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Photosynthetic characteristics of mangrove seedlings in chronosequence of restored and recolonized stands under field conditions

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ABSTRACT.—Mangrove forests are the dominant ecosystems on tropical and subtropical coasts, subjected to widespread degradation and land conversion, such as aquaculture. To restore mangrove cover, mangrove seedlings were planted in coastal fringes and abandoned ponds. Most restoration reports were focused on seedling survival and growth rates. However, physiological conditions of mangrove seedlings, in terms of photosynthetic characteristics under field conditions, have seldom been studied. Mangrove seedlings from restored "planted" (5, 8, 15, and 30 yr old) and recolonized (5 and 20 yr old) stands were monitored for a year to assess their photosynthetic performance. These were compared with a reference system consisting of mature, natural stands of unknown ages. Chlorophyll fluorescence–based parameters, leaf temperature differential (LTD), and relative chlorophyll content (SPAD) were measured. At younger restored and recolonized stands, actual photosystem II (PSII) efficiency (Phi2) and PSII maximum efficiency (F_v'/F_m') of the seedling leaves were lower compared to natural stands. Yields of nonregulatory energy dissipation (PhiNO) and electron transport rates (ETR_{PSII}) were higher in younger restored and recolonized stands than natural stands. This suggests excess energy production which can lead to potential damage to photosystems. The lower photosynthetic efficiency and higher potential damage of seedling leaves may reflect suboptimal environmental conditions in both the restored and recolonized stands. The photosynthetic efficiency tended to improve as the age of the stands mature. This study provides the first physiological measurements of mangrove seedlings under different field conditions in the Philippines and highlights the role of photosynthetic regulation for seedling establishment and growth.

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Mangrove forests provide essential ecological and socio-economic benefits, such as protecting shorelines, supporting biodiversity and fisheries, and playing a key role in carbon sequestration and storage (Dahdouh-Guebas et al. 2021). However, they are under threat due to widespread degradation and conversion for other economic activities, such as aquaculture (Luo et al. 2022). The sustainable use of mangrove forests requires a thorough understanding of the ecological and physiological processes by which mangrove forests are affected by, and recover from both natural and anthropogenic disturbances.

Healthy mangroves are linked to the stability and productivity of the forest. An appropriate stage to begin to understand physiological processes in relation to ecological patterns is at the seedling level, because this phase of life history is an important determinant of forest structure (Ball 2002). Seedling recruitment and growth contribute to the stability of the forest but are challenging in inherently stressed environments such as mangrove forests (Ewel and Baldwin 2024). In the occurrence of a disturbance (i.e., typhoons), seedlings initiate post-typhoon recovery (Duke 2001, Salmo 2021). The survival and growth of established mangrove seedlings, and their progression to the sapling stage, are primarily determined by the availability of light and nutrients (Padilla et al. 2004), hydrogeomorphic settings (Ewel and Baldwin 2024), soil chemistry (van Bijsterveldt et al. 2020), and sensitivity to physicochemical stress factors (Xu et al. 2023, Matsuo et al. 2024). However, the dynamics of mangrove seedlings under various stand conditions remain largely unknown.

In the Philippines, mangroves exist in various stand conditions (natural, restored, and recolonized) and are influenced by different climatic and geomorphological conditions (Corcino et al. 2023). "Natural stands" (herein, NAT stands) are mangroves that naturally occur on the site without any direct or indirect human intervention. "Restored stands" (herein, RES stands) refer to planted stands. "Recolonized stands" (herein, COL stands) are abandoned ponds that were naturally recolonized/revegetated with mangroves.

Abandoned ponds often represent highly degraded and stressful environments to growing mangroves (Xiong et al. 2021). Stressed conditions reduce or disrupt photosynthetic metabolism, and thus the capacity for orderly energy dissipation and increase vulnerability to photoinhibition (Ball 2002). The stressful physicochemical conditions following pond construction (e.g., removal/excavation, vegetation clearing, and changes in hydroperiod) can probably decrease the photosynthetic efficiency of recolonizing mangroves. In the Philippines, about 317,500 ha of mangroves (about 70% of the total mangrove cover in 1990s, Walters 2000) have been converted to aquaculture ponds. However, some of these aquaculture ponds have been abandoned and were naturally recolonized by mangroves (delos Santos et al. 2022, Salvaña et al. 2024). Other aquaculture ponds were included in more active mangrove restoration programs implemented in the 1990s where mangrove seedlings were planted with varying success (Wodehouse and Rayment 2019, Salmo 2021). Several restoration reports include seedling survival, mortality, recruitment, and growth rates over a short period of time (Padilla et al. 2004, Wodehouse and Rayment 2019). However, physiological conditions of mangrove seedlings, in terms of photosynthetic characteristics under field conditions, have seldom been studied.

Stress adversely affects the growth, development, and overall "ecosystem health" of mangroves (D'Addazio et al. 2023). Depending on the nature, occurrence/persistence,

and magnitude of stress, the effects are manifested in the vegetation structure, productivity, and photosynthetic performance of mangroves (Rovai et al. 2013, Salmo 2021, Krauss et al. 2023). The health and response of plants are widely assessed through photosynthetic characterization in other taxa (Liu et al. 2023, Moustaka and Moustakas 2023) but rarely applied in mangrove seedlings under field conditions due to inherent difficulty in field sampling. Photosynthesis is expected to vary with species, stand ages, ecosystem health, and geomorphic conditions (López-Hoffman et al. 2006, Cadiz et al. 2021) in response to, and/or as adaptation mechanisms against stress (e.g., leaf thickness, thermo-regulation, increased efficiency, etc. (Deva et al. 2020, Chen et al. 2022, Sturchio et al. 2023). Recently, photosynthetic capacity is assessed using chlorophyll fluorescence–based parameters due to its simplicity, high-throughput advantages, and nondestructive method (Maxwell and Johnson 2000, Walker et al. 2018). In a stressful environment, such as the case of former mangroves that were converted into aquaculture ponds (with sparse vegetation and toxic sediment), photosynthesis is expected to be constrained and less efficient. In contrast, restored mangroves (of different ages) might have better photosynthetic efficiency and could be similar to that of healthy natural mangroves.

In mangroves, photosynthetic measurements are mostly conducted under controlled conditions, either in greenhouse or mesocosm experiments, but is rarely investigated under field conditions. Values for photosynthetic efficiency of photosystem II (PSII) and other chlorophyll fluorescence values for mangrove seedlings have been focused in response to salinity (Chen et al. 2022), light (Kitao et al. 2003), and flooding (Salas-Rabaza et al. 2024) under controlled conditions in greenhouse or mesocosm experiments. But the actual physiological response of the seedlings at the mangrove stands where those studies were done is not known. Studies under field conditions are necessary to provide a more realistic and ecologically relevant setting for scientific investigations.

In this study, we used the photosynthetic characteristics of mangrove seedlings to investigate the relative health of mangrove seedlings across a chronosequence of restored "planted" mangrove stands and naturally recolonized stands with intact mangrove forests as the reference (natural stands). We hypothesized that the photosynthetic performance of mangrove seedlings in RES and COL stands, differ significantly from NAT stands due to residual stressors following mangrove degradation.

Materials and Methods

Site Description.—The study was conducted in Ormoc Bay, mideastern Philippines (Fig. 1). Mangroves in Ormoc Bay receive freshwater and sediment inputs from Bao River. Some areas were once converted into fishponds, but many of these fishponds were abandoned over time and have since been naturally recolonized by mangroves (approximately 20 yr). Planting initiatives have been underway since the 1990s, comanaged by the city government and the Naungan-San Juan Mangrove Planters Association (NSJMPA). The mangroves in Ormoc Bay are generally categorized into natural (NAT), restored (RES), and recolonized (COL) stands (Gerona-Daga et al. 2024a). NAT stands are of unknown ages that naturally occur on the site without any direct human intervention (e.g., planting; considered as reference sites). RES stands refer to "planted stands" and as a result of previous

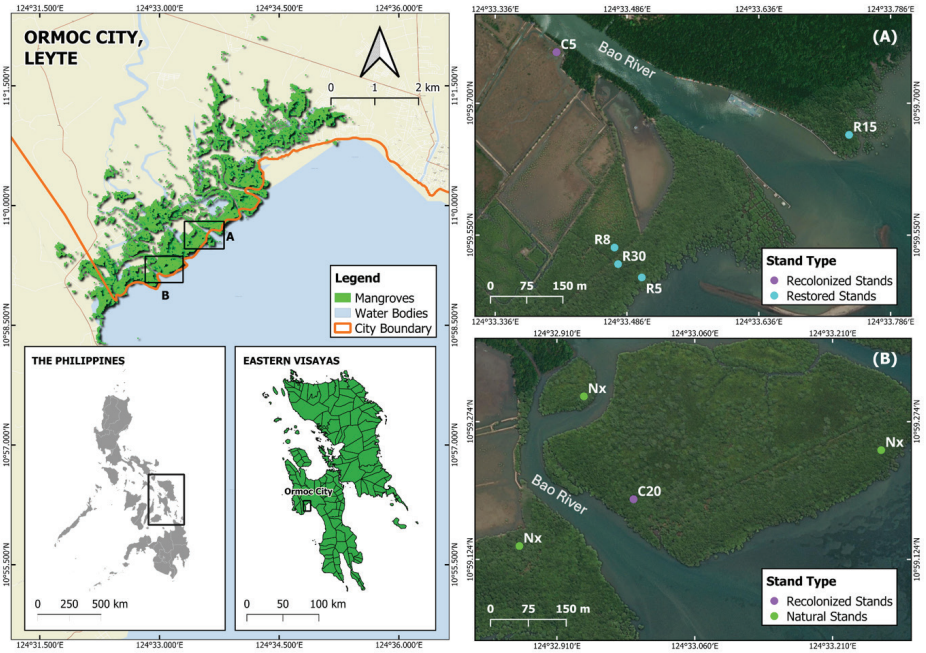

Figure 1. Location of the study sites in Ormoc, mideastern Philippines relative to the Philippine archipelago (left panel: bottom left) and the eastern Visayas region (left panel: bottom right). Permanent plots were established in restored "planted" stands (blue circles), recolonized stands (purple circles), and natural stands (green circles). Restored "planted" stands are marked as R5 (5 yr old), R8 (8 yr old), R15 (15 yr old), and R30 (30 yr old). Recolonized stands are marked as C5 (5 yr old) and C20 (20 yr old). Natural stands of unknown ages are marked as Nx.

mangrove planting projects. The estimated ages for RES stands varied based on the time of plantation, which were approximately 5, 8, 15, and 30 yr old (herein as R5, R8, R15, and R30 stands). 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 and 20 yr old (herein as C5 and C20 stands). The estimated ages of RES and COL stands were based on local accounts/records complemented with local maps and satellite images. Eleven mangrove tree species were observed, generally codominated by *Avicennia marina* and *Sonneratia alba*. However, only five genera of seedlings were noted, with *Avicennia* present in all stands. Younger RES stands are typically dense, with tree densities ranging from 2249 to 5178 trees ha^{-1} (Table 1, Supplementary Table S1).

Triplicate 7 m–radii plots were established in each stand type except in 5-yr stands where 5 m–radii plots were used. In total, 27 plots (9 NAT, 12 RES, and 6 COL) were monitored monthly from June 2022 to July 2023 (except for November–December 2022 due to frequent torrential rains). Porewater salinity and water temperature were measured per plot using Horiba (U-51, Essex UK).

Field Sampling.—Pulse-amplitude modulation (PAM) fluorometry, relative chlorophyll content, and leaf temperature differential (LTD) measurements were carried out using a MultispeQ v2.0 (Michigan, US) device. The device was calibrated using the CaliQ calibration system (https://photosynq.com/caliq) and

Table 1. Stand structure and climatic conditions in natural, restored and recolonized mangrove stands in Ormoc, Philippines. R5 (5 yr old), R8 (8 yr old), R15 (15 yr old), and R30 (30 yr old) are restored "planted" stands; C5 (5 yr old) and C20 (20 yr old) are naturally recolonized stands. Nx are natural stands of unknown ages.

Stand code	Stand type	Species	Tree density (trees ha^{-1})	Relative humidity (%)	Air temperature (°C)	Water temperature (°C)	Porewater salinity (ppt)	Redox potential (mV)
Nx	Natural	Mixed species	2,533	60.97 (0.30)	32.88 (0.12)	28.17 (0.55)	27.04 (3.41)	−75.00 (30.37)
R5	Restored	*A. marina*–dominated	2,249	58.63 (0.23)	33.71 (0.07)	28.80 (0.10)	28.58 (0.25)	−60.00 (5.04)
R8	Restored	*A. marina*–dominated	5,178	58.93 (0.13)	34.35 (0.09)	29.05 (0.11)	31.70 (1.26)	−251.33 (21.74)
R15	Restored	*S. alba*–dominated	1,537	60.41 (0.13)	33.07 (0.09)	28.83 (0.26)	25.86 (0.15)	−125.00 (9.00)
R30	Restored	*A. marina*–dominated	1,732	57.28 (0.13)	34.36 (0.09)	28.68 (0.11)	28.98 (0.67)	−177.66 (33.89)
C5	Recolonized	Mixed species	1,655	56.60 (0.19)	34.92 (0.08)	28.93 (0.26)	25.01 (0.15)	−114.00 (15.72)
C20	Recolonized	Mixed species	2,858	58.38 (0.22)	34.34 (0.08)	29.38 (0.12)	29.48 (0.29)	−184.00 (15.72)

linked to the web-based PhotosynQ platform (https://photosynq.org; Kuhlgert et al. 2016). Measurements were taken from the first fully expanded leaf (after the apical bud) of mangrove seedlings (n = 10 seedlings per genus per plot). Mangrove seedling identification was conducted up to the genus level due to the difficulty in differentiating the morphological characteristics of mangroves at the seedling stage. Samplings were performed on clear days from 0900 to 1400 hr (cf. Cadiz et al. 2021). To avoid light intensity effects, leaf measurement was taken without altering the leaf angle (i.e., leaf was not pulled out) and not covered or shaded by the researcher.

Chlorophyll Fluorescence, Absorbance, and Environmental Variable Measurements.—Using the Rapid Information Dense Experimental Sequence (RIDES) protocol (Photosynthesis RIDES 2.0) available on the PhotosynQ platform (https://photosynq.org/), measurements were initiated automatically upon clamping the leaf. The Photosynthesis RIDES 2.0 protocol was selected as it is very high throughput for field measurements (Marie et al. 2024). A single leaf measurement took about 20 s (*see* schematic diagram by Kanazawa et al. 2021). MultispeQ v2.0 enables the rapid capture of fluorescence parameters during steady-state illumination in the field (Kuhlgert et al. 2016) without dark adaptation (Tietz et al. 2017).

Saturation pulse chlorophyll fluorescence yield parameters (F_s, F_m' and F_0') in light-adapted leaves were measured (cf. Kuhlgert et al. 2016, Fernández-Calleja et al. 2020). Steady-state fluorescence yield, F_s, was collected under continuous actinic light. The sample was exposed to a brief saturating light pulse (about 10,000 µmol photons m^{-2} s^{-1} at 650 nm) to obtain an estimate of the maximal fluorescence yield under steady-state illumination, F_m'. Immediately after the saturation pulse, the actinic light was switched off. A pulse of far-red light (6 s pulse at 5 µmol photons m^{-2} s^{-1} at 730 nm) was applied to fully oxidize the plastoquinone pool and Q_A. This allowed the measurement of F_0' in the presence of steady-state levels of NPQ, but with all PSII centers oxidized (Baker 2008). These measurements allowed the calculations of fluorescence-based photosynthetic parameters which are useful indicators of plant's health status (Genty et al. 1989, Kuhlgert et al. 2016).

Physiological Parameters.—The actual photosystem II efficiency (Phi2) is a measurement of photosynthetic efficiency (Cadiz et al. 2021). Photoprotective nonphotochemical quenching (PhiNPQ) is the ratio of incoming light (excited electrons) lost through regulated nonphotochemical quenching (which is an indicator of photoprotection; Sooriyapathirana et al. 2021). On the other hand, yield of nonregulatory energy dissipation (PhiNO) is the ratio of incoming light (excited electrons) that is lost in nonregulated processes and can cause photodamage (Gitau et al. 2023). PSII maximum efficiency (F_v'/F_m') is a parameter that describes the maximum operating efficiency in the light-adapted state (Murchie and Lawson 2013). Additionally, fluorescence-based electron transport rate (ETR_{PSII}) and nonphotochemical quenching based on the rapid "total" NPQ method (designated as NPQt; Tietz et al. 2017) were measured. The selected parameters represented in this manuscript were chosen due to proven sensitivity to mangrove's health status (Rovai et al. 2013, Cadiz et al. 2021, Wang et al. 2022).

The associated macro code of the RIDES 2.0 protocol (https://photosynq.org/macros/photosynthesis-rides-2-0) automatically calculated the abovementioned parameters. The summation of Phi2, PhiNPQ, and PhiNO is equal to one (Kuhlgert

et al. 2016). An overview of the equations used in the protocol can be found on PhotosynQ's webpage "documentation" under the subsection "references and parameters" (https://help.photosynq.com/#measurements). ETR was calculated using formula: ETR = 0.84 × 0.5 × Phi2 × photosynthetically active radiation (PAR; Krall and Edwards 1992, Ibrahimova et al. 2021). Soil plant analysis development (SPAD) readings indicate greenness, which is the direct representation of relative chlorophyll content (Liu et al. 2023). Relative chlorophyll content (designated as SPAD) was estimated using the relative transmissions of red (650 nm) and infrared (940 nm) light (Fernández-Calleja et al. 2020). Leaf temperature differential (LTD) was calculated as the difference between the air and leaf temperatures (Kuhlgert et al. 2016).

Data Analyses.—Data were analyzed using repeated-measures design. Due to high data variability, the nonparametric Aligned Ranks Transformation Analysis of Variance (ART ANOVA; Mansouri et al. 2004) was used to determine if photosynthetic parameters significantly varied with stand type (NAT vs RES vs COL) and stand ages. For all the parameters, data from different genus per stand were pooled. Post hoc comparisons were made using Tukey's test to determine pairwise differences ($P < 0.05$). Principal component analysis (PCA) was conducted to assess the affinities of photosynthetic parameters among stand types. Spearman-rank correlation (SRC) was used to test the association among leaf thickness, relative chlorophyll content, and photosynthetic parameters. All data analyses and visualizations were implemented in R Statistical Software (R v4.2.2 and RStudio v2023.06.0+421).

Results

Higher Photosynthetic Efficiency and Lower Potential Damage in Mature Stands.—The photosynthetic characteristics significantly varied across stand types and ages (Fig. 2A–F, Supplementary Tables S2 and S3). The COL stands [mean (SE) = 0.51 (0.10)] had the least photosynthetic efficiency (Phi2) that were 4% to 9% lower than the RES [0.53 (0.10)] and NAT [0.56 (0.06)] stands (Fig. 2A; $F = 130.12$, $P < 0.001$). The Phi2 values were generally lower in younger stands that became comparable with NAT stands as age increased. Photoprotection (PhiNPQ) was significantly higher by 41% in younger RES [R5: 0.24 (0.13)] and COL [C5: 0.24 (0.08)] stands than the NAT [0.17 (0.07)] stands (Fig. 2B, $F = 94.26$, $P < 0.001$). Seedlings from R8 [0.28 (0.05)] and C5 [30 (0.08)] stands have 4% to 11% higher potential to photodamage (PhiNO) than NAT [0.27 (0.04)] stands (Fig. 2C; $F = 22.39$, $P < 0.001$). The PSII maximum efficiency (F_v'/F_m') in younger RES [R5: 0.71 (0.004)] and COL stands [C5: 0.72 (0.002)] were significantly lower by 4% and 3% than NAT [Nx: 0.75 (0.001)] stands (Fig. 2D; $F = 49.24$, $P < 0.001$). The nonphotochemical quenching (NPQt) values and electron transport rates (ETR_{PSII}) of mature RES and COL stands were comparable with NAT stands (Fig. 2E–F; $P > 0.05$). Younger RES [R5: 0.99 (0.05)] and COL [C5: 0.89 (0.02)] stands had significantly higher NPQt by 50% and 34% than NAT [Nx: 0.67 (0.02)] stands (Fig. 2E; $F = 48.96$, $P < 0.001$). ETR_{PSII} in younger RES [R5: 41.85 (2.10)] and COL [C5: 28.90 (1.23)] stands were significantly higher by 145% and 70% than NAT [Nx: 17.04 (0.54)] stands (Fig. 2F, $F = 53.55$, $P < 0.001$). There was a strong correlation between Phi2 and PhiNPQ ($\rho = -0.86$; $P < 0.001$) but weak

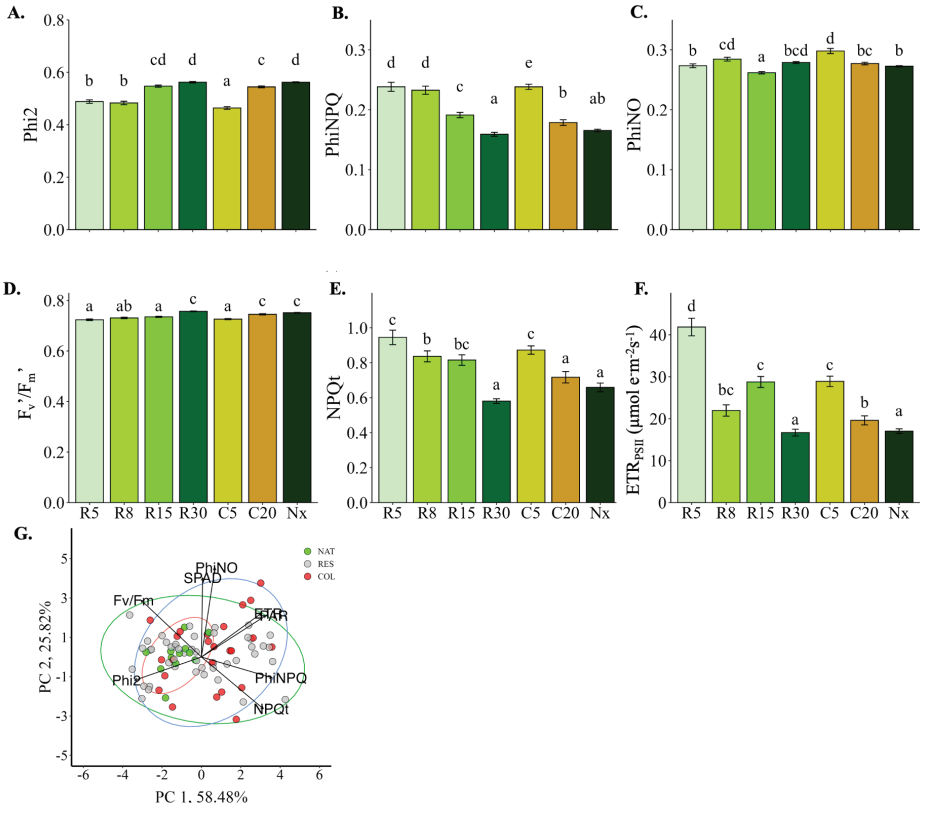

Figure 2. Photosynthetic parameters of mangrove seedlings from different ages of restored and recolonized stands, with reference to natural stands: (A) Phi2, actual photosystem II efficiency, (B) PhiNPQ, ratio of incoming light (excited electrons) lost through regulated nonphotochemical quenching, (C) PhiNO, ratio of incoming light (excited electrons) that is lost in nonregulated processes and can cause photodamage, (D) Fv′/Fm′: photosystem II (PSII) maximum efficiency, (E) NPQt, nonphotochemical quenching based on the NPQt method, (F) ETRPSII: PSII electron transport rate, (G) PCA plot based on photosynthetic parameters under different stand types. R5 (5 yr old), R8 (8 yr old), R15 (15 yr old), and R30 (30 yr old) are restored "planted" (RES) stands; C5 (5 yr old) and C20 (20 yr old) are naturally recolonized (COL) stands; Nx are natural (NAT) stands of unknown ages. Data are presented as the mean (standard error). Different letters above columns indicate significant differences across stand ages ($P < 0.05$).

between Phi2 and PhiNO ($\rho = -0.18$; $P < 0.001$; Supplementary Table S4). The PCA plot showed varying affinities of photosynthetic parameters. PC1 and PC2 accounted for 58.48% and 25.82% of variations, respectively. PAR ($\rho = 0.42$), ETR ($\rho = 0.42$), and Phi2 ($\rho = -0.42$) contributed the highest sources of variation in PC1 (Fig. 2G). RES stands have closer resemblance with COL stands due to comparable F_v'/F_m', NPQt, ETR_{PSII}, LTD, and SPAD values (Supplementary Table S2).

Leaf Thermoregulation.—Leaf thickness significantly varied with stand types and with ages (within RES and COL stands; $P < 0.001$; Supplementary Tables S2 and S3). The R8 [0.83 (0.05) mm] and C20 [0.73 (0.03) mm] have 20% and 6% thicker leaves than the natural stands [0.69 (0.01) mm]. *Sonneratia* seedlings had the thickest leaves in both RES (0.73–2.53 mm) and COL (1.03–1.14 mm) stands (Supplementary Table

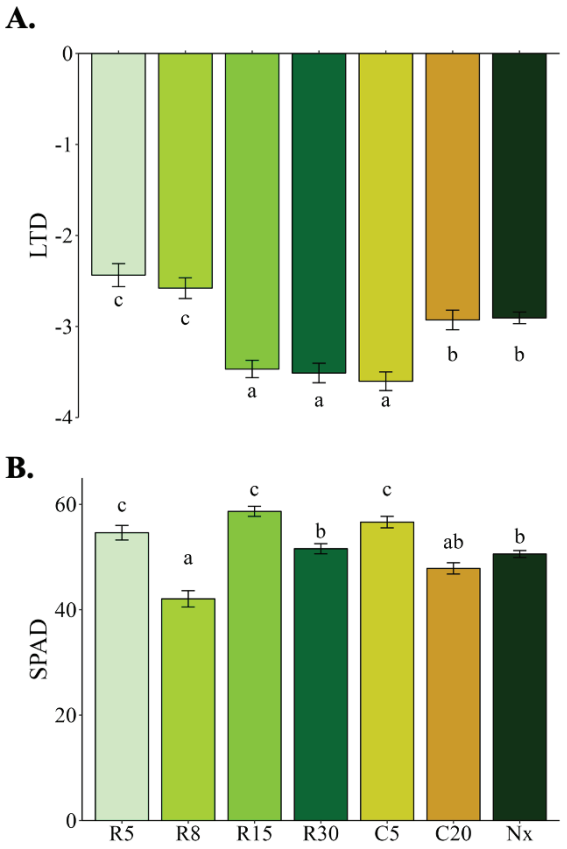

Figure 3. (A) Leaf temperature differential (LTD) and (B) relative chlorophyll content (SPAD) of mangrove seedlings from different ages of restored and recolonized stands, with reference to natural stands. R5 (5 yr old), R8 (8 yr old), R15 (15 yr old), and R30 (30 yr old) are restored "planted" stands; C5 (5 yr old) and C20 (20 yr old) are naturally recolonized stands; Nx are natural stands of unknown ages. Data are presented as the mean (standard error). Different letters above columns indicate significant differences across stand ages ($P < 0.05$).

S5). The leaf thickness was significantly correlated with SPAD ($\rho = 0.13$, $P < 0.01$; Supplementary Table S4). The mean LTD ranged from –3.60 °C in C5 to –2.90 °C in NAT, and varied between the NAT and RES and COL, but not between RES and COL (Fig. 3A; Supplementary Tables S2, S3, S6).

Lower Relative Chlorophyll Content in Younger Stands.—Relative chlorophyll content (SPAD) significantly varied across stands types and ages ($P < 0.001$; Fig. 3B; Supplementary Tables S2 and S3). Younger RES stand [R8: 42.07 (1.55)] have 17% lower SPAD than the NAT [50.58 (0.65)] stands but the more mature RES [51.58 (0.95)] and COL [47.85 (1.07)] stands have comparable values with the NAT stands (Fig. 3B; Supplementary Table S2). Among genera, *Sonneratia* seedlings [69.62 (3.03)] had the highest SPAD in the NAT stands, *Aegiceras* [63.89 (2.87)] in the RES stands, and *Avicennia* [44.40 (1.40)] in the COL stands (Supplementary Table S7).

Discussion

Our study provides empirical data on the photosynthetic characteristics of mangrove seedlings from chronosequences of RES and COL stands. Here, we reported lower photosynthetic efficiency (Phi2) and higher potential photodamage (PhiNO) in mangrove seedlings from young stands that tend to improve as they mature (Fig. 2A–C). These photosynthetic characteristics indicate potential damage to the photosynthetic apparatus of seedlings (from recolonized stands), and probably a suboptimal growing conditions in restored mangroves. Overall, our data allowed us to understand the photosynthetic characteristics of mangrove seedlings in different ages of restored and recolonized stands and seedlings' potential vulnerability to persistent and long-lasting impacts of pond construction and operations.

Previous studies have shown that stressed conditions may inhibit PSII photochemistry due to related build-up of reactive redox intermediates which can occur more rapidly than the activation of photoprotective NPQ (Kanazawa et al. 2021). The changes in PSII activity can be rapidly diagnosed by measuring chlorophyll fluorescence (Lichtenthaler et al. 2005, Walker et al. 2018). The Phi2 reflects PSII photochemistry activity; it is significantly lower in seedlings from younger RES and COL stands than from NAT and mature RES stands (Fig. 2A). This suggests that the suboptimal environmental conditions in younger RES and COL stands adversely modified the PSII photochemistry in seedling leaves. PhiNPQ is a component of nonphotochemical quenching and reflects the fraction of regulated photoprotective thermal dissipation, thus protecting PSII from photodamage (Kramer et al. 2004). Photoprotection (PhiNPQ; Fig. 2B) decreases with stand age and almost matches values with the natural stands. Mature stands generally have taller trees (5.71–6.11 m) and wider tree diameter (8.36–13.52 cm) provides higher canopy shade (Table 1) that nurtures seedling growth. In contrast, younger COL stands consist of smaller trees (<5 m tree height, 8.32 cm tree diameter) with more open space that can potentially expose growing seedlings to higher light intensities leading to photodamage. Salmo et al. (2013) observed that soil temperature decreased as stands aged due to the development of mangrove canopy cover that provides shading which regulates absorption of solar radiation. Moreover, in mangrove leaves, the ambient light frequently exceeds the light saturation point, causing excess light energy and potentially leading to photoinhibition (Kitao et al. 2003). Photoinhibition is the light-induced reduction in photosynthetic efficiency and is usually associated with damage to the D1 PSII reaction center protein (Townsend et al. 2018, Murchie and Ruban 2020). However, under intense illumination, the surplus of absorbed energy often results in photoinhibition and diminished photosynthetic efficiency (Chen et al. 2022) which could be the case in younger RES and COL stands. According to FAO (1994), a stand density of 2500 stems ha^{-1} is adequate for restocking degraded mangrove areas. In our study, the younger restored and recolonized stands exhibited higher tree densities, exceeding 4000 trees ha^{-1}, likely due to dense planting (Gerona-Daga et al. 2024a) and unobstructed water flow that facilitates seedling accumulation (C5 stand). This high tree density can also lead to resource competition, potentially limiting PAR and nutrients for seedlings and saplings, thereby negatively reducing stand productivity (Wang'ondu et al. 2014).

A decline in F_v'/F_m' indicates a decline in PSII maximum efficiency and probably a disturbance in or damage to the photosynthetic apparatus (regular F_v/F_m value in

dark-adapted leaves, 0.74–0.85; Lichtenthaler et al. 2005). F_v'/F_m' ratios of seedlings in younger RES [R5: 0.71 (0.004)] and COL [C5: 0.72 (0.002)] stands were significantly lower than NAT [Nx: 0.75 (0.001)] stands and mature RES [R30: 0.75 (0.001)] and COL [C20: 0.74 (0.001)] stands (Fig. 2D), suggesting that photoprotection is insufficient (Fig. 2B, E) and that seedlings from younger RES and COL stands experienced greater stress levels and probably a higher degree of photoinhibition (Xu et al. 2023). In COL stands, the stressful physicochemical conditions following pond construction, such as soil removal/excavation, vegetation clearing, and changes in hydroperiod, can significantly alter PSII photochemistry. Excavation and prolonged exposure of soil to air can result in the formation of acid sulfate soils. When these soils are subsequently flooded, acid ions like hydrogen (H), ferrous (Fe), and aluminum (Al) are released into the water (Xiong et al. 2021). These ions can be toxic. Such environmental stresses can reduce or disrupt photosynthetic metabolism, enhancing the vulnerability to photoinhibition and reducing the capacity for orderly energy dissipation (Ball 2002).

Chlorophyll is the main light-harvesting pigment and reaction center that primarily influences light interception, consequently influencing photosynthetic performance (Guidi et al. 2019). Chlorophyll fluorescence measurements are commonly used indicators of photosynthetic capacity in mangroves (Chen et al. 2022, Xu et al. 2023), but rarely applied in seedlings under field conditions (Table 2). The weak association between leaf thickness and SPAD (Supplementary Table S4) was similarly reported on mangroves in Thailand (Cadiz et al. 2021) and China (Zhao et al. 2019). Its low association with SPAD can be attributed to the variation in species composition between stands. Different species have different leaf structures and thickness (Zhao et al. 2019, Li et al. 2022). While thicker leaves generally have higher photosynthetic rates (in most terrestrial plants; Pauli et al. 2017) this is not necessarily the case for mangroves as they have to adapt to the salinity-induced physiological drought (Cao et al. 2023). To maintain photosynthesis, leaves must be continuously supplied with water, as such water deficits are often associated with leaf thickness (Pauli et al. 2017). Studies on morphological and anatomical features such as palisade to spongy mesophyll ratio, size and stomata aperture, leaf area, and mesophyll tissue volume have demonstrated important relationships with photosynthesis due to its importance in avoiding high light intensities (Li et al. 2022)

The cooler temperature (more negative LTDs) of mangrove seedlings from RES and COL stands indicates the ability of the seedlings to shift the temperature distribution experienced by the leaf surface to a range in which physiological function is maintained. This is an important mechanism to avoid the adverse effects of heat stress. Experimental studies have imposed different temperatures to induce heat stress in plants, i.e., 40 °C in *A. marina* (Liu and Wang 2020). Asian mangrove species exhibit high photosynthetic tolerance (P_{HT}), with critical temperature (T_{Crit}, temperature that causes initial damage) at 40.7 °C and T_{50} (temperature that causes initial 50% damage to photosystem) that may reach (on average) 9.76 °C higher than T_{Crit} (Li et al. 2022). In most C3 plants, including mangroves, photosynthesis declines above 35 °C as a result of a reduction in the activation state because it limits carbon fixation and subsequently, net photosynthesis (Sage et al. 2008). In this study, all mangrove stands have lower air and leaf temperatures (Supplementary Table S6) indicating that leaf thermal regulation plays an important role in maintaining photosynthesis. The markedly higher (more negative) LTD in younger COL (C5) stands (Fig. 3A) reflects a possible adaptation to prevailing temperature.

Table 2. Comparison of photosynthetic parameters in restored, recolonized, and natural stands in Ormoc, Philippines and other mangroves worldwide.

Location	Phi2	PhiNPQ	PhiNO	Fv/Fm	NPQt	ETR_{PSII}	SPAD	NPQ	Stand type/condition	Reference
Ormoc, Philippines	0.49–0.56	0.16–0.24	0.26–0.28	0.71–0.75§	0.59–0.99	17–42	42–58	- - -	Restored (5–30 yr)	Present study**
	0.46–0.54	0.18–0.24	0.28–0.30	0.72–0.74	0.72–0.89	20–29	48–57	- - -	Recolonized (5–20 yr)	- - -
	0.56	0.17	0.27	0.75	0.67	17	51	- - -	Natural	- - -
Trang, Thailand	0.48–0.65	0.09–0.37	0.15–0.31	- - -	- - -	- - -	42–71	- - -	Restored (10–25 yr)	Cadiz et al. 2021*
	approx 0.50–0.60	approx 0.1–0.2	approx 0.20–0.30	- - -	- - -	- - -	approx 37–72	- - -	Natural	- - -
Guangxi, China	approx 0.03–0.05	- - -	- - -	approx 0.75–0.79	- - -	approx 40–100	- - -	approx 0.25–0.31	Natural	Xu et al. 2022*
Sta. Catarina Is., Brazil	- - -	- - -	- - -	approx 0.65–0.70	- - -	- - -	- - -	- - -	Restored (10–12 yr)	Rovai et al. 2013*
	- - -	- - -	- - -	approx 0.60–0.69	- - -	- - -	- - -	- - -	Natural	- - -
Tainan, Taiwan	- - -	- - -	- - -	0.38–0.80	- - -	approx 40–65	- - -	- - -	Greenhouse/ salinity stress-induced	Chen et al. 2022**
	- - -	- - -	- - -	0.3–0.5	- - -	25–40	- - -	- - -	Control	- - -
Pohnpei Is., Micronesia	- - -	- - -	- - -	0.78–0.83	- - -	approx 10–115	- - -	- - -	Natural	Kitao et al. 2003*

Note: Phi2, actual photosystem II efficiency; PhiNPQ, photoprotective nonphotochemical quenching; PhiNO, yield of nonregulatory energy dissipation, Fv/Fm, maximal quantum efficiency of PSII; ETR, electron transport rates, NPQt, nonphotochemical quenching based on the rapid "total" NPQ method; ETR_{PSII}, electron transport rate; SPAD, relative chlorophyll content; NPQ, nonphotochemical quenching. Photosynthetic measurements taken from (**) seedlings and (*) mature trees; - - -, not reported; §, reported as Fv´/Fm´: PSII maximum efficiency.

Extensive mangrove loss due to conversion to aquaculture has long been documented in the Philippines, and practically in most Southeast Asian countries (also referred to as "fishpond boom" and "shrimp fever"; Song et al. 2021). Pond construction, and pond disuse associated with the heavy applications of fertilizers and pesticides lead to alterations to the physicochemical properties of soil, hydrological conditions, and the flora and fauna composition (Stevenson 1997, Green 2022, Meng et al. 2022). Due to poor water and sediment qualities (Towatana et al. 2002, van Bijsterveldt et al. 2020, Hongwiset et al. 2022), seedling recruitment and establishment in the abandoned ponds are constrained. These unfavorable conditions limit seedling recruitment and growth, and those seedlings that initially grow can be further stressed with lower photosynthetic efficiency. The dense vegetation in R8 and C5 (Table 1) may indicate vegetation recovery (Gerona-Daga et al. 2024a), however phosphorus (P) resorption is extremely high in COL stands (probably as a result of P depletion due to soil excavation and vegetation clearing during pond construction; Gerona-Daga et al 2024b). Leaf litter contributes poorly to the soil P pool which likely resulted in the delay of soil recovery which consequently reduced stand productivity (Loiola et al. 2023). Complete recovery of healthy mangroves may take 20–30 yr if large scale damage has resulted from a disturbance (Lewis et al. 2016). In Indonesia, when pond walls/dikes were removed and tides were reconnected, natural recruits were observed after about 10–12 yr (Sidik et al. 2021). When the vegetation and sediment conditions improved postplanting (ca 10–20 yr), it is possible that the photosynthetic characteristics of restored seedlings will be similar to that of seedlings from healthy natural mangroves (Cadiz et al. 2021). Due to a long history of failed massive mangrove planting in coastal fringes (Zimmer et al. 2022), proactive restorations are now advocated to be implemented in mid- to upper-intertidal abandoned ponds (Lovelock et al. 2022). Our results, however, showed that while the abandoned ponds are potential restoration areas, the perturbed conditions need to be repaired prior to planting. More importantly, further studies on seedling growth and establishment in abandoned ponds are recommended for science-based restoration and management.

Conclusions

Characterization of photosynthetic performance using chlorophyll fluorescence–based measurements is a useful indicator in documenting changes or progress of seedling growth. Our findings revealed that seedlings from younger RES and COL stands are "stressed" as indicated by lower photosynthetic efficiency (Phi2), lower PSII maximum efficiency (Fv′/Fm′), and higher potential damage (PhiNO). ETR_{PSII} induction was higher in younger restored and recolonized stands, resulting in excess energy production that may lead to potential damage. Photoprotection (PhiNPQ and NPQt) decreases with stand age and almost matches values with the natural stands. Collectively, these results support our hypothesis that mangrove seedlings in RES and COL stands differ significantly from NAT stands due to residual stressors following mangrove degradation. Further, our study highlights that although abandoned ponds are potential restoration areas, they pose great challenges to seedling survival and growth.

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