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Interspecific associations of mangrove species and their preferences for edaphic factors and water quality

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Abstract. *Marpaung BA, Budiadi, Pertiwiningrum A, Lestari LD, Nurjanto HH, Widiyatno. 2022. Interspecific associations of mangrove species and their preferences for edaphic factors and water quality. Biodiversitas 23: 4626-4635.* Scientists from different regions have reported failures of mangrove restorations that were predicted due to the unsuitability of the species for the habitats. Habitat preferences should become an important consideration for mangrove restoration and management. This study aimed to find interspecific associations between species and examine the edaphic factors and water quality suitable for mangroves. Eight research stations (and 24 sample plots) were established purposively based on the vegetation structure and salinity levels in successful mangrove restorations in East Lampung in 2020. In each plot, vegetal data and sediment and water samples were taken. The species domination was analyzed using the important value index (IVI), and interspecific associations were determined using a 2x2 contingency table. The edaphic factors and water quality were analyzed using principal component analysis (PCA) to find factors that had significant correlations among others. The effects of the edaphic factors and water quality on species regeneration were analyzed using multiple linear regression by backward elimination to develop a model of habitat preferences for mangroves. Based on the results, *Avicennia marina* and *Rhizophora* sp. were the dominant species in all the zones. Still, the lack of interspecific association ($\chi^2_{hit} < \chi^2_{0.05}$) showed that both species had different preferences for the habitat. We found four principal components (PCs) of edaphic factors—i.e., the environmental (soil and surface) temperature, dusty clay and Ca, inorganic nitrogen (NH_4-N and NO_3-N), and Mg—and two PCs of water quality, i.e., nontoxic pollutants (total suspended solids and turbidity) and anthropogenic factors (NO_2-N and PO_4-P), as predictors for multiple linear regression. The seedlings of *A. marina* had no specific preferences for edaphic factors but significantly preferred nontoxic pollutants (R^2 = 0.619), while the seedlings of *Rhizophora* spp. significantly preferred a specific environmental temperature, dusty clay and Ca, and inorganic nitrogen (R^2 = 0.768), and nontoxic pollutants (R^2 = 0.755). Combining *A. marina* and *Rhizophora* spp. in mangrove restorations should be avoided. Therefore, spatial planting patterns or sequential planting based on the succession stages of the habitat could be established.

Keywords: *Avicennia*, mangrove zone, restoration, *Rhizophora*, succession

INTRODUCTION

Mangroves grow along intertidal zones, and they morphologically and physiologically adapt well to such extreme environments (Alongi 2009; Wang et al. 2019). Mangroves are parts of estuaries and coastal ecosystems that have various functions and uses and, therefore, must be conserved and protected (Barbier et al. 2011). On the other hand, mangroves are sensitive to many habitat changes caused by natural or anthropogenic activities, including fisheries and deforestation (Maulidar and Samosir 2016; Goldberg et al. 2020). Southeast Asian countries, including Indonesia, contribute 0.26 to 0.66% to global mangrove deforestation annually (Hamilton and Casey 2016; Richards and Friess 2016). Mangrove deforestation in Indonesia is caused by fishery activities or pond establishment, cutting, land-use change to estate plantations or agricultural land, coastal development, and natural disasters (Ilman et al. 2016; Eddy et al. 2021). The deforestation decreases species diversity, density, and environmental services (Nordhaus et al. 2019).

Mangrove restoration is, globally, mainly conducted through the direct plantation on site (Lee et al. 2019). However, some failures in mangrove restoration have been reported, including in Indonesia (Nusantara et al. 2015), with a low survival rate that is probably due to the species' incompatibility with the habitats (Kodikara et al. 2017; Wodehouse and Rayment 2019). Many key factors that are usually considered in mangrove restoration are the salinity, pH, slope, wind velocity, tidal period and length, and depth of mud, although optimizing a single factor can significantly improve the survival rate of the mangroves (Win et al. 2019; Charrua et al. 2020; Jalil et al. 2020). In fact, optimizing the salinity, inundation period, and depth of the mud only stimulates zone formation (Faridah-Hanum et al. 2019; Win et al. 2019; Jalil et al. 2020).

Each mangrove species has certain preferences of habitat that influence its regeneration and survival rate

(Peng et al. 2016; Wodehouse and Rayment 2019; Sreelekshmi et al. 2020). Comprehensive research on the habitat preferences of mangrove species regarding edaphic factors and water quality has been conducted in India (Das et al. 2019), whereas in Indonesia, research on habitat preferences is still based on the individual analysis of variables such as the pH, diluted oxygen, salinity, temperature, depth of the mud, and slope (e.g., in Poedjirahajoe et al. 2017; Matatula et al. 2019). Research on water quality usually encompasses the relationship between the rate of pollution and the growth of mangrove vegetation (Heriyanto and Suharti 2019; Sari et al. 2019). The studies partially correlate the vegetation with edaphic factors or water quality; in fact, the characteristics should show reciprocal multivariate relationships (Cooray et al. 2021). Edaphic factors affect the ecophysiology, composition, and structure of mangrove species (Hossain and Nuruddin 2016), while the water quality is able to identify the existence of anthropogenic resources in the ecosystem (Maurya and Kumari 2021).

Knowledge about the habitat preference of a mangrove species should be developed because it determines success in mangrove restorations (Lee et al. 2019; Wodehouse and Rayment 2019). Habitat preferences can be researched through empirical studies on successful mangrove restorations (e.g., in the study of Oh et al. 2017) by measuring changes in mangrove landcover over time and the existence of interspecific relationships (Lewis 2009; Liu et al. 2017). Yuliasamaya et al. (2014) mentioned the successful regeneration of a mangrove area on the East coast of Lampung Province between 2004 and 2013, and our preliminary survey also found a significant increase in land cover in the area between 2010 and 2020. On the site, we conducted a field survey to analyze the interspecific association between mangrove species, and to improve the knowledge of habitat preferences for mangrove regeneration based on edaphic factors and water quality.

MATERIALS AND METHODS

Study area

The research was conducted in a mangrove area in Purworejo village, East Lampung District (5º 29’ 53.41” - 5º 29’ 53.84’’ LS and 105º 47’ 52.96” - 105º 50’56.84) (Figure 1). Based on a preliminary survey, the mangrove land cover in the location increased from 58 ha (in 2010) to 508 ha (in 2020). In order to study the habitat preference of the successful mangrove, we collected data on the stand composition and structure, took soil and water samples in August 2020, and continued with laboratory analysis until March 2021.

Procedures

The locations and distributions of the research stations are shown in Figures 1a and 1b. Based on the salinity levels referred to Barik et al. (2018), the locations were divided into oligohaline (salinity: 5-15 ppm), mesohaline (15.1-25 ppm), and polyhaline (> 25 ppm), and represented the established stations (Figure 1c). Stations S1, S2, S3, and S6 are colonization areas for natural and planted *Rhizophora* spp., and are seedling dominant (S1) and sapling dominant (S2, S3, and S6). Stations S1 to S8 are also colonization areas for the natural regeneration of *A. marina* and are seedling dominant (S1), sapling dominant (S2 and S3), and pole and tree dominant (S4, S5, S6, S7, and S8).

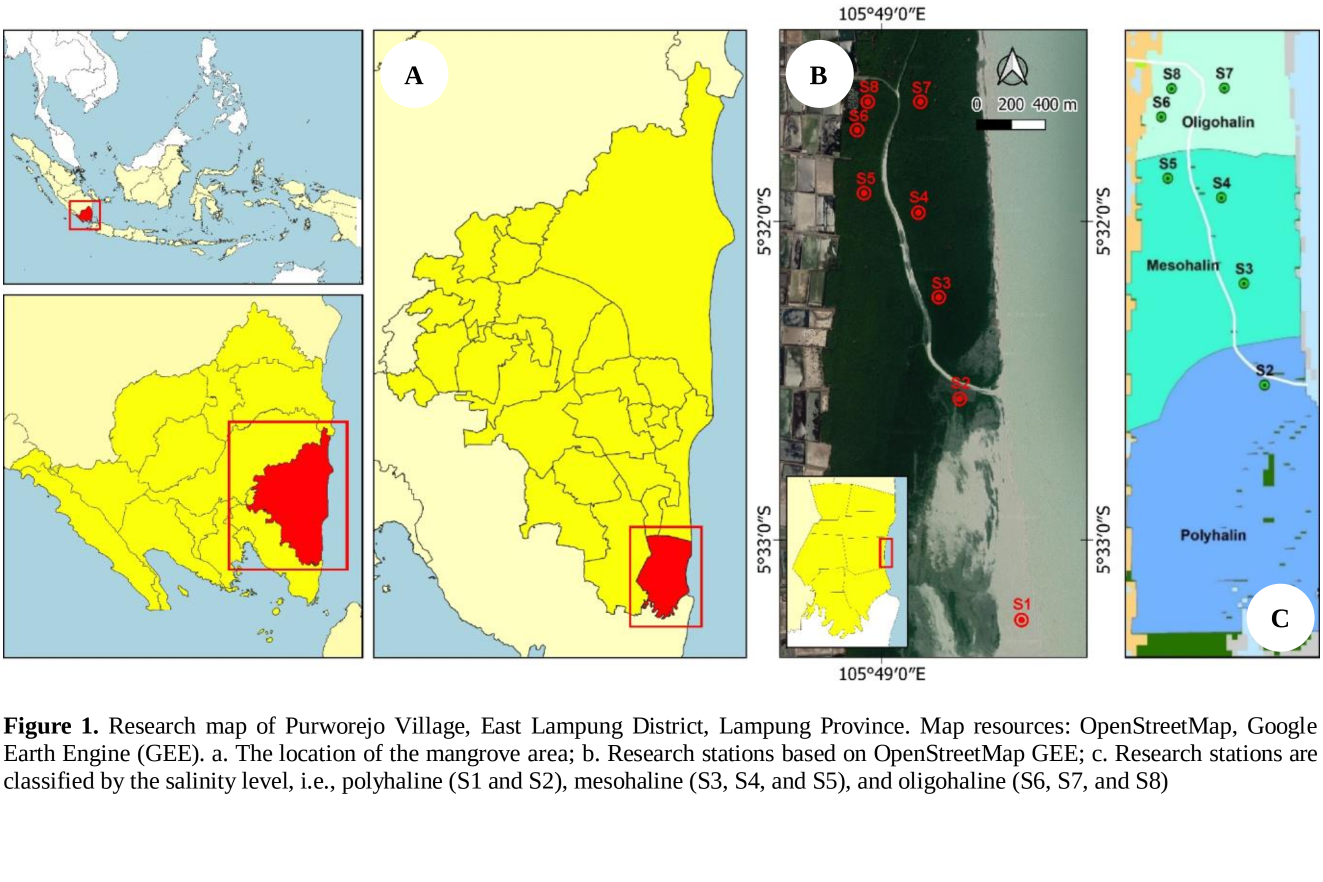


Figure 1. Research map of Purworejo Village, East Lampung District, Lampung Province. Map resources: OpenStreetMap, Google Earth Engine (GEE). a. The location of the mangrove area; b. Research stations based on OpenStreetMap GEE; c. Research stations are classified by the salinity level, i.e., polyhaline (S1 and S2), mesohaline (S3, S4, and S5), and oligohaline (S6, S7, and S8)

In each station, we established three plots of 10 m x 10 m (refer to Kauffman and Donato 2012), with a 50 m distance between the plots, making a total of 24 units. Measurements for all the vegetation were taken, including species identification (refer to Noor et al. 1999); the height for the seedlings; and the stem diameter and total height for the saplings, poles, and trees. Mangroves were classified as seedlings (less than 1.5 m in height), saplings (less than 10 cm in diameter), and trees (more than 10 cm in diameter) (Istomo et al. 2020). The stem diameter was measured at a 130 cm height from the stem base (Kauffman and Donato 2012). The samples for soil analysis, water, and microsite data were taken in three diagonal spots in the main plots. From the spots, samples for soil chemical analysis were taken using the disturbed method at a 20 cm depth and mixed to obtain composite samples. The samples for soil physical analysis were taken using the undisturbed method with a soil ring (4.8 cm in diameter and 5.0 cm in height) at a soil depth of 10 cm. The water samples from each main plot were combined into composite samples. Microsite data, including soil temperature, surface temperature and humidity were taken directly at the same time when soil samples were taken in the main plots. The method and results for the soil properties and water quality analyses are provided in Tables 1 and 2.

Data analysis

In each plot, measurements of the relative density (RD), relative frequency (RF), and relative dominance (RDom) of the stands were conducted to calculate the important value index (IVI) (Cintron and Schaeffer Novelli 1984). Interspecific associations were analyzed using a 2 x 2 contingency table (Ludwig and Reyolds 1988), and hypothetically, every dominant species was independent (or no significant associations were found). Hypothetical tests were conducted using chi-square (χ^2) tests and Yates corrections to determine the significance of species associations, and the Ochiai index (OI) to evaluate interspecific correlations (refer to Li et al. 2008; Liu et al. 2017). Principal component analysis (PCA) was utilized to measure the ordination axes (Peres-Neto et al. 2003), by analyzing the edaphic characteristics and water quality in each salinity zone. Varimax rotation was utilized to simplify the interpretation of the variables (Acal et al. 2020), and the Kaiser criterion (eigenvalue > 1.0) was utilized to determine the number of selected principal components (PCs) (Gholizadeh et al. 2016). A significant correlation between single variables could be recognized by a loadings value ±0.5 (Williams et al. 2010). The PCA was then visualized using the "ggplot" package in RStudio (Wickham 2016). Analysis of similarity (ANOSIM) (Somerfield et al. 2021) was employed to measure the similarity and dissimilarity of variables between groups (or mangrove zones), using the PAST software (Hammer et al. 2001).

The stand densities (N ha^{-1-}) of the seedlings and saplings were regarded as response variables, while PCs selected from the results of the PCA were regarded as predictors for multiple linear regression by the backward elimination method (Rhyma et al. 2020) using RStudio's "olsrr" package (Hebbali 2020). The formula for the multiple linear regression analysis was as follows (Abdel-Salam 2008):

$$Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} \cdots + \beta_k X_{ki} + \varepsilon_i$$

Note: i = 1,2,3…, n; $\beta 0$ = the value of Y, when X_1, X_2, and $X_k = 0$; εi = the error; the values of $\beta 1$ to βk are for each increasing or decreasing value of X_1 to Xk

RESULTS AND DISCUSSION

Vegetation structure and interspecific association

Four true mangrove species composed the ecosystem in the location: *Avicennia marina* (Forssk.) Vierh. (Acanthaceae), *Rhizophora stylosa* Griff. (Rhizophoraceae), *Rhizophora mucronata* Lamk. (Rhizophoraceae), and *Excoecaria agallocha* L. (Euphorbiaceae) (Table 3).

For the seedling stage, the highest density was found in the polyhaline zone of *R. stylosa* (1282 individuals per ha), while for the sapling stage, it was in the mesohaline zone of *A. marina* (2967 individuals per ha). For the tree stage, the oligohaline and mesohaline zones were dominated by *A. marina*. In general, *A. marina* and *R. stylosa* were found in all the zones, while *E. agallocha* was only found in very low numbers (IVI: 12.2%) in the oligohaline zone (Table 3). A higher IVI value reflects a significant contribution of a species in the community and its habitat preference (Kiruba-Sankar et al. 2018; Rani et al. 2018). *A. marina* is adaptive to all the intertidal zones and tolerates low- to high-salinity conditions (Jayatissa 2006; Tamin et al. 2011; Basyuni et al. 2019; Cheng et al. 2020), whereas *R. stylosa* can grow well under medium salinity, but its growth capability declines under high salinity (Kanai et al. 2014; Basyuni et al. 2019).

Excoecaria agallocha was not considered for interspecific associations due to the low number of individuals per ha, and therefore, in all of the zones, there were species pairs of *A. marina*-*R. stylosa*, *A. marina*-*R. mucronata*, and *R. stylosa*-*R. mucronata* (Table 4). The results from the analysis of interspecific associations showed that there was no clear association between *A. marina* and *Rhizophora* sp. in any of the zones ($\chi^2_{hit} < \chi^2_{0,05}$). The relationships between *A. marina* and *Rhizophora* spp. tended to be negative, reflecting the fact that the two species have different habitat preferences. The Ochiai index (OI) was not very meaningful because the three species pairs had no associations. The lack of associations between species reflects the fact that each species in the community tends to be independent (Liu et al. 2017). As stated by Hilmi et al. (2021) based on research in Segara Anakan, no interspecies associations were found for mangrove species, and clusters of similar species tended to be established. The species clusterization is related to mangrove zonation; i.e., *A. marina* is found along river flows and close to land, while *Rhizophora* spp. is usually found in the centers of estuaries (Putri et al. 2015; Sreelekshmi et al. 2020; Triest et al. 2020), but some cases of homogeneity also result from planting activities (Pham et al. 2019; Wang et al. 2021).

Table 1. Edaphic variables in different salinity zones in the coastal area of East Lampung, Indonesia (mean ± SE)

Variable	Salinity zones			Method	References
	Oligohaline	Mesohaline	Polyhaline		
pH H_2O	7.8 ± 0.05 ^{b}	7.7 ± 0.1^{b}	8.1 ± 0.03^{a}	Extract, 1:5	(Kargas et al. 2020; Pan et al. 2019)
EC (dS/m)	0.01 ± 0.00^{a}	0.01 ± 0.0^{a}	0.010 ± 0.0^{a}	Potentiometer	(Yin and Yan 2020)
Redox (mV)	353.7 ± 6.4^{a}	359.4 ± 3.2 ^{a}	354.5 ± 2.0^{a}	Extract, 1:5	(Duan et al. 2020)
Organic C (%)	2.5 ± 0.20^{a}	2.6 ± 0.12 ^{a}	1.6 ± 0.06^{b}	Walkley and Black	(Budiadi 2020)
CEC (cmolc/kg)	30.5 ± 0.67^{a}	29.0 ± 0.56^{a}	24.2 ± 0.4^{b}	NH_4 acetate 1N, pH 7	(Ukpong 2000)
NH_4-N (ppm)	130.0 ± 25.7^{b}	83.3 ± 8.2^{b}	275.3 ± 63.8^{a}	Morgan-Wolf, spectrophotometer	(Eviati and Sulaeman 2009)
NO_3-N (ppm)	48.0 ± 5.04^{b}	49.8 ± 5.4^{b}	187.7 ± 54.9^{a}	Morgan-Wolf, spectrophotometer	(Eviati and Sulaeman 2009)
P (ppm)	5.0 ± 0.71^{a}	3.0 ± 0.24^{a}	3.2 ± 0.31^{a}	Morgan-Wolf	(Kumawat et al. 2017)
Calcium (ppm)	717.1 ± 49.5^{a}	805.4 ± 35.5^{a}	699.3 ± 24.2^{a}	Morgan-Wolf	(Kumawat et al. 2017)
Ca (ppm)	4521.4 ± 1362.5^{ab}	2234.2 ± 298.5^{b}	5173.3 ± 472.7^{a}	Morgan-Wolf	(Kumawat et al. 2017)
Mg (ppm)	3597.6 ± 81.1^{a}	3652.2 ± 112.0^{a}	3368.5 ± 92.6^{a}	Morgan-Wolf	(Kumawat et al. 2017)
Fe (ppm)	7.8 ± 0.8^{a}	9.1 ± 0.4^{a}	5.0 ± 0.7^{b}	Morgan-Wolf	(Kumawat et al. 2017)
Texture	Dusty clay	Dusty clay	Dusty clay	Pipette method	(Dewi et al. 2014)
Bulk density(g/mL)	0.4 ± 0.1^{b}	0.4 ± 0.02^{b}	0.46 ± 0.0^{a}	Core method	(Al-Shammary et al. 2018)
Particle density (g/mL)	1.9 ± 0.1^{b}	2.0 ± 0.1^{ab}	2.1 ± 0.0^{a}	Core method	(Das et al. 2019)
Soil temperature (˘C)	27.8 ± 0.40^{b}	27.2 ± 0.2^{b}	31.8 ± 0.9^{a}	Soil thermometer	(Poedjirahajoe et al. 2017)
Surface temp. (°C)	31.9 ± 0.33^{b}	31.4 ± 0.3^{b}	33.1 ± 0.5^{a}	Thermohygrometer	(Dimara et al. 2021)
Humidity (%)	76.7 ± 1.9^{b}	85.4 ± 1.7^{a}	78.0 ± 1.0^{b}	Thermohygrometer	(Dimara et al. 2021)

Note: different superscript letters indicate significance for variables in different salinity zones; α = 0.05

Table 2. Water quality variables for different salinity zones in the coastal area of East Lampung, Indonesia (mean ± SE)

Variable	Salinity zones			Method	References
	Oligohaline	Mesohaline	Polyhaline		
TSS (mg/L)	652.0 ±280.2^{a}	175.3 ± 91.6^{b}	2289.7 ± 880.5^{a}	*In House Method*	BBTKLPP Yogyakarta
Turbidity (NTU)	915.0 ± 383.5^{a}	226.4 ± 89.9^{b}	2324.2 ± 458.2^{a}	SNI 06-6989.25-2005	(KLHK 2019)
Salinity (‰)	12.4 ± 0.2^{c}	19.1 ± 0.8^{b}	26.4 ± 0.6^{a}	*In House Method*	BBTKLPP Yogyakarta
pH	7.4 ± 0.0^{a}	7.4 ± 0.1^{a}	7.3 ± 0.03^{a}	SNI 6989.11-2019	(KLHK 2019)
DO (mg/L)	6.5 ± 0.7^{a}	5.0 ± 0.5^{b}	6.3 ± 0.70^{a}	APHA 2012, Section 4500 - OG	(APHA 2017)
NO_3-N (mg/L)	1.1 ± 0.2^{ab}	0.7 ± 0.1^{b}	2.8 ± 0.55^{a}	APHA 2017, Section 4500 - NO3B	(APHA 2017)
NO_2-N (mg/L)	0.7 ± 0.1^{a}	0.4 ± 0.1^{a}	0.01 ± 0.0^{b}	SNI 06-6989.9-2004	(KLHK 2019)
NH_3 (mg/L)	0.01 ± 0.01^{b}	0.06 ± 0.02^{a}	0.08± 0.01^{a}	SNI 06-6989.30-2005	(KLHK 2019)
PO_4-P (mg/L)	0.06 ± 0.03^{ab}	0.21 ± 0.09^{a}	0.03 ± 0.09^{b}	APHA 2012, Section 4500 P-D	(APHA 2017)
SO_4 (mg/L)	989.0 ± 114.2^{ab}	1114.6 ± 278.5^{a}	92.3 ± 21.1^{b}	SNI 06-6989.22-2004	(KLHK 2019)

Note: different superscript letters indicate significance for variables in different salinity zones; α = 0.05. *In House Method:* sample testing procedure following standard methods printed on the equipment; BBTKLPP: Balai Besar Teknik Kesehatan Lingkungan dan Pengendalian Penyakit

Table 3. Species densities and important value indices (IVIs) of different salinity zones of the coastal area of East Lampung, Indonesia

Salinity zones	Species	Seedling		Sapling		Tree		Number of species
		N ha^{-1}	IVI	N ha^{-1}	IVI	N ha^{-1}	IVI	
Oligohaline	Am	78	170.8	1400	228.2	811	269.5	3
	Rs	11	29.2	365	71.8	11	18.2	
	Ea	-	-	-	-	22	12.2	
Mesohaline	Am	-	-	2967	261.0	778	300.0	2
	Rs	-	-	344	39.0	-	-	
Polyhaline	Am	217	56.0	467	138.6	-	-	3
	Rs	1283	134.6	383	95.0	-	-	
	Rm	17	9.4	167	66.4	-	-	

Note: Am = *Avicennia marina;* Rs = *Rhizophora stylosa;* Rm = *Rhizophora mucronata*, Ea = *Excoecaria agallocha*; IVI= important value index; IVI of seedling (%) = RD+RF; IVI of sapling and tree (%) = RD+RF+RDom

Table 4. Interspecific associations of dominant mangrove species in the coastal area of East Lampung, Indonesia

Salinity zones	Species pairs	χ^2_{hit}	$\chi^2_{0.05}$	Association	Correlation	Ochiai Index (OI)
Oligohaline	*A. marina-R. stylosa*	0.141	3.841	No significant	Negative	0.41
Mesohaline	*A. marina-R. stylosa*	0.000	3.841	No significant	Negative	0.58
	A. marina-R. stylosa	0.141	3.841	No significant	Negative	0.72
Polyhaline	*A. marina-R. mucronata*	0.000	3.841	No significant	Negative	0.52
	R. stylosa-R. mucronata	1.524	3.841	No significant	Positive	0.50

PCA analysis for edaphic factors and water quality

The results from the analysis of edaphic factors and water quality are shown in Tables 1 and 2. Eighteen variables of edaphic factors were tested, including three soil physical properties, five soil chemical properties, seven macro- and microelements, and three other environmental variables. Ten variables of water quality were tested, including three physical variables, two chemical variables, and five water ions. The results from the PCA based on the zonation are visualized in biplots in Figure 2.

The oligohaline and mesohaline zones had similar edaphic factors ($R_{oligohaline-mesohaline}$ = 0.0415, $p > 0.05$) and water quality ($R_{oligohaline-mesohaline}$ = 0.031, $p > 0.05$), while the polyhaline tended to be different. The edaphic factors in the oligohaline zone were significantly different from those in the polyhaline zone ($R_{oligohaline-polyhaline}$ = 0.2651, $p < 0.05$; $R_{mesohaline-polyhaline}$ = 0.748, $p < 0.05$). The water quality in the oligohaline and mesohaline zones was also significantly different from that in the polyhaline zone ($R_{oligohaline-polyohaline}$ = 0.3457, $p < 0.05$; $R_{mesohaline-polyohaline}$ = 0.6783, $p < 0.05$). Of the edaphic factors, organic C and Fe showed a strong correlation in the oligohaline and mesohaline zones, and Mg and CEC also showed a strong correlation in the mesohaline zone. The soil temperature, bulk density, particle density, soil pH, NO_3-N, and NH_4-N had a strong intercorrelation in the polyhaline zone. The SO_4 concentration, NO_2N, and PO_4P had an intercorrelation in the mesohaline zone, while the salinity and NO_3-N had an intercorrelation in the polyhaline zone. In oligohaline and mesohaline zones, poles and trees were dominant and showed a strong correlation with mangrove nutrition. The polyhaline zone is a habitat for young mangroves and showed strong correlations with inorganic nitrogen and soil physical properties.

The strong correlation for organic C in the mesohaline and oligohaline zones reflects the fact that the total soil organic carbon (SOC) increases along with the stand growth of mangrove species (Alongi 2009). In the case of Mg in the mesohaline zone, Alongi (2021) also stated that Mg is present in seawater but is low in high-salinity environments. The common forms of nitrogen are NH_4+ and NO_3- (Reef et al. 2010; Abbasi et al. 2017; Alongi 2021), which showed strong correlations in the polyhaline zone, but the denitrification activity and N assimilation decrease with an increase in seawater salinity (Shiau et al. 2017; Wang et al. 2018). Anthropogenic sources (such as SO_4, NO_2-N, and PO_4) in the mesohaline zone probably originate from fertilizer waste from farming activities, fish ponds, or industries upstream (as for Wu et al. 2017; Maurya and Kumari 2021).

The results from the PCA of the edaphic factors showed four principal components (PCs) with eigenvalues > 1.0 (Table 5), which explained 83.25% of the total data variance, with PC values of 52.10%, 12.58%, 9.95%, and 8.61% for PC1, PC2, PC3, and PC4, respectively. The principal components for the edaphic factors were: The soil and surface temperature, which described the effect of environmental temperatures on mangrove development (PC1). The soil textures and calcium content represented substrates dominated by mud with similar Ca concentrations in the three mangrove zones (PC2). NH_4-N and NO_3-N, which represented the inorganic nitrogen in the zones (PC3). Magnesium, which describes the availability of the main nutrients in the habitats (PC4).

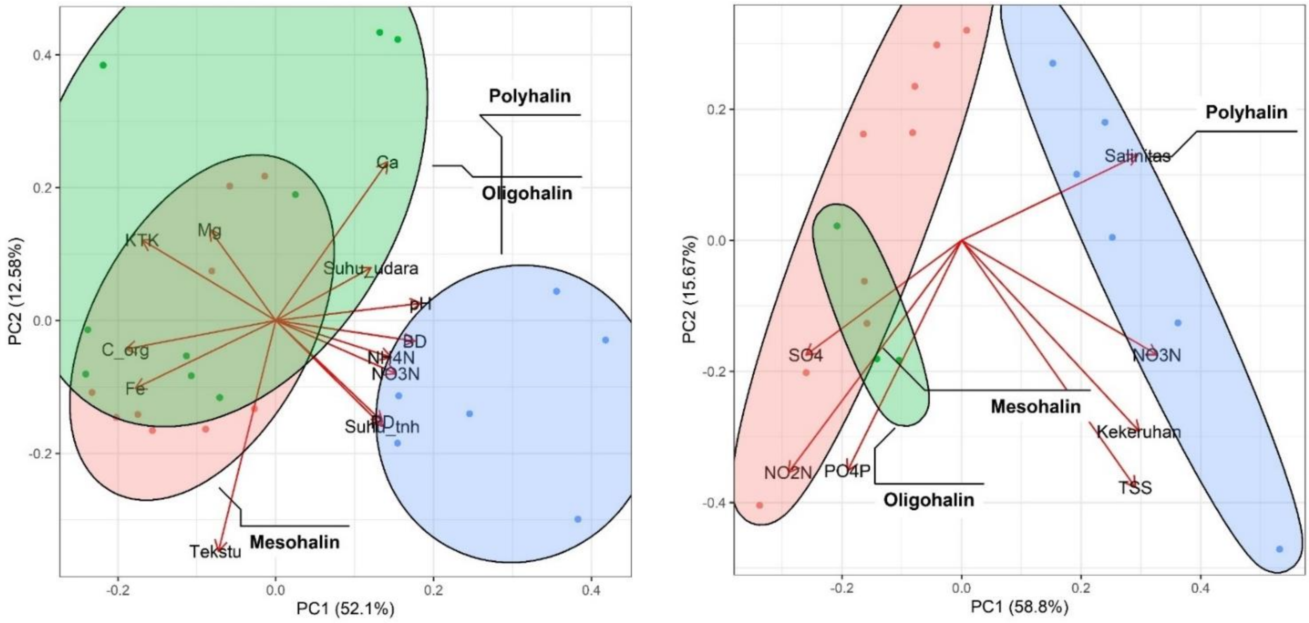
The results from the PCA for the water quality showed two PCs with eigenvalues > 1.0, which explained 74.47% of the total data variance, with PC values of 58.80% and 15.67% for PC1 and PC2, respectively. The principal components of the water quality were: The total suspended solid (TSS) and turbidity or muddiness, which represented nontoxic pollutants from suspended materials and nutrients (PC1). The NO_2-N and PO_4-P concentrations, which represented anthropogenic influences (PC2).

The edaphic factors and water quality from the loadings influenced the adaptability and development of the mangrove species. For instance, an increase in air temperature every year influences changes in the mangrove ecosystem, species composition, phenology, productivity, and species distribution (Srivastava et al. 2015; Ward et al. 2016). The optimum rate of photosynthesis is reached at a leaf surface temperature of 28-32^{o}C, and it is terminated at 38-40^{o}C (Gilman et al. 2008). Silt-loam soil mostly results from sedimentation, and a high rate of sedimentation decreases the mangrove density, reduces the oxygen supply to the root, and reduces the growth rate (Van Santen et al. 2007; Sidik et al. 2016; Nordhaus et al. 2019). The forms of inorganic nitrogen studied in this research were NH_4-N and NO_3-N, which are growth-limiting factors for mangroves (see, for example, Reef et al. 2010 and Alongi 2021), while Mg is not (Alongi 2021). In terms of the water quality attributes, nontoxic pollutants disturb the ecosystems when above their maximum thresholds (for example, see Effendi 2003).

Habitat preferences of *A. marina* and *Rhizophora* spp.

Multiple regression analysis was performed to examine the roles of edaphic factors and water quality regarding the stand density of *A. marina* and *Rhizophora* spp., and multiple linear regression models were developed (Table 6).

The seedling density of *A. marina* seedlings was not affected by edaphic factors but was positively affected by nontoxic pollutants (R^2 = 0.619). The seedling density of *Rhizophora* spp. was positively affected by the soil and surface temperature, and inorganic N, but negatively affected by a clay substrate and Ca (R^2 = 0.768), and nontoxic pollutants (R^2 = 0.755). The sapling density of *A. marina* was negatively affected by the inorganic N, nutrients, and soil and surface temperature (R^2 = 0.726), but there was no effect on water quality, whereas the sapling density of *Rhizophora* spp. was not affected by specific factors of soil and water quality.



A **B**

Figure 1. Principal component analysis (PCA) biplot of edaphic factors and water quality in the coastal area of East Lampung, Indonesia. A. Biplot of edaphic factors; B. Biplot of water quality. (Abbreviations: Oligohalin: oligohaline, mesohaline: mesohaline, polyhalin: polyhaline, Tekstur: texture, KTK: cation-exchange capacity, Suhu_udara: air temperature, Suhu_tnh: soil temperature, BD: bulk density, Kekeruhan: dissolved oxygen, TSS: total suspended solid, salinitas: salinity level)

Table 5. Principal component loading values (varimax rotation) of edaphic factors and water quality in the coastal area of East Lampung, Indonesia

Edaphic factors					Water quality		
Variables	**PC1**	**PC2**	**PC3**	**PC4**	**Variables**	**PC1**	**PC2**
NH_4-N			0.627*		TSS	0.633*	
NO_3-N			0.591*		Turbidity	0.559*	
pH	0.314	0.174		-0.101	Salinity	0.161	0.401
Organic C	-0.226	-0.257		0.221	NO_3-N	0.478	0.139
CEC	-0.294			0.367	NO_2-N		-0.612*
Ca		0.570*	-0.158	-0.112	PO_4-P	0.147	-0.517*
Mg	0.124		0.145	0.592*	SO_4		-0.412
Fe	-0.132	-0.325	-0.157				
Texture	0.111	-0.609*	-0.128	-0.318			
BD	0.145	0.142	0.110	-0.260			
PD			0.173	-0.477			
Soil temperature	0.523*	-0.273	0.258				
Surface temperature	0.646*		-0.236	0.187			
Eigenvalue	2.602	1.278	1.137	1.058	Eigenvalue	2.029	1.047
Variance (%)	52.1	12.58	9.95	8.61	Variance (%)	58.8	15.67
Cumulative (%)	52.1	64.68	74.63	83.25	Cumulative (%)	58.8	74.47
Kaiser-Meyer-Olkin (KMO) = 0.718					Kaiser-Meyer-Olkin (KMO) = 0.748		
Bartlett Sphericity Test < 0.05					Bartlett Sphericity Test < 0.05		

Note: *loading values ±0.5 indicate variables are significantly correlated

Table 6. Multiple linear regression model of edaphic factors and water quality for stand density of *A. marina* and *Rhizophora* spp. in the coastal area of East Lampung, Indonesia

Species	Predictor variables	Response	Model	Sig.	R^2	adj R^2	RMSE
A. marina	Edaphic	Seedling density ($N\ ha^{-1}$)	0.93 + 0.22[TEMPERATURE]	0.0122	0.253	0.219	1.009
	Water quality		0.77 + 0.43[NONTOXIC POLLUTANS]	0.0001	0.619	0.595	0.719
	Edaphic	Sapling density ($N\ ha^{-1}$)	2.58 - 0.65[NITRO] - 0.35[Mg] - 0.31[TEMPERATURE]	0.0000	0.726	0.685	0.770
	Water quality		2.39 - 0.45[NONTOXIC POLLUTANS]	0.0092	0.354	0.313	1.279
Rhizophora spp.	Edaphic	Seedling density ($N\ ha^{-1}$)	0.78 + 0.38[TEMPERATURE] - 0.35[SUBSTRAT-CA] + 0.27[NITRO]	0.0000	0.768	0.734	0.670
	Water quality		1.05 + 0.60[NONTOXIC POLLUTANS]	0.0000	0.755	0.739	0.719
	Edaphic	Sapling density ($N\ ha^{-1}$)	1.08 + 0.96[Mg]	0.0001	0.490	0.467	1.062
	Water quality		1.44 + 0.60[ANTRO]	0.0837	0.175	0.124	1.421

Note: TEMPERATURE: soil and surface temperature; SUBSTRAT-CA: mud texture and Ca; NITRO: inorganic nitrogen; Mg: magnesium; NONTOXIC POLLUTANS: total suspended soil and dissolved oxygen; ANTRO: anthropogenic factors. Level of significance α: 0.05, except for the water quality and sapling density regression, for which the level of significance $\alpha = 0.1$

Based on the results for the effect of the temperature of the environment, (Hastuti et al. 2012; Akaji et al. 2019) stated that the photosynthetic rate of *Rhizophora* sp. increased at 25ºC and decreased at 30ºC, while the photosynthesis of *A. marina* was inhibited at 37ºC. Magnesium is needed in photosynthesis, and it has been found to be deposited in the stems and branches of *R. stylosa*, and in the leaves of *A. marina* (Alongi 2021). In addition to the nutrients, it is reported that the maximum stem growth of *R. apiculata* is observed with a supply of N > 10 $Nm^{-2}d^{-1}$ and P ≈ 6-8 mmol $Pm^{-2}d^{-1}$, whereas *A. marina* at N ≈ 10 mmol $Nm^{-2}d^{-1}$ shows no specific trend of P requirements (Alongi 2011). Based on their spatial distribution and temporal patterns, *A. marina* can be planted in the lower elevation or forepart of the mangrove zone (Aung et al. 2011; Ren et al. 2011), whereas *R. mucronata* is better to be planted in the higher elevation or adjacent to the mainland (Basyuni et al. 2018) in the restoration programs. Regarding the stand density, Asaeda et al. (2016) mentioned that the seedling and sapling density was positively correlated with the density of the mother trees of *R. stylosa* and A. *marina*. However, biological or reproductive success is due to the production of flowers, fruits, and viable seeds (Primavera and Esteban 2008; Jorge et al. 2015) at 3-5 years for most mangroves, 5 years for *A. marina*, and 3-5 years for *R. mangle* (Clarke 1992; Vozzo 2002; Primavera and Esteban 2008), or the sapling phase (Clarke 1992).

In conclusion, research into the habitat preferences of mangrove species by simultaneously using edaphic factors and water quality in Indonesia has not yet developed. Selecting species incompatible with habitats can promote failure in restoration programs. *Rhizophora* spp. and *A. marina*, the two most famous mangroves for restoration programs, have no interspecific associations; i.e., they tend to have negative relationships. The edaphic factors that significantly affect mangroves are the environmental temperature, clay content and Ca, inorganic N, and Mg, while the water quality factors are nontoxic pollutants and anthropogenic factors. At the seedling and sapling stages, *A. marina* and *Rhizophora* spp. prefer distinct habitats for stand development. Combining *A. marina* and *Rhizophora* spp. in restoration programs must be avoided. Future research should perform sequential data collection to obtain the spatiotemporal trends of the edaphic factors and water quality.

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