″ longitude, and belongs to the Visayan Sea biogeographic region. Mangroves in Ormoc Bay receive freshwater and sediment inputs from Bao River. Some areas were converted to fishponds. Over time, some of these fishponds were abandoned and subsequently recolonized by mangroves through natural recolonization process (~20 yrs). Planting projects have been conducted since the 1990s and is co-managed by the city government and Naungan-San Juan Mangrove Planters Association (NSJMPA). The mangroves in Ormoc Bay are generally categorized into natural, restored, and recolonized stands (Fig. 1; Supplementary Fig. 1). "Natural stands" (hereafter referred to as NAT stands) are mangroves of unknown ages that naturally occur on the site without any direct human intervention. "Restored stands" (hereafter referred to as RES stands) refer to "planted" stands. The estimated ages for RES stands in 2022 varied based on the time of plantation, which were approximately 5-, 8-, 15-, and 30-yrs old (hereafter referred to as R5, R8, R15, and R30 stands). "Recolonized stands" (hereafter referred to as COL stands) were abandoned aquaculture ponds that were naturally recolonized/regenerated with mangroves. The estimated ages for COL stands varied based on the time of pond abandonment, which were 5-, 12- and 20-yrs old (hereafter referred to as C5, C12, and C20 stands). Remnants of aquaculture pond construction were observed in COL stands, such as waterways (C5 stand) and dikes (intact dikes in C12 stand; partially destructed dikes in C20 stand; Supplementary Fig. 1). The estimated ages of the stands were based on local accounts/records complemented with local maps. Younger RES stands are characteristically dense with tree densities ranging from 2,249 to 5,178 trees/ha. Through the years, mature RES stands tended to have similar stand structure with the NAT stands (Table 1). Ormoc is categorized under Cluster I climate with a dry season from March to April (100–200 mm) and wet season from June to January (320–580 mm; Corporal-Lodangco and Leslie, 2017).

In each mangrove stand, triplicate 7 m-radii plots were established except in 5-yr stands where 5 m-radii plots were used. Plots were also distributed based on tidal positions (as landward [LW], midward [MW], and seaward [SW]). The classification was based on the following features: 1) SW zone is situated at the intertidal zone where mangroves are daily submerged to seawater. Mangrove stands in the SW zone are directly exposed to the tidal fluctuations and currents. Surface elevation in the SW zone ranges from −0.1 m to 0.2 m (mean sea level, MSL), 2) Mangrove stands in the MW zone are situated between the SW and LW zones, where surface elevation ranges from 0.3 to 0.4 m, and 3) Mangrove stands in the LW zone are situated inland that extends ~1 km from the shoreline. Surface elevation in the LW zone ranges from 0.6 m to 3 m. In addition, the presence of intact dikes in C12 stand as well as the partially destructed dikes in C20 stand limits water exchanges from tide. Thus, poor draining was observed in C12 and C20 stands especially during spring tides. Mangroves in Ormoc Bay are influenced by semi-diurnal tides with tides that range from 1.1 m to 2.3 m. In total, 30 plots (9 NAT, 12 RES, and 9 COL) were monitored from April 2022 to March 2023.

2.2. Mangrove litterfall production

Litterfall production was investigated using a 1-m^2 (mesh size of 2 mm) litter trap from each plot. Three replicate litter traps were set in each mangrove stand type, resulting in 30 litter traps in total. The litter trap was suspended by ropes between trees about 2 m above ground level to avoid being reached by maximum tidal water level. Monthly litterfall collection started in April 2022 until March 2023 for all plots, except for the C12 stand which started in November 2022 due to difficulty of access to the site. Litterfall samples were air-dried and sorted into three main categories: leaves (apical buds and stipules), woods (i.e., branches and twigs), and reproductive parts (i.e., flower buds, flowers, fruits, and propagules). Individual litterfall components were oven-dried at 80 °C for 48–72 h until constant weight (cf. Wang'ondu et al., 2014). The rate of litter fall was calculated by dividing the DW of litter (g DW/m^2) by the number of days in each collection date and reported as Mg/ha/yr.

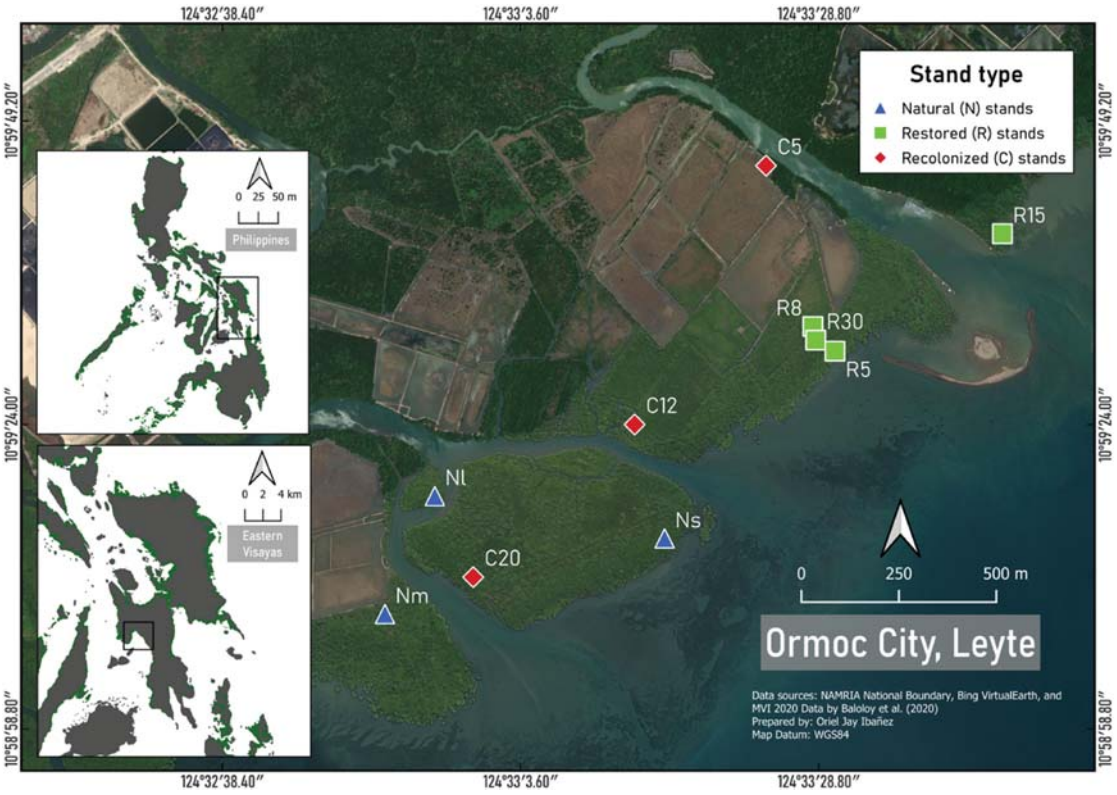

Fig. 1. Location of study sites in Ormoc, Leyte relative to PHL archipelago (top left) and Eastern Visayas region (bottom left). Permanent monitoring plots comprises natural stands (blue triangle), restored stands (green squares), and recolonized stands (red diamond). Ns (seaward), Nm (midward), Nl (landward) are natural stands of unknown ages; R5 (5 yrs old), R8 (8 yrs old), R15 (15 yrs old), and R30 (30 yrs old) are restored 'planted' stands; C5 (5 yrs old), C12 (12 yrs old), and C20 (20 yrs old) are naturally recolonized stands. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Stand structure characteristics in natural, restored and recolonized mangrove stands in Ormoc, Philippines. R5 (5 yrs old), R8 (8 yrs old), R15 (15 yrs old), and R30 (30 yrs old) are restored 'planted' stands; C5 (5 yrs old), C12 (12 yrs old), and C20 (20 yrs old) are naturally recolonized stands. Nx are natural (NAT) stands of unknown ages. SW: seaward, MW: midward, LW: landward.

Stand code	Stand type	Zonation	Species	Tree density (trees/ha)	Basal area (m^2/ha)	Diversity (H')	Evenness (E)	Dominance (D)
Nx	Natural	SW-LW	Mixed species	2,533	13.99	1.30	0.51	0.47
R5	Restored	SW	*A. marina*-dominated	2,249	23.75	0.90	0.56	0.47
R8	Restored	LW	*A. marina*-dominated	5,178	27.77	0.29	0.21	0.86
R15	Restored	SW	*S. alba*-dominated	1,537	18.74	0.90	0.65	0.48
R30	Restored	MW	*A. marina*-dominated	1,732	27.69	0.54	0.34	0.75
C5	Recolonized	LW	Mixed species	1,655	12.27	1.03	0.64	0.45
C12	Recolonized	SW	Mixed species	4,413	17.41	0.19	0.28	0.91
C20	Recolonized	MW	Mixed species	2,858	20.02	0.68	.0.33	0.73

2.3. Leaf litter decay sampling

The litterbag experiment was employed to determine the decay kinetics of leaf litter (Karberg et al., 2008) in all mangrove stands. Freshly fallen or easily handpicked yellowish senescent leaves of *Avicennia marina* were collected, weighed, and placed in litter bags (~50 g for each litter bag). Leaf litter samples were standardized by collecting *A. marina* leaves as it is the common species in all plots. Litterbags were made of nylon fibre mesh (200 mm × 200 mm, mesh size 1 mm^2), and closed using cable ties. Four litter bags were randomly placed on the sediment surface for each plot and tied with nylon rope to the roots. The litterbag experiment lasted for 42 days, with an intermediate sampling after 7, 14, and 21 days. The time period selected was based on previous leaf litter decay experiments which are apparently the most active decay phases from 14 to 70 days (Mamidala et al., 2023; Pradisty et al., 2022). Hence, an ideal timeline of 42 days to cover the largest mass loss from the mangrove leaf litter was thought to be most appropriate. The litterbag experiment was carried out in two sampling periods, during the wet season from September to October and the dry season from March to April to account for seasonal variations. Leaf litter decay was estimated using the dry:fresh weight ratio of leaf litter from each litter bag. Leaf litter decay rates (K) were calculated using a single-component exponential decay model:

$$X_t = X_0\, e^{-Kt}$$

where X_t is the percentage of the initial material X_0 remaining after time t (days) and K is a decay coefficient (d^{-1}). The times required for the decomposition of leaf half-life ($t_{0.50}$), 95 % ($t_{0.95}$), and 99 % ($t_{0.99}$) lifespan were computed (Pradisty et al., 2021; Karberg et al., 2008).

2.4. Sediment accretion and root biomass sampling

Short-term sediment accretion was measured using makeshift acrylic corers (6.5-cm diameter; 25 cm-height). This method was relatively

inexpensive and required minimal manpower for installation, though it is potentially vulnerable to erosion from physical processes such as rainfall, currents, and wave resuspension (similar to the feldspar marker-horizon method; Swales and Lovelock, 2020). Despite a shorter observation period (similar to the sediment traps and ruler method; Thomas and Ridd, 2004), the use of makeshift acrylic corers remains a cost-effective and practical approach in documenting short-term sediment accretion. An acrylic corer was buried up to 20-cm length for each plot and collected every 3–4 months for measurement. Sediment accretion sampling was carried out in two sampling periods, April 2022 and December 2022. Sediment accretion rate was based on measuring the thickness of a vertical sediment section divided by the number of days in each collection date (Saad et al., 1999).

Belowground root biomass (BRB) was determined from the same cores deployed for sediment accretion sampling. For each sampling period, three cores were taken (n = 30) from each stand, except for the C12 stand where makeshift acrylic cores were deployed in December 2022 due to difficulty of access to the site. The sediment core was subdivided at different depths (5-cm interval for the 0–5 cm layer and subsequently 2-cm intervals for the 5–25 cm layer) to trace the downcore BRB variation. Core samples were placed in sealed bags and stored at −18 °C until analysis. Samples were then air-dried for ~5 days, then oven-dried for 24 h at 60 °C. To separate roots from the sediment, each depth section was initially grounded using mortar and pestle, then dry-sieved for 5 min using a sieving tower (BIOBASE BK-TS200 laboratory test sieve, China) (including sieves of 0.06 mm, 0.13 mm, 0.25 mm, 0.50 mm, 2 mm, and 4 mm). Roots mixed with sediments after dry sieving were manually picked using forceps. Root samples were then rinsed with distilled water for complete removal of sediments then oven-dried at 60 °C to constant weight. Root biomass was calculated as the dry weight ratio of roots to the surface area of the soil column (Zhang et al., 2021; Adame et al., 2014).

2.5. Data analysis

Due to high data variability, the non-parametric Aligned Ranks Transformation Analysis of Variance (ART ANOVA; Mansouri et al., 2004) was used to determine if litterfall production and sediment accretion rates varied with stand types (NAT vs RES vs COL), ages (Nx, R/C<forest age>), and zonation (SW vs MW vs LW). Post hoc comparisons were made using Tukey's test to determine pairwise differences ($p \leq 0.05$). A one-way analysis of variance (ANOVA) was used to compare leaf litter decay rate and root biomass across stand types, ages, and zonation. The root biomass values were pooled for the entire depth. For downcore BRB variation, mean per depth was calculated (5-cm interval for 0–5 cm layer and 2-cm intervals for 5–25 cm layer). Data were tested for normality and homogeneity of variance using the Shapiro–Wilk test and Levene's test, respectively. Leaf litter decay data was untransformed while root biomass data was square-root transformed to conform with the normality test. Post hoc analyses of leaf litter decay rate and sediment accretion were performed using Tukey's test. Data uncertainty was expressed as mean ± s.e.m. Data analysis and visualization were performed using R ver. 4.2.2 and RStudio ver 2023.06.0 + 421.

3. Results

3.1. Litterfall production

Total litterfall production significantly varied among stand types, zones, and ages (Fig. 2A–C; $p < 0.001$). RES (8.31 ± 0.54 Mg/ha/yr) and COL (12.29 ± 1.59 Mg/ha/yr) stands have 30 % and 48 % higher total litterfall production than NAT stands (6.35 ± 0.44 Mg/ha/yr; $F = 6.42$, $p = 0.001$). Landward stands (11.62 ± 1.27 Mg/ha/yr) have 57 % and 61 % higher total litterfall production than SW (7.38 ± 0.58 Mg/ha/yr) and MW (7.23 ± 0.51 Mg/ha/yr) stands (Fig. 2B; $F = 5.5$, $p = 0.001$). Younger restored (R8: 10.05 ± 1.15 Mg/ha/yr) and recolonized stands

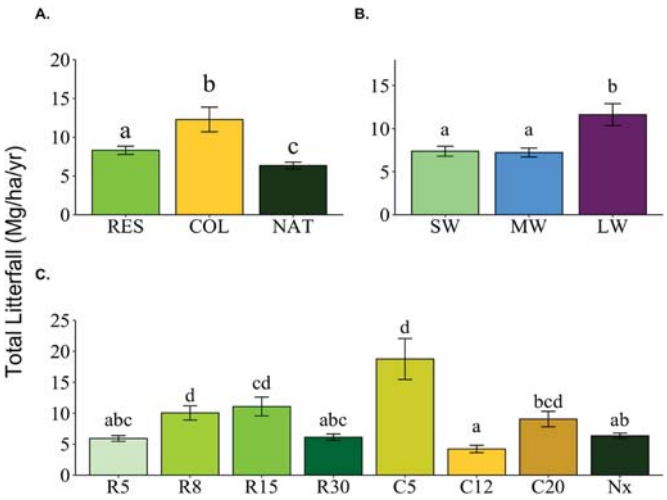

Fig. 2. Total litterfall production (Mg/ha/yr) of mangroves in Ormoc Bay, Philippines according to A) stand types, B) zonations, and C) stand ages. Different letters above the error bars indicate a significant difference between stands (at α = 0.05; Tukey's HSD test). Younger stands have higher total litter production compared to mature stands. R5 (5 yrs old), R8 (8 yrs old), R15 (15 yrs old), and R30 (30 yrs old) are restored 'planted' (RES) stands; C5 (5 yrs old), C12 (12 yrs old), and C20 (20 yrs old) are naturally recolonized (COL) stands; Nx are natural (NAT) stands of unknown ages. SW: seaward, MW: midward, LW: landward.

(C5: 18.75 ± 3.31 Mg/ha/yr) have 58 % and 195 % higher total litterfall production than the NAT (6.35 ± 0.43 Mg/ha/yr) stands but the more mature RES (R30: 6.13 ± 0.50 Mg/ha/yr) and COL (C20: 9.05 ± 1.25 Mg/ha/yr) stands have comparable values with the NAT stands (Fig. 2C).

In all stand ages, leaves contributed the highest percentage to total litterfall production (Supplementary Table 1). In RES stands, leaves accounted for 69–76 % of the total litterfall, while wood and reproductive parts contributed 9–12 % and 13–19 %, respectively. Leaves accounted for 58–94 % of the total litterfall in COL stands, whereas wood and reproductive parts contributed 6–11 %, and 12–25 %, respectively. In NAT stands, leaves accounted for 73–83 % of the total litterfall, while wood and reproductive parts contributed 6–10 % and 6–19 %, respectively.

3.2. Leaf litter decay

Initial rapid mass loss was observed in all stand types, zones, and ages during the first 14 days, followed by a slower mass loss at 21st and 42nd day (Fig. 3A–D). Decay patterns of all stand ages fitted a single negative exponential model ($R^2 > 0.90$; Supplementary Table 2). Leaf litter decay rates significantly varied across stand ages (within RES and COL stands, $p < 0.001$; Fig. 3A) and zonation ($F = 8.9$, $p < 0.001$; Fig. 3B). Mass loss between time intervals significantly varied among stand types ($p < 0.001$), with significant differences found between the 14th and 21st d (within RES and COL stands). After 21 d, younger RES (R8: 18.37 ± 2.45 %) and COL stands (C5: 17.11 ± 1.28 %) have 49 % and 38 % higher remaining mass proportion of leaf litter than the NAT (12.35 ± 1.24 %) stands (Fig. 3C and D). The half-lives ($t_{0.50}$) in different stand ages ranged from 6 to 12 days and the total life ($t_{0.99}$) of the leaf litter, until complete decay, was projected from 43 to 84 days (Supplementary Table 2).

3.3. Pattern of total root biomass

Root biomass significantly varied across stand types ($F = 12.15$, $p < 0.001$) and ages ($F = 4.47$, $p < 0.001$; Fig. 4A and B). RES (49.20 ± 6.76 Mg/ha) and COL (13.78 ± 2.69 Mg/ha) stands have 45 % and 85 %

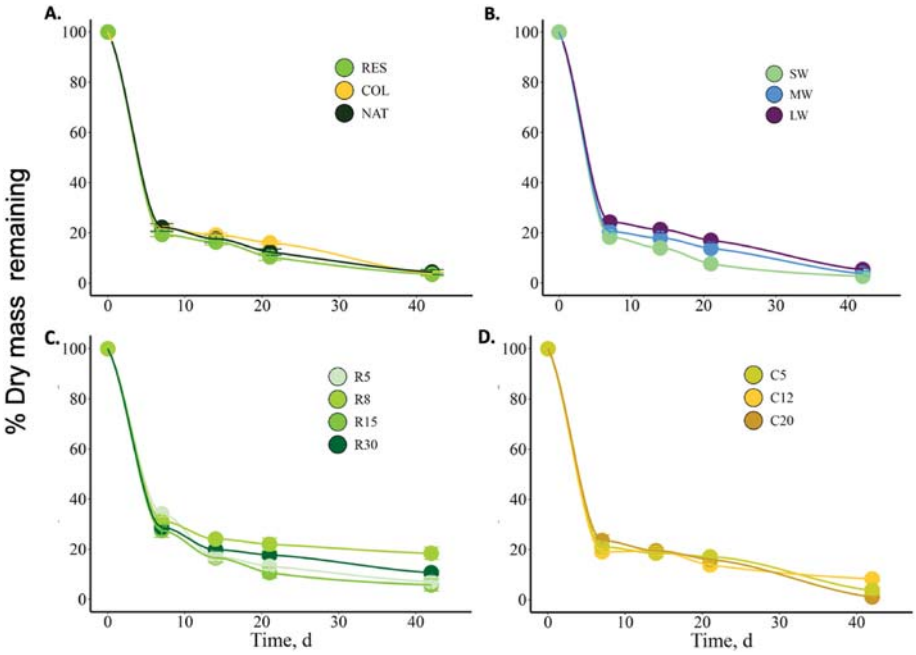

Fig. 3. Remaining dry mass (%) of *A. marina* leaf litter in different A) stand types, B) zonations, and stand ages of C) restored stands, and D) naturally recolonized mangrove stands. Younger stands have higher remaining mass proportion than mature stands. R5 (5 yrs old), R8 (8 yrs old), R15 (15 yrs old), and R30 (30 yrs old) are restored 'planted' (RES) stands; C5 (5 yrs old), C12 (12 yrs old), and C20 (20 yrs old) are naturally recolonized (COL) stands; NAT are natural stands of unknown ages. SW: seaward, MW: midward, LW: landward.

lower root biomass than NAT stands (89.88 ± 16.12 Mg/ha). Root biomass in RES stands ranged from 13.28 ± 3.44 Mg/ha to 66.69 ± 0.73 Mg/ha and differed significantly by age ($F = 5.57$, $p < 0.001$) with lowest root biomass from R5 stand (13.28 ± 3.44 Mg/ha). Root biomass in COL stands ranged from 5.42 ± 2.29 Mg/ha to 19.49 ± 4.19 Mg/ha and differed significantly by age ($F = 5.06$, $p < 0.05$) with lowest root biomass from C5 stand (5.42 ± 2.29 Mg/ha). More mature RES and COL stands have higher root biomass than younger stands of the same stand type although not comparable with NAT stands (Fig. 4B). Root biomass significantly varied with stand types and depths ($F = 5.88$, $p < 0.001$; Fig. 4C), with zones and depths ($F = 1.77$, $p = 0.001$; Fig. 4D), and with ages and depths among RES and COL stands ($F = 4.76$, $p < 0.001$; Fig. 4E and F). In general, root biomass increased with depth in NAT stands, but not pronounced among different ages of RES and COL stands (Fig. 4E and F).

3.4. Sediment accretion pattern

Sediment accretion rate did not vary across stand types, but varied significantly within RES ($F = 3.51$, $p < 0.05$) and COL stands ($F = 3.27$, $p < 0.05$). SW (9.23 ± 0.97 cm/yr) stands have 82 % and 91 % higher accretion rate compared to MW (4.83 ± 0.95 cm/yr) and LW (5.06 ± 1.26 cm/yr) stands, respectively (Table 2). Younger RES (R5: 10.06 ± 1.53 cm/yr) and COL (C5:8.27 ± 1.76 cm/yr) stands have 69 % and 22 % higher accretion rates than NAT stands (5.96 ± 0.91 cm/yr). More mature RES (R30: 6.34 ± 1.38 cm/yr) and COL (C20: 4.34 ± 2.16 cm/yr) stands have comparable accretion rates with NAT stands ($F = 2.4$, $p > 0.05$).

4. Discussion

Our study provides empirical data on litterfall production, leaf litter decay, root biomass, and sediment accretion across chronosequence of restored and recolonized mangrove stands. Litterfall production and root biomass increased with age, and then decreased as it matures in restored stands. Leaf litter decay varied between stand types and among restored and recolonized stands of different ages with higher mass proportion remaining in younger RES and COL stands. Our results showed wide range of sediment accretion rates in different stand ages (1.1–10.1 cm/yr) in both restored and recolonized stands. There are limited available data in the Philippines on mangrove litterfall production, leaf litter decay, root biomass, and sediment accretion for our study to compare with. Moreso on literatures that involve chronosequence of restored and recolonized stands. Our results provide empirical evidence on the contribution of restored and recolonized mangroves on productivity and the potential of naturally recolonized abandoned ponds as priority restoration areas.

4.1. Litterfall production pattern in chronosequence of mangrove stands

The return of ecosystem services following restoration initiatives is important in assessing its success (or failures; Lovelock et al., 2022). Healthy and recovered ecosystems are expected to show enhanced structural productivity compared to disturbed systems (e.g., abandoned ponds; Herbeck et al., 2020; McKee and Faulkner, 2000). Our results showed productivity differences among stand types and within restored and recolonized stands, with higher total litterfall production in younger stands that tend to resemble mature stands (Fig. 2C). Productivity differences can be attributed to a combination of stand ages and management practices (Zaman et al., 2023; Azman et al., 2021; Hanggara et al., 2021). The litterfall production pattern in terms of stand age reported in our study followed typical patterns in forest stand development where younger forests showed increased aboveground net productivity then stabilized as stands mature (Berger et al., 2004). A stand density of 2500 stems/ha is sufficient to restock a degraded mangrove stand (FAO, 1994). In our study, however, younger restored and recolonized stands had a high tree density exceeding 4,000 trees/ha due to dense planting (*pers. obs.*) and unobstructed water flow that accumulates seedling recruits (C5 stand). Such density may contribute to initial higher litterfall production in younger stands. High tree density can lead to competition for resources, including the potential shielding of seedlings (and saplings) from photosynthetic active radiation and hence negatively affect stand productivity (Wang'ondu et al., 2014). In an overcrowded *Kandelia obovata* stand in Okinawa, Japan, self-thinning resulted in a

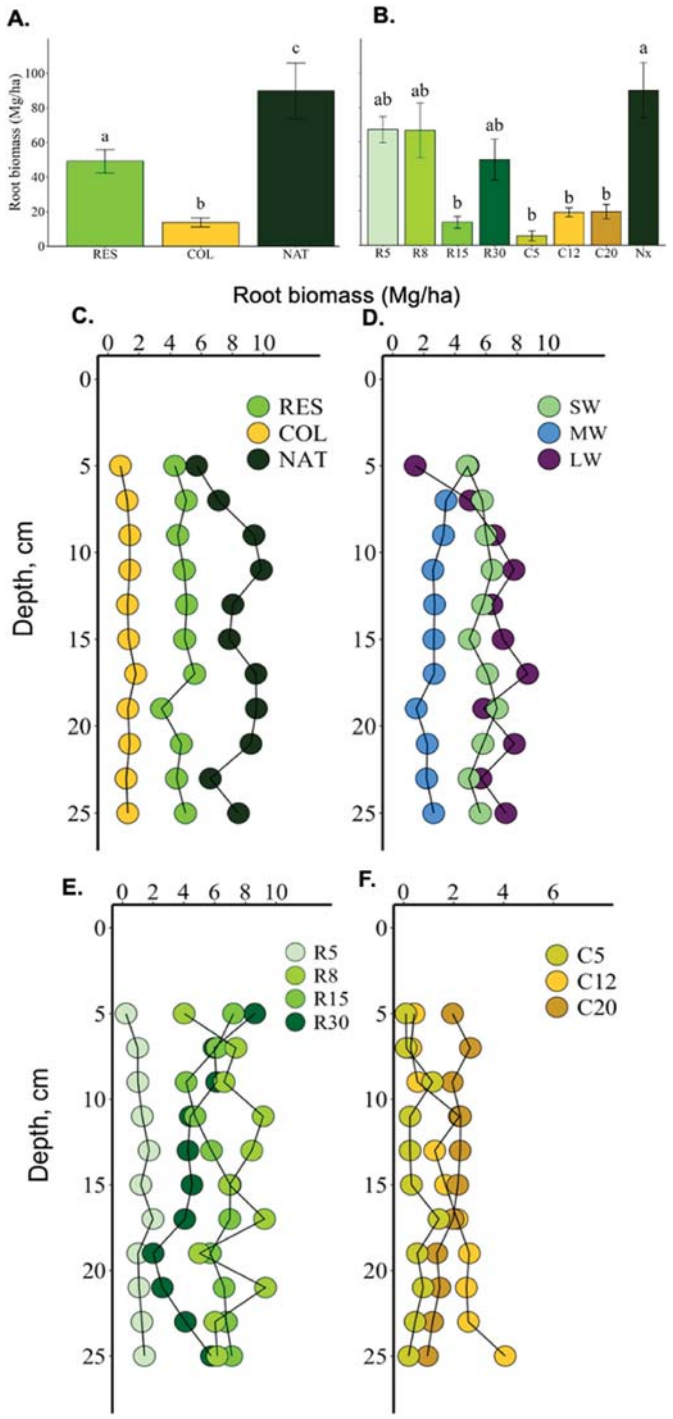

Fig. 4. Total root biomass (Mg/ha) according to A) stand types, B) stand ages; and its down-core distribution according to C) stand types, D) zonations, and stand ages of E) RES, and F) COL stands. Points for down-core BRB variation were mean values for each depth interval (5-cm interval for the 0–5 cm layer and subsequently 2-cm intervals for the 5–25 cm layer). Different letters above the error bars in A) and B) indicate a significant difference between stands (at $\alpha = 0.05$; Tukey's HSD test). R5 (5 yrs old), R8 (8 yrs old), R15 (15 yrs old), and R30 (30 yrs old) are restored 'planted' (RES) stands; C5 (5 yrs old), C12 (12 yrs old), and C20 (20 yrs old) are naturally recolonized (COL) stands; Nx are natural (NAT) stands of unknown ages. SW: seaward, MW: midward, LW: landward.

Table 2
Sediment accretion rates in chronosequence of restored and recolonized mangrove stands in Ormoc, Philippines. R5 (5 yrs old), R8 (8 yrs old), R15 (15 yrs old), and R30 (30 yrs old) are restored 'planted' stands; C5 (5 yrs old), C12 (12 yrs old), and C20 (20 yrs old) are naturally recolonized stands. Nx are natural (NAT) stands of unknown ages. SW: seaward, MW: midward, LW: landward.

Stand code	Stand type	Zonation	Species	Accretion rate (cm/yr)
Nx	Natural	SW	Mixed species	5.1 ± 0.9
R5	Restored	SW	*A. marina*-dominated	10.1 ± 1.5
R8	Restored	LW	*A. marina*-dominated	1.1 ± 0.2
R15	Restored	SW	*S. alba*-dominated	9.8 ± 2.6
R30	Restored	MW	*A. marina*-dominated	6.3 ± 1.6
C5	Recolonized	LW	Mixed species	8.3 ± 1.8
C12	Recolonized	SW	Mixed species	9.7 ± 1.1
C20	Recolonized	MW	Mixed species	4.3 ± 2.2

decrease in tree density and nearly constant annual leaf litterfall (Sharma et al., 2012). In the process of self-thinning, space becomes available for the remaining trees. Consequently, the surviving trees can extend more branches and develop more leaves, leading to an increase in mean leaf mass per tree as the stand matures (Sharma et al., 2012; Analuddin et al., 2009). The higher litterfall production in the LW zone compared to SW and MW zones can be attributed to tree density (~2,000–5,000 trees/ha) and differential allocation of photosynthetic products between leaf and non-leaf components of a mangrove (Salas-Rabaza et al., 2024). Mangroves in the SW zone are exposed to several additional stresses including inundation with high salinity water and exposure to erosion due to wind and waves (particularly during typhoons; Salmo, 2021). Preferential allocation of photosynthetic products to trunk and root growth (Salas-Rabaza et al., 2024; Castañeda-Moya et al., 2011) over leaf production provides a stable support system (Krauss and Osland, 2020).

Litterfall input in Ormoc (restored: 8.31 Mg/ha/yr, recolonized: 12.29 Mg/ha/yr, natural: 6.35 Mg/ha/yr; Fig. 2A) lies within the range of tropical mangrove litterfall production (3–18 Mg/ha/yr globally, 5–18 Mg/ha/yr SEA; Table 3). Management practices (i.e., selective pruning or harvesting has been widely reported to affect litterfall production). In Japan, artificial thinning of *Kandelia obovata* stands showed decreasing litterfall production with increasing thinning intensity although annual litterfall production did not significantly vary between control and artificially thinned plots (Kamara and Kamruzzaman, 2020). However, selective pruning of *Rhizophora mangle*-dominated forest in Florida, USA showed decreased litterfall production (Parkinson et al., 1999). The significantly higher total litterfall production in younger recolonized stand (C5: 18.75 Mg/ha/yr) can be potentially attributed to stand age and soil fertility. C5 stand receives freshwater inputs that may contribute to the nutrient source of the stand (Fig. 1; Supplementary Fig. 1). Consequently, the complete destruction of dikes has introduced tidal water exchange to the abandoned ponds, potentially adding nutrient load to the site. Krauss et al. (2006) reported soil fertility as a contributing factor to stand development and hence litterfall production. In China, plant biomass production is enhanced with soil fertility due to increased access to available resources (i.e. water, light, nitrogen; Bai et al., 2021). Our results provide evidence on litterfall productivity variations in restored and recolonized stands in Ormoc, which is valuable for pro-active restoration, especially the need to restore water flow in abandoned ponds.

4.2. Leaf litter decay pattern in chronosequence of mangrove stands

The decay pattern reported in our study followed a single exponential function with differences in the remaining mass over time in the

Table 3
Comparison of annual total litterfall production (Mg/ha/yr) of restored and recolonized stands in Ormoc, Philippines and other mangrove forests worldwide.

Location	Stand type	Genus/Species	Total litterfall (Mg/ha/yr)	Reference
Central Visayas, Philippines	Planted (30 yrs)	*Avicennia, Rhizophora, Sonneratia*	24.05–30	Rafael and Calumpong (2018)
	Natural	*Avicennia, Rhizophora, Sonneratia*	30.22–35.55	
Panay Is, Philippines	Planted (19 yrs)	*Rhizophora*	12.7	Ogawa et al. (2022)
	Natural	*Avicennia*	16.4	
		Sonneratia		
Trang, Thailand	Planted (10–25 yrs)	*Rhizophora*	13.25	Cadiz et al. (2021)
	Natural	*Avicennia, Bruguiera, Xylocarpus*	11.9	
Bali, Indonesia	Planted (14- >15yrs.)	*Rhizophora*	13.96	Pradisty et al. (2021)
	Natural	*Avicennia, Ceriops, Rhizophora, Sonneratia*	10.18	
Ca Mau, Vietnam	Planted (6–35 yrs)	*R. apiculata*	9.42–18.79	Clough et al. (2000)
Gazi Bay, Kenya	Planted (5–13 yrs)	*R. mucronata and S. alba*	5.22–10.15	Wang'ondu et al. (2014)
	Natural	*R. mucronata* and *S. alba*	8.36–10.15	
Okinawa, Japan	Natural thinning	*Kandelia obovata*	10.10	Kamara and Kamruzzaman (2020)
	Artificial thinning (15%–30% stems removed)		8.50–8.97	
SW Florida, USA	Natural	*R. mangle* dominated	3.73	Parkinson et al. (1999)
	Selective pruning (~50% of lateral branches pruned)		3.05	
Atrato River Delta, Southern Caribbean, Colombia	Natural	*R. mangle* dominated	20	Riascos and Blanco-Libreros (2019)
Ormoc, Philippines	Restored (5 yrs)	*Avicennia,*	5.90	This study
	Restored (8 yrs)	*Sonneratia*	10.05	
	Restored (15 yrs)		11.08	
	Restored (30 yrs)		6.13	
	Recolonized (5 yrs)	*Avicennia,*	18.75	
	Recolonized (12 yrs)	*Sonneratia*	4.23	
	Recolonized (30 yrs)		6.13	
	Natural	Mixed species	6.35	

different stands. Based on decay rates, Ananda et al. (2008) categorized litter decay rates into fast (K > 0.01), medium (K = 0.005–0.01), and slow (K < 0.005) types. Our results showed fast leaf litter decay rates of *A. marina* in all stand ages (0.06–1.20 K/d; Supplementary Table 2). Our reported fast leaf litter decay rates can be attributed to the tropical conditions suitable for higher microbial activity and rapid litter decay (Zhai et al., 2021). The decay rate of *A. marina* in our study are comparable with the decay rate of *A. officinalis* in India (0.03 K/d, Mamidala et al., 2023) and higher compared to *R. apiculata* in Malaysia (0.013 K/d, Kamal et al., 2020), *Bruguiera gymnorrhiza* in Japan (0.02 K/d, Mfilinge et al., 2002), and *Acrostichum aureum* in Indonesia (0.0074–0.0081 K/d, Pradisty et al., 2021). Previous studies have reported interspecific variation in leaf litter decay and concomitant release of nutrients (Mamidala et al., 2023; Bosire et al., 2005). These can be attributed to differences in C:N ratio with fast decay of detrital material with high N-content (or low content of phenolics, lignins or cellulose, Lang et al., 2024). Pradisty et al. (2021) reported that leaf phenolic compounds slow down litter decay microbial activity. Other than plant litter quality, substrate differences, and faunal association, management practices are thought to affect litter decay. Bosire et al. (2005) reported improved decay rates of *S. alba* and *R. mucronata* in reforested plantations (~8 yrs) compared to degraded stands due to improved site conditions in reforested stands. The higher remaining mass proportion of leaf litter in the LW zone compared to SW and MW zones (Fig. 3B) can be partly explained by the infrequent tidal inundation in the upper parts of the mangrove shore, where leaf litter accumulates and decomposes *in situ* or consumed by associated fauna (Pradisty et al., 2022). In SW zone, increased submergence of leaf litter was previously described to accelerate speed of decay (Dhaou et al., 2022). The physical impact of tides on leaves can accelerate leaf fragmentation (Mamidala et al., 2023). Moreover, longer exposure time to saline water inundation can trigger leaf litter decay through sulfate reduction, compensating the general notion of reduced decay under anaerobic conditions (Arnaud et al., 2020). Leaf litter in the SW zone substantially contributes to nutrient source to adjacent coastal ecosystems (Gerona-Daga et al., 2024; Mamidala et al., 2023).

4.3. Patterns of root biomass in chronosequence of restored and recolonized stands

The measured BRB in this study from a chronosequence of recolonized stands increased as stand age, while BRB values from chronosequence of restored stands did not show a distinct pattern (Fig. 4B and E). The BRB pattern in chronosequence of recolonized stands in this study, resembles those found in replanted stands in Thailand and Kenya (Tamooh et al., 2008; Alongi and Dixon, 2000) wherein root biomass increased with age. In Thailand, a 5-yr *R. apiculata* planted stand had 8, 169 Mg/ha of live root biomass and increased to 12,590 Mg/ha at 25 yrs. Similarly, a 6 yr-old *R. mucronata* planted stand in Kenya had 653 Mg/ha of root biomass; at 12 yrs, the root biomass increased to 2,171 Mg/ha (Tamooh et al., 2008). In our study, the lower total root biomass in R15 stand compared to mature R30 stand can be attributed to species variation (Adame et al., 2017). *S. alba* dominates the R15 stand in contrast to the other restored stands with dominating *A. marina* (Table 1). Lang'at et al. (2013) observed higher root biomass in mangrove stands where the dominating species is *A. marina*. However, the sampling technique employed (i.e., core method vs trench method, positioning of cores, etc.) may also underestimate the values in mature stands. For example, the positioning of the cores relative to the tree trunks may have led to the underestimation of root biomass of *A. alba* natural stand in Malaysia (18.88 Mg/ha; Muhammad-Nor et al., 2019).

The BRB from recolonized stands increased with stand age (5–19 Mg/ha; Fig. 4B and Fig. 4F) but were lower compared to the range reported for mangroves worldwide (Supplementary Table 3). This probably reflects the slow recovery of root biomass in previously abandoned ponds. The stressful physico-chemical conditions following pond construction, such as soil removal/excavation, vegetation clearing, and changes in hydroperiod, can significantly slow down the recovery of root biomass. Excavation and prolonged exposure of soil to air can lead to the formation of acid sulfate soils. When these soils are later flooded, acid ions such as hydrogen (H), ferrous (Fe), and aluminum (Al) are released into the water, which is toxic and can inhibit root growth (Xiong et al., 2021). Vegetation clearing negatively impacts nutrient

pools in mangroves because of the sudden reductions in both above-ground and below-ground biomasses including litterfall, and consequently nutrient inputs (Grellier et al., 2017; Singh et al., 2015). Nutrient availability is required for root growth to obtain water and nutrients (Medina-Calderón et al., 2021; Torres et al., 2021). Additionally, with barriers to hydrologic flows imposed by pond dykes, longer inundation time increases hydrogen sulfide and decreases soil redox potential (Chen et al., 2023) which can decrease root growth and hence, biomass. In a glasshouse experiment of *A. germinans* seedling, flooding decreased root biomass due to increased production of hydrogen sulfide (Adame et al., 2017; Cormier et al., 2015; Krauss et al., 2006). In planted *K. obovata* stands, increasing inundation time decreases oxygen demand for fine root growth, which further reduces fine root biomass (Chen et al., 2023).

Here, we analyzed BRB from the top 25 cm of soil, considered as the tide-sensitive layer, where inundated water affects root growth (Komiyama et al., 2020). In Thailand, inundated water from the Trat River caused higher root biomass in the riverine *Avicennia* zone (Hongwiset et al., 2021). In our study, mangrove stands in the LW zone receive direct freshwater input from Bao River which creates a favorable condition for root growth due to physiological and osmotic pressures (Komiyama et al., 2020). In addition, the LW zone is dominated by high density of *A. marina* (Table 1), a fast-growing species with a dense cable-root system concentrated in the topsoil (Tamooh et al., 2008).

4.4. Sediment accretion pattern in the chronosequence of mangrove stands

Our study provides empirical evidence on the rapid short-term accretion rates of Ormoc mangrove forest. The wide range of sediment accretion rates in different stand ages (1.1–10.1 cm/yr) reflect variations in sediment delivery controlled by hydroperiod and distance from both the river and the intertidal flats, which supply sediments via wave-driven resuspension to the mangrove forest (Swales and Lovelock, 2020). Our reported values are nevertheless within the range of values measured in other mangrove forests (0.02–16.3 cm/yr) where fluvial and tidal sediment depositions are evident, measured primarily using feldspar marker beds, sediment traps, and ^{210}Pb dating technique, and over longer time scales (~5 yr; Supplementary Table 4). Using artificial marker horizon, Saad et al. (1999) reported sediment accretion rates of 0.66–1.46 cm/yr at an estuarine mangrove in Terengganu, Malaysia. Higher sediment accretion rates (1.8–2.5 cm/yr) were reported in mangroves near the riverbank in Kamora Estuary, Indonesia using sediment traps (Setyadi et al., 2021). Considering stand age, younger stands were reported to have higher sediment accretion rates due to high structural complexity of the mangrove forest floor and the ability of young forests to trap and retain sediments. Similar pattern was observed in our study where R5 and C5 stands showed 98 % and 68 % higher sediment accretion rates compared to NAT stands (Table 2). Such sediment accretion improvement in restored and recolonized stands is beneficial for mangrove-seedling recruitment (Albers and Schmitt, 2015) and hence productivity of mangroves. However, monitoring permanent plots is suggested to track sediment dynamics and prevent the burial of roots and seedlings that can potentially interrupt root and soil gas exchange, and eventual death of seedlings and trees (as observed in common Thailand mangroves; Thampanya et al., 2002).

4.5. Implications for mangrove conservation, restoration, and research

Mangrove restoration has been implemented in many parts of Southeast Asia, including the Philippines, with monogeneric planting as the most dominant strategy (Gerona-Daga and Salmo, 2022). However, the long history of massive mangrove planting on coastal fringes has often failed to meet its restoration objectives. These failures are mainly due to large-scale dense planting of mangroves conducted in inappropriate or unsuitable sites and poor site/species matching (Wodehouse and Rayment, 2019). Thus, proactively restoring the mid-to upper--intertidal abandoned aquaculture ponds previously occupied by mangroves are potential areas for restoration (Lovelock et al., 2022). Our study provides evidence on the recovery of mangrove forest productivity in restored stands following reported trajectory patterns in mangrove vegetation (Azman et al., 2021; Salmo et al., 2013). Younger restored stands have low species diversity and high tree density, ranging from 2, 000 to 5,000 trees per hectare (Table 1). Higher tree density in mangrove forests leads to increased litterfall production (Wang'ondu et al., 2014) and root biomass (He et al., 2021). Although leaf litter decay rates were considered fast (Ananda et al., 2008) across stand types and ages, having a balance between fast and slow decaying litter is important to provide readily available nutrients for plant uptake (and microbes), and provide a longer-lasting pool of nutrients to be released into the soil environment more evenly over time.

From the measured parameters in chronosequence of restored and recolonized stands, litterfall production increased and tended to stabilize as it matured. As litterfall accumulates on the forest floor, it undergoes decay, contributing organic materials and nutrients to the forest floor and soils (Lang et al., 2024; Bosire et al., 2005). The accumulation of litterfall in forest floor can be attributed to the increase in foliage density aboveground (reflected as tree density; Table 1), and related increase in BRB with stand age (Fig. 4B) which additionally help in binding and stabilizing sediments, further facilitating sediment accretion (Table 2). Aside from stand age, root biomass can also vary with stand structure (as observed in R8, *A. marina* dominated stand vs R15, *S. alba* dominated stand). Following mangrove degradation, naturally recolonized stands from this study showed varying recovery patterns (to no distinct pattern as observed in sediment accretion rate with stand age) in terms of litterfall production and decay, and root biomass. Mangrove degradation slowed leaf litter decay (Fig. 3A and D; Supplementary Table 2) and constrained root growth (as evidenced by the lower root biomass in COL stands; Fig. 4A, B, and F). However, our observed recovery on litterfall production and decay, and root biomass from recolonized stands may vary from other abandoned ponds due to differences in extractive pressures and pond management practices.

Our study showed a huge potential contribution of recolonized stands on mangrove productivity as evidenced by the higher litterfall production compared to natural stands. Interestingly, younger recolonized stands showed exceptionally high litter production and sediment accretion rates. Assisted natural regeneration by restoring hydrology, such as removing dikes and pond walls, is a cost-effective method in restoring abandoned ponds (Sidik et al., 2021; Djamaluddin et al., 2018). Waterborne seeds and propagules of mangroves from adjacent natural stands are not hindered or blocked and thus facilitate seedling recruitment (Wang'ondu et al., 2014). The absence of dike in the younger recolonized stand contributed to its high species diversity as opposed to the recolonized stand with intact dikes (C12, Table 1) which may explain the differences in litterfall production and sediment accretion. In abandoned ponds, the severity of damage (i.e. application of fertilizers, vegetation clearing, longevity, etc.) is expected to affect its long-term recovery. The establishment of long-term permanent plots for monitoring recovery trajectories both in restored and recolonized stands is highly suggested.

In 1994, there were approximately 232,000 ha of aquaculture ponds in the Philippines, some of which are active, while others have been abandoned or underdeveloped (Salmo and Gianan, 2019; Castillo et al., 2017a). Between 2000 and 2012, an estimated additional 522 ha of mangroves were converted to aquaculture (Castillo et al., 2017b). In total, these conversions amount to approximately 232,520 ha. Assuming that 50 % of these ponds are abandoned, underutilized, or underdeveloped (AUU) (Salmo and Gianan, 2019), and using our study's litterfall production rate in recolonized mangrove stands (12.29 Mg/ha/yr), the potential for carbon storage can be calculated. With a conversion factor of 0.45 for litter to carbon concentration (Kauffman and Donato, 2012), the Philippines could gain an additional ~642,975 Mg C/yr of annual

carbon storage from litterfall in recolonized mangrove stands. But this carbon supply can only be gained, once AUU ponds have been naturally recolonized for at least 5 yrs. Similarly, the approximately 116,260 ha of AUU ponds in the Philippines (cf. Salmo and Gianan, 2019) offers an opportunity to study the changes in litterfall production and decay, root biomass, and sediment accretion to advance our understanding on the recovery dynamics of AUU ponds.

Our study documented short-term sediment accretion rates in chronosequence of RES and COL stands using makeshift acrylic corers. The use of makeshift acrylic corers may be a cost-effective approach in studying sediment dynamics, however, it can potentially overestimate sediment accretion due to the design of the acrylic corer. The protruding body of the acrylic corer can set as 'trap' to the sediment particles and might disturb the surrounding flow hydrodynamics. In improving the design of such studies, complementary measurements, such as the vertical activity profiles of radioisotopes (i.e., ^{210}Pb, Jupin et al., 2023; Wigand et al., 2021) and Rod Surface-Elevation Table–Marker Horizon method(RSET-MH; Rogers et al., 2006) can be employed. Several studies have demonstrated the reliability of these methods in coastal wetlands, mostly from the United States, Australia, Caribbean (MacKenzie et al., 2023; Webb et al., 2013), and a few in Southeast Asia (Friess et al., 2019). In particular, less attention has focused on tracking trajectory patterns of sediment dynamics in chronosequence of mangrove stands (restored or recolonized; passive restoration vs active restoration). Studies of sedimentation dynamics with annual to decadal time scales are essential to improve our understanding of sedimentary processes in restored and recolonized mangroves for science-based management and policy formulation.

5. Conclusions

Here, we found that restored stands showed clear progression in litterfall production and decay, and root biomass with age. However, our results for the recolonized stands (to our knowledge is the first report for Philippine mangroves with natural recolonization), showed contrasting patterns for root biomass. There was no discernible pattern for sediment accretion with stand age. Younger restored and recolonized stands showed higher litterfall production and total root biomass due to higher tree density. In view of litterfall dynamics and root biomass, multispecies planting is suggested in future mangrove restoration projects to sustain the coastal food web, improve the soil nutrient pool, and enhance coastal protection. Moreover, our results demonstrated the varying recovery potentials of naturally recolonized abandoned ponds in terms of litterfall dynamics, root biomass, and sediment accretion after abandonment. Monitoring permanent plots is suggested for adaptive management strategies and to improve restoration outcomes.

CRediT authorship contribution statement

Maria Elisa B. Gerona-Daga: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Richard A. MacKenzie:** Writing – review & editing, Funding acquisition. **Severino G. Salmo III:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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