

RESEARCH ARTICLE

Hydrological repair and invasive grass removal restore *Rhizophora racemosa* mangrove communities in West Africa

Claudia M. Agraz Hernández^{1,2} , Ebénézer Houndjinou³, Jordan E. Reyes Castellanos¹, Carlos A. Chan Keb⁴, Juan Osti Saénz¹, Julio C. Chávez Barrera⁵, Janique Etienne⁶, Romain L. Glèlè Kakai⁷, Robert Puschendorf^{2,8} 

Mangrove ecosystems face significant threats from climate change and human activities. In West Benin, the invasive grass *Paspalum vaginatum* disrupts sedimentation and hydrology, creating anoxic conditions and nutrient imbalances. To address this, we implemented a cost-effective restoration strategy focused on hydrological repair, engaging local communities to excavate 26 artificial channels and clear 19 existing ones, restoring tidal flow to 30 ha of degraded mangrove forest. Of this, 20 ha were planted with *Rhizophora racemosa* propagules, while 10 ha remained unplanted due to unsuitable micro-topographic conditions. This intervention, costing \$1394.3 USD per hectare, adjusted sediment levels to match natural micro-topography, enabling hydrological recovery and suppressing *P. vaginatum*. The return of *Sesuvium portulacastrum* stabilized sediments, improved nutrient retention, and facilitated mangrove regeneration. Over 24 months, restoration efforts improved physicochemical parameters, reduced ammonium and acidity, and supported the planting of 250,000 *R. racemosa* propagules at 25 propagules/m² across 20 ha. At 785 days post-planting, survival reached 90%, promoting natural recolonization by mangroves along channel edges and by *S. portulacastrum* in adjacent unplanted areas. The 10 ha not reforested exhibited low *P. vaginatum* colonization, reinforcing the effectiveness of hydrological repair. This study presents a scalable, low-cost restoration model that integrates hydrological repair and pioneer species facilitation to enhance mangrove recovery. While still in early recovery, this community-driven approach establishes a strong foundation for long-term ecological restoration.

Key words: community-driven restoration, environmental stress, hydrological repair, invasive plant, mangroves

Implications for Practice

- Hydrological repair, the process of restoring natural water flow and tidal exchange, should be prioritized alongside propagule planting as it effectively reestablishes functional habitats and enhances long-term ecosystem resilience.
- Reestablishing natural tidal flooding cycles in mangroves impacted by siltation and erosion strengthens their capacity to withstand climate extremes, such as prolonged droughts, and adapt to gradual changes like rising sea levels.
- By comparing key physicochemical parameters of interstitial water and soil topography between healthy mangroves and adjacent degraded sites undergoing hydrological repair, it is possible to optimize the timing of planting to maximize survival and minimize the risk of planting too early, when substrate conditions remain unsuitable for propagules.

Introduction

Mangroves are among the most productive and ecologically important ecosystems, providing critical services such as carbon sequestration, habitat for biodiversity, food resources, and

Author contributions: CMAH, EH, JERC, JOS, RLGK, JE conceptualized and designed the study; CMAH, RLGK, JCCB collected and analyzed the data; CMAH, CACK provided guidance for data interpretation; CMAH, CACK, RLGK, RP contributed to the writing, reviewing, and editing of the manuscript; all authors approved the final version.

¹Instituto EPOMEX, Universidad Autónoma de Campeche, Avenida Agustín Melgar s/n between Juan de la Barrera and Calle 20, Colonia Buenavista, San Francisco de Campeche CP 24039, Campeche, Mexico

²Address correspondence to C. M. Agraz Hernández, email clmagraz@uacam.mx and R. Puschendorf, email robert.puschendorf@plymouth.ac.uk

³Ecole d'Aménagement et de Gestion de l'Environnement, Faculté des Sciences Agronomiques (FSA), Université d'Abomey-Calavi, Abomey-Calavi, Benin

⁴Facultad de Ciencias Químico Biológicas, Universidad Autónoma de Campeche, Avenida Agustín Melgar s/n entre Juan de la Barrera y Calle 20, Colonia Buenavista, San Francisco de Campeche CP 24039, Campeche, México

⁵División de Ciencias Biológicas y de la Salud, CBS, Universidad Autónoma Metropolitana Unit Iztapalapa, Ciudad de México, México

⁶Fonds Français pour l'Environnement Mondial, 5 Rue Roland Barthes 75598, Paris Cedex 12, France

⁷Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, Cotonou 04 BP 1525, Benin

⁸School of Biological and Marine Sciences, University of Plymouth, Devon PL24 8AA, UK

© 2025 The Author(s). Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

doi: 10.1111/rec.70084

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70084/supinfo>

reproductive grounds for commercially valuable fish species. They also play a vital role in coastal protection and biodiversity conservation (Feller et al. 2017). Despite their importance, mangroves are increasingly threatened by anthropogenic pressures and climate change (Romañach et al. 2018; Agraz-Hernández et al. 2022). Between 1980 and 2005, global mangrove cover declined by 23% (FAO 2007), disrupting essential ecosystem functions and promoting the proliferation of invasive species, which impede natural recovery processes (Biswas et al. 2018).

Mangrove decline in Africa continues to be a critical issue. In Benin, 62% of mangrove cover was lost between 1988 and 2001 (Zanvo et al. 2022). This decline is further exacerbated by climate change, as mangroves in the region naturally occur in areas experiencing increasingly extreme seasonal rainfall patterns (Hounvou et al. 2023). Proximity to expanding human populations also subjects these ecosystems to industrial and urban wastewater pollution. Additionally, ecosystem fragmentation and hydrological alterations caused by artificial channels—constructed to transport sediments for salt production—along with wood extraction for artisanal fishing and firewood collection, represent significant local threats to Benin's mangroves (Teka et al. 2019).

Mangrove degradation facilitates the spread of invasive species, especially *Paspalum vaginatum* (Sw.) Godr. This grass invades degraded habitats, forming dense monocultures that displace native vegetation. Originally introduced for livestock feed and golf courses, *P. vaginatum* proliferates in fragmented mangrove ecosystems. Its dense root system accelerates sedimentation, raises sediment levels, and releases allelopathic compounds that inhibit native species germination and disrupt sediment microbial communities (Zhang et al. 2019; Zheng et al. 2023). By creating a persistent, stable state, this species impedes the survival and growth of mangrove propagules, complicating restoration efforts (Biswas et al. 2018).

The invasion of *P. vaginatum* disrupts the composition, structure, and function of mangrove ecosystems (Andrieu et al. 2019). Its invasive success is widely documented across coastal regions, attributed to its tolerance of brackish environments and prolonged flooding (Duncan & Carrow 1999). The continued degradation of mangroves caused by this grass has long-term consequences for coastal communities, aggravating poverty and increasing vulnerability to extreme weather events (Teka et al. 2019).

Implementing ecological restoration projects is essential to reversing mangrove degradation, particularly those that actively engage local communities in management processes (Borrini-Feyerabend & Hill 2015; Agraz Hernández 2024). However, despite international restoration efforts, mangrove projects often fail because propagules or seedlings are planted before addressing the underlying stressors, and insufficient measures are taken to improve environmental conditions (Lewis 2005). In areas where mangroves have been displaced by invasive species, there is a notable lack of studies on their ecological impacts and effective control strategies. Developing and implementing control measures, while generating data on the success of restoration approaches, is critical to supporting large-scale projects

for climate change mitigation and job creation, particularly in vulnerable and impoverished communities.

This research aimed to test whether hydrologic repair, combined with appropriate micro-topographic relief, could re-establish the hydrological conditions found in nearby healthy mangroves, thereby promoting suitable conditions for propagule establishment and survival. In this context, “micro-topographic relief” refers to centimeter-scale variations in sediment elevation across the restoration area, integrated with broader hydrological restoration efforts (Flores-Verdugo et al. 2007). These efforts involve recovering and creating a channel system similar to those in healthy mangroves, ensuring appropriate conditions to support key ecological processes. Variations in soil level, measured in centimeters, are critical for controlling tidal flow, salinity gradients, and sediment oxygenation. These variations create favorable conditions for natural mangrove recolonization. Additionally, they support the establishment and ecological functioning of vegetation such as *Sesuvium portulacastrum* L., which stabilizes sediments and facilitates nutrient cycling (Villavicencio et al. 2024). The study focused on the hydrological rehabilitation of 30 ha and the planting of 20 of these hectares in the Djégbadji wetland, located in the municipality of Ouidah, Benin, West Africa, while also addressing the challenges posed by the invasive grass *P. vaginatum*. In parallel, the project actively involved the local community in planting, implementation, environmental monitoring, and evaluation. This participatory approach sought to deepen the community's understanding of mangrove ecosystems and empower them to implement low-cost restoration techniques, handcrafted by the community, to maximize long-term sustainability. These efforts represent an essential first step toward the long-term goal of mangrove planting.

Methods

Study Area

The study area is in the Ouidah district of the Republic of Benin, West Africa. It features a hydrographic network of lakes and lagoons fed by the Kouffo and Mono rivers originating from the southwest basin (Ahouangninou 2013). It is bordered by the Atlantic Ocean to the south, Abomey-Calavi to the east, Grand-Popo to the west, and Kpomassè and Tori-Bossito to the north (Fig. 1). The region typically has two rainy seasons, April–July and September–November, with dry seasons December–March and in August. Annual precipitation ranges from 700 to 1400 mm, with average annual temperatures between 23 and 32°C (Obada et al. 2021). In Cotonou, Benin, tides have a mean range of approximately 1.5 m, with maximum recorded heights of 1.7 m and minimums of −0.2 m (Tide Table, n.d.). According to Flores-Verdugo et al. (2007), *Rhizophora racemosa* thrives at intermediate elevations within this tidal range, with roots partially exposed during low tide and periodically inundated, ensuring proper oxygenation and nutrient access. The hydroperiod should avoid prolonged anoxia and excessive desiccation.

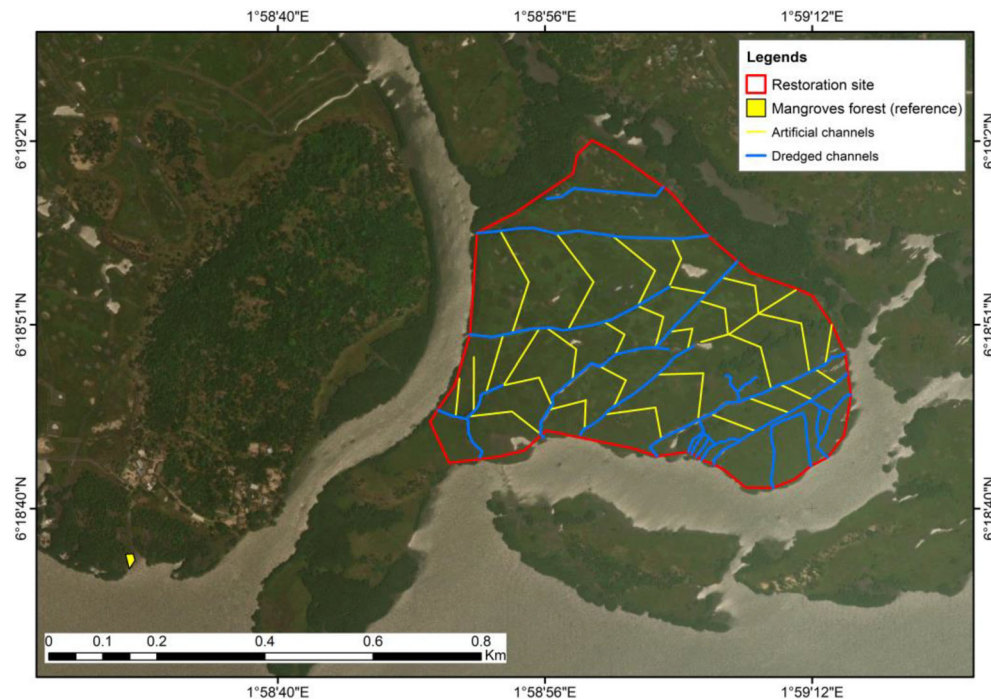


Figure 1. Location of the restoration and reference sites within the study area, showing the design and placement of artificial channels and community-dug channels at the restoration site in the Djègbadji district, Ouidah, Benin, Africa.

Along the coastline lies Ramsar site 1017, an extensive wetland near Djègbadji, Ouidah municipality. Spanning approximately 66 km², these mangroves constitute about 0.2% of Africa's mangrove coverage. Six mangrove species have been identified, with *R. racemosa* and *Avicennia germinans* L. as the most dominant. However, the Ouidah district's mangroves are highly degraded (Corcoran et al. 2007), with the wetlands increasingly dominated by invasive species, including *Paspalum vaginatum*, *Philoxerus vermicularis* L., and *Acrostichum aureum* L. (Biswas et al. 2018), occupying a distinct ecological niche. It often establishes itself in areas where physicochemical conditions improve but soil elevation remains suboptimal for mangrove growth. In such cases, *Sesuvium portulacastrum* acts as a pioneer species, aiding in soil recovery, nutrient recycling, and the creation of microhabitats that capture floating propagules and facilitate mangrove establishment (Lewis 2005; McKee et al. 2007; Villavicencio et al. 2024).

The municipality's population has grown rapidly, increasing from 76,555 inhabitants in 2002 to 162,034 in 2013 (INSAE 2016), which has exerted considerable pressure on the area's natural resources. Economic activities such as agriculture, fishing, and hunting engage approximately 13% of the local population (INSAE 2016). Among these, fishing is the predominant livelihood in several districts, while salt production, extracted from mangrove sediment, represents a vital economic activity, predominantly undertaken by women (Teka et al. 2019; Agoungbome et al. 2020).

Reference Site Selection and Environmental Parameters

We selected two monospecific mangrove forests adjacent to the restoration site as references: one dominated by *R. racemosa* (6°18'36.29"N, 1°58'30.63" E) and the other by *A. germinans* (6°18'36.72"N, 1°58'30.77" E). *Rhizophora racemosa* was chosen for planting due to its dominance and compatibility with the restoration site's conditions after hydrological repair. Sediment micro-topography and environmental assessments conducted in March 2018 determined planting timing (Fig. 1). Micro-topographic relief significantly influences interstitial water properties—salinity, oxygenation, and hydroperiod—critical to mangrove distribution (Flores-Verdugo et al. 2007). The restoration site's micro-topography closely matched *R. racemosa* habitats. However, the topography of the *A. germinans* forest did not align with the reforested 20 ha, so its data was excluded.

We installed piezometers at the reference and restoration sites to collect interstitial water and measure physicochemical parameters and nutrients. Two piezometers were placed in the *A. germinans* forest, two in the *R. racemosa* forest, and seven in the restoration site. To sample interstitial water from zones with the highest root biomass, we constructed piezometers from polyvinyl chloride (PVC) tubes, 25.8 cm in diameter and 1.5 m in length, perforated with 1 cm holes down to 30 cm (Agraz Hernández et al. 2011). The piezometers were constructed from 1.5 m long PVC tubes, perforated from the bottom up to 30 cm. They were installed with the perforated end buried 50 cm deep into the sediment, leaving 1 m above the sediment surface, and their locations were georeferenced

(Agraz-Hernández et al. 2022). From February 2018 to October 2020, we measured salinity, redox potential, and nutrient concentrations in the interstitial water monthly at the reference and restoration sites. The piezometers were drained and allowed to refill before the new water was used for sampling and measurements. Before each measurement, we drained the piezometers. We determined salinity by extracting water with a hose and measuring it using a refractometer (ATAGO, Inc., range: 0–100 PSU; Agraz-Hernández et al. 2022). Redox potential was measured with a portable multimeter (HACH HQ40d, Loveland, CO, U.S.A.) equipped with an oxidation–reduction potential (ORP) probe capable of detecting values from -1200 to $+1200$ mV, suitable for both oxidizing and reducing environments.

To analyze nutrient concentrations, we collected water samples in 50 mL polypropylene bottles pre-washed with 5% hydrochloric acid and rinsed with distilled water. At each site, we filled two bottles per piezometer using a manual vacuum pump connected to a hose. We preserved one bottle with two drops of phenol to stabilize ammonium (NH_4^+) and used the second bottle to measure nitrite (NO_2^-), nitrate (NO_3^-), phosphates (PO_4^{3-}) and sulfates (SO_4^{2-}). We stored the samples in coolers with ice, transported them to the laboratory, and kept them at -4°C until analysis. All samples were analyzed within 3 months using ion chromatography (Agraz-Hernández et al. 2018).

Diagnosis and Hydrological Repair of the Restoration Site

Baseline evaluations of interstitial water physicochemical parameters were conducted throughout 2018 to assess the extent of degradation and guide the design of artificial channels for hydrological repair. These evaluations included measurements of salinity (PSU), redox potential (mV), temperature ($^\circ\text{C}$), and nutrient concentrations such as ammonium and SO_4^{2-} . The chemical properties of interstitial water, including acidity or alkalinity (pH) and redox potential (an indirect indicator of oxygen availability), were also assessed to ensure alignment with reference site conditions. The methodology was adapted from restoration approaches applied in Mexico by the Laboratorio de Humedales Costeros con especialidad en Mangles at the Universidad Autónoma de Campeche (Agraz Hernández 2024).

Micro-topographic relief, defined as centimeter-scale variations in sediment elevation within the 30 ha of restoration, was identified as a critical factor influencing hydrodynamics, salinity, sediment oxygenation, and habitat suitability for mangrove species and associated vegetation. These fine-scale variations shaped the ecological conditions necessary for successful restoration (Agraz Hernández 2024). A sediment micro-relief survey, conducted using Real-Time Kinematic (RTK) positioning, provided high-precision data with a margin of error of 5 mm. Two differential global positioning system units paired with a high-frequency amplified antenna recorded coordinates, referencing the National Geodesic database in real-time or during post-processing to ensure accuracy. Micro-topographic data allowed classification of the restoration site into zones based on flooding

levels—maximum, moderate, and minimal—guiding species selection, planting timing, and channel excavation.

Using micro-topographic data and the values and concentrations of physicochemical parameters of interstitial water, a network of artificial channels was designed to restore tidal flow and hydrological connectivity. The restoration design focused on the lowest sediment elevations to improve tidal inflow, thereby replicating natural tidal cycles (hydroperiods) and enhancing oxygenation and salt dilution in the sediment. Channels were strategically constructed to mimic natural tidal conditions, with specific channels for water entry (high tide) and others for water outflow (ebb tide). This ensured optimal flooding patterns, appropriate flooding frequency and duration, and shorter water residence times. Additionally, hydrological repair increased freshwater input, further improving habitat conditions essential for mangrove regeneration.

Large primary channels were excavated and connected directly to rivers and estuaries. Secondary channels were constructed and linked to primary channels, forming a network that restored water flow across the restoration area. Additionally, community-constructed channels, historically excavated for sediment extraction and salt production, were cleared of silt to further improve hydrological connectivity (Table S1; Figs. 1 & S1–S7). Maintenance included clearing blockages and addressing opportunistic vegetation growth, ensuring the stabilization of the system.

Post-hydrological repair monitoring from April 2019 to December 2021 tracked physicochemical parameters to confirm alignment with reference site conditions. Community members manually removed surviving *P. vaginatum* 1 year after hydrological repair using a handcrafted tool called “Alín” (from the Fon dialect; Fig. S2). These efforts confirmed that hydrological repair created favorable conditions for the preselected species *R. racemosa* and guided the optimal timing for planting efforts.

Planting of *R. racemosa* Propagules

We selected *R. racemosa* for planting due to its dominance in the reference forest and compatibility with the restoration site’s environmental conditions. Planting began only after salinity and redox potential at the restoration site aligned with those of the reference site following hydrological repair. The micro-topographic distribution of *R. racemosa* in areas where *P. vaginatum* had either been removed or experienced high mortality was compared with that of the reference site, predominantly occupied by *R. racemosa*.

Mature propagules were collected manually between October and December 2019, corresponding to the species’ reproductive phenology and favorable interstitial water conditions (Akodekou 2022). Field teams gathered propagules from parent trees at the reference site, discarding those damaged by herbivory. Propagules were transported using community boats and sacks to prevent physical damage, dehydration, and sun exposure.

Planting was conducted across 20 ha, with 10 ha excluded due to unsuitable micro-topographic conditions, specifically elevations that were too high, exceeding the range suitable for

R. racemosa establishment (Table S1; Figs. S1–S7). The planted areas were categorized as follows: (a) zones where *P. vaginatum* died due to hydrological repair, allowing tidal action to remove sediment and lower the elevation; (b) zones where *P. vaginatum* was manually cleared, reducing sediment elevation; (c) zones already having micro-topographic relief similar to the reference forest. Categories (a) and (b) thus reached similar soil elevations as the reference forest after these processes. Propagules were planted at a density of 250,000 per hectare, spaced 20 cm apart (25 propagules/m²), and embedded 3–5 cm into the substrate.

Propagule Growth and Survival

We monitored propagule growth and survival over 785 days using six 5 × 5 m plots randomly distributed across the 20-ha restoration site. Evaluations were conducted every 30 days for the first 300 days, with a final assessment at 785 days. Each plot was analyzed separately. Due to the lack of significant differences among plots (checked initially but results not shown), data were pooled for overall analysis.

Within each plot, 12 seedlings were labeled and monitored for total height using a Mitutoyo Advanced Onsite Sensor vernier, providing an accuracy of ±0.025 mm and a measurement interval of 0.0005–0.01 mm. Measurements began at the zero node following the protocol of Duke and Pinzón (1992). Mortality was assessed monthly within each plot and across the entire restoration site, with site-wide mortality trends extrapolated from plot-level data. As with growth rates, mortality showed no significant differences among plots ($p > 0.05$). Pooled data were used to calculate overall mortality for the restoration site.

Data Analysis

We used multivariate principal component analysis (PCA) to identify the most significant variables explaining the environmental conditions at each site before hydrological repair. A t test was performed to compare the physicochemical conditions of interstitial water between the restoration and reference sites before restoration. To evaluate the effects of restoration at the degraded mangrove site, we performed a two-way analysis of variance (ANOVA) to assess changes in water conditions before and after hydrological repair.

Propagule height growth was evaluated using linear regression, while mortality patterns were best modeled using a quadratic regression, which revealed an initial increase in mortality, followed by stabilization and a subsequent decline. Differences in relative survival across evaluation times were analyzed using one-way ANOVA. A post hoc test was conducted using Fisher's least significant difference (LSD) method to determine which time points exhibited significant differences in survival.

Normality and homoscedasticity were tested using the Shapiro–Wilk and Levene tests ($\alpha = 0.05$). Since the data violated normality assumptions, the variables were transformed using the Box-Cox method. All statistical analyses were conducted using XLSTAT-Ecology v.2018.5, Minitab 18, and STATISTICA V.12, with a significance level set at $\alpha = 0.05$.

Results

Hydrological Repair and Environmental Changes Post-Restoration

Between January and March 2019, hydrological repair included the excavation of 26 artificial secondary channels measuring 1.5 m wide and 1.0 m deep, totaling 5166.8 m³ of material over 3714 m in length with the support of 180 people from the Ouïdah community. These channels were connected to 19 pre-existing channels, which were originally dug by the community for fishing and sediment salt. Maintenance involved clearing 10,737.8 m³ of silt, forming an interconnected network spanning 7158.5 m (Fig. 1). This network enhanced tidal inflow, reduced water retention times, and improved sediment oxygenation.

Post-hydrological repair monitoring from April 2019 to December 2021 revealed substantial changes in the physicochemical conditions of interstitial water at the restoration site (Table 1). Salinity decreased significantly from 21.7 to 13.3 PSU, aligning with conditions at the reference site (10.8 PSU; Table 2). Redox potential decreased from −96.7 to −172.1 mV, maintaining hypoxic conditions, compared to the reference site, which remained anoxic at −363 mV (Table 1). SO₄^{2−} concentrations decreased by 49.3%, while pH increased significantly, surpassing reference site levels and indicating higher alkalinity. Detailed data and additional analyses supporting these findings are provided in Table S1 and Figs. S1–S7.

Nutrient concentrations, including ammonium and NO₂[−], remained stable at both sites throughout the monitoring period, with no significant differences before or after restoration (Table 2). Temperature also showed no significant variation between sites and across the monitoring period (Table 2). These results indicate that hydrological repair successfully altered key

Table 1. Two-way analysis of variance with respect to the physicochemical parameters of the interstitial water (salinity, redox potential, pH, and temperature) between the restoration and the *R. racemosa* forest of the reference site and the environmental conditions (before and after hydrological repair), with a significance level of p less than 0.05. See Table S1 and Figs. S1–S7 for detailed data. *df*, degrees of freedom.

Parameter	Factor	df	F	p
Salinity (PSU)	Site	1	11.11	<0.001
	Condition	1	28.73	<0.0001
	Site × condition	1	4.73	<0.030
	Error	327		
Redox potential (mV)	Site	1	391.47	<0.0001
	Condition	1	1.51	0.220
	Site × condition	1	12.43	<0.0001
	Error	327		
pH	Site	1	8.32	<0.004
	Condition	1	86.11	<0.0001
	Site × condition	1	9.66	<0.002
	Error	327		
Temperature (°C)	Site	1	1.79	0.182
	Condition	1	0.06	0.801
	Site × condition	1	0.05	0.828
	Error	327		

Table 2. Comparison of physicochemical parameters in interstitial water between the restoration site and the *Rhizophora racemosa* forest reference site before and after restoration, using a *t* test. This analysis was conducted prior to hydrological repair in the Djegbadji district wetland, Ouidah, Benin, Africa. NS, not significant; S, significant. Parameters: NO₂[−] (nitrite), NO₃[−] (nitrate), NH₄⁺ (ammonium), PO₄^{3−} (phosphate), SO₄^{2−} (sulfates). See Table S1 and Figs. S1–S7 for detailed data.

Parameters	df	T	p	Significance
pH	56	0.40	0.691	NS
Redox potential (mV)	104	18.56	0.0001	S
Salinity (PSU)	117	3.59	0.0001	S
Temperature (°C)	111	1.73	0.086	NS
NO ₂ [−] (mg/L)	76	0.68	0.497	NS
NO ₃ [−] (mg/L)	101	1.96	0.050	S
NH ₄ ⁺ (mg/L)	62	0.33	0.742	NS
PO ₄ ^{3−} (mg/L)	76	0.92	0.363	NS
SO ₄ ^{2−} (mg/L)	90	1.12	0.269	NS

parameters, creating conditions favorable for mangrove planting.

PCA provided further insights into environmental drivers prior to restoration (2018). At the reference site, 78% of the variance in environmental conditions was explained by two components: the first correlated PO₄^{3−}, NO₃[−], ammonium, and SO₄^{2−} with temperature (42%), while the second linked salinity and SO₄^{2−} with redox potential (36%; Table 3). At the restoration site, 65.7% of the variance was explained by three components: ammonium and NO₃[−] were inversely related to pH, salinity, and SO₄^{2−} (31.6%), while NO₃[−], PO₄^{3−}, salinity, and redox potential were linked to temperature in the remaining components (18.9 and 15.1%, respectively; Table 4).

Monitoring of *Rhizophora racemosa* Propagules

Following hydrological repair and the alignment of salinity and redox potential with reference site conditions, 5,760,000 propagules of *Rhizophora racemosa* were collected for planting. Of these, 760,000 propagules (13.2%) were discarded due to physical damage, herbivory, boring, or dehydration, leaving 5,000,000 propagules to be planted across 20 ha at a density of

Table 3. Principal component analysis (PCA) of physicochemical parameters in interstitial water at the *Rhizophora racemosa* forest reference site in Ouidah, Africa (2018, before restoration). The first two principal components explain 78% of the total variance. See Table S1 and Figs. S1–S7 for detailed data.

Parameters	Component 1 (42%)	Component 2 (36%)
pH	−0.259573	−0.401046
Temperature (°C)	−0.461003	−0.120358
Redox potential (mV)	−0.183056	0.508630
Salinity (PSU)	−0.087715	0.534142
NO ₂ [−] (mg/L)	0.181074	0.0903243
NO ₃ [−] (mg/L)	−0.383253	−0.286736
PO ₄ ^{3−} (mg/L)	−0.507787	−0.076407
SO ₄ ^{2−} (mg/L)	−0.363982	0.381432
NH ₄ ⁺ (mg/L)	−0.32999	−0.197378

Table 4. Principal component analysis (PCA) of physicochemical parameters in interstitial water at the degraded mangrove site in Ouidah, Africa (2018, before restoration). The first three principal components account for 65.7% of the total variance. See Table S1 and Figs. S1–S7 for detailed data.

Parameter	Component I (31.6%)	Component II (18.9%)	Component III (15.1%)
pH	−0.509	0.194	−0.024
Temperature (°C)	0.055	0.112	−0.615
Redox potential (mV)	−0.073	−0.407	0.617
Salinity (PSU)	−0.397	0.329	0.179
NO ₂ [−] (mg/L)	0.008	0.641	−0.090
NO ₃ [−] (mg/L)	0.300	0.119	−0.035
PO ₄ ^{3−} (mg/L)	−0.160	0.422	−0.443
SO ₄ ^{2−} (mg/L)	−0.518	0.146	0.015
NH ₄ ⁺ (mg/L)	0.437	0.226	0.047

250,000 propagules per hectare (Table S1; Figs. S1–S7). Planting in this area included planting along the edges of artificial channels to stabilize channel walls and reduce sedimentation.

Paspalum vaginatum remained undetected in planted areas during the monitoring period. However, natural recolonization of *R. racemosa* propagules occurred along artificial channel edges, and occasional propagules and established seedlings of *Avicennia germinans* were observed in zones colonized by *Sesuvium portulacastrum* (Fig. 2).

High mortality of *P. vaginatum* was documented in the 10 ha that were not reforested due to micro-topographic conditions unsuitable for *R. racemosa*, as the elevation was above the species' maximum distribution range. Subsequently, recolonization by *S. portulacastrum* was observed, indicating further sediment stabilization (Fig. 2).

The average growth rate in height for *R. racemosa* seedlings reforested from hypocotyls was 0.22 ± 0.05 cm/day, exhibiting a linear trend during the measurement period ($r^2 = 0.93$; Fig. 3A). Mortality followed a quadratic model, showing an initial increase (Fig. 3B), followed by a stabilization phase up to 300 days, and then a subsequent decrease by 785 days. Notably, mortality peaked at 10% between days 240 and 300 (Fig. 3B).

Regarding the survival rate, the highest value was recorded between 30 and 60 days post-planting, at 97%, while the lowest value was observed at 785 days, at 87%. Despite these variations, no significant differences were found across the evaluation times (Fig. 3C; $p = 0.114$).

In the 10 ha that were not planted due to unsuitable micro-topographic conditions, natural recruitment of *R. racemosa* was observed following hydrological repair, particularly in areas initially colonized by *S. portulacastrum*. This natural recruitment progressively increased, further stabilizing sediments and enhancing mangrove establishment.

Discussion

The global decline of mangrove ecosystems underscores the urgent need for restoration strategies that are both ecologically tailored and grounded in robust, evidence-based techniques.

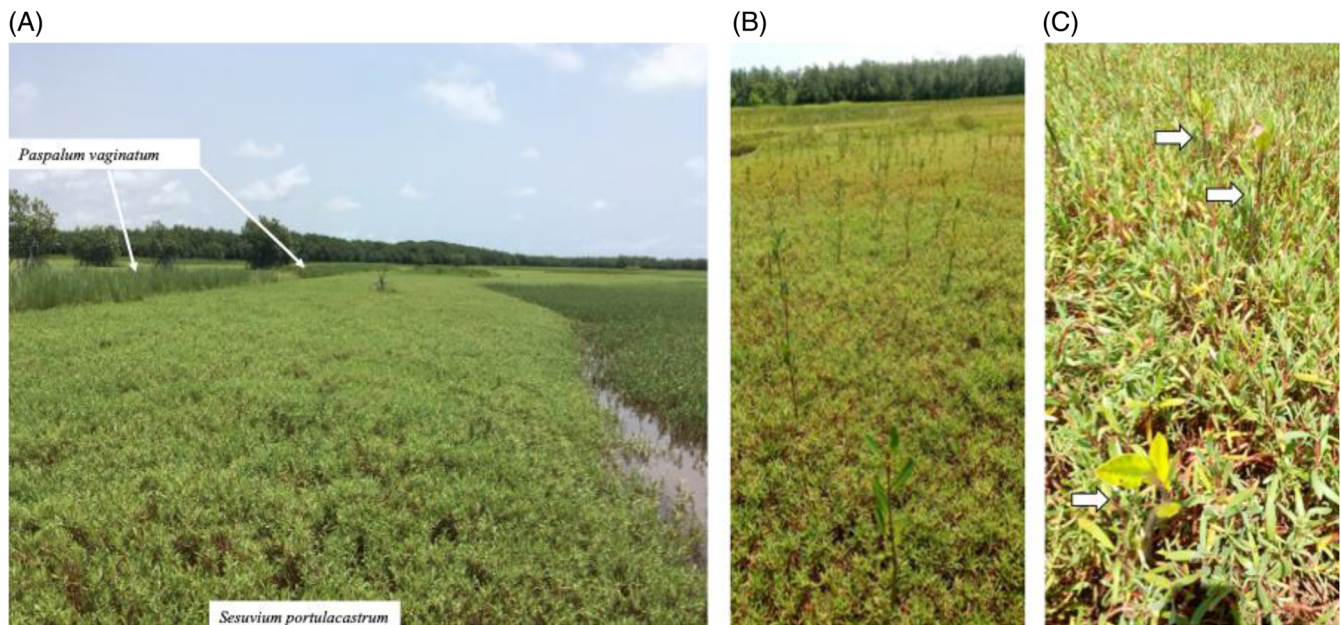


Figure 2. (A) Non-planted areas where *Paspalum vaginatum* exhibited 100% mortality resulting from hydrological repair. (B) Initial colonization by *Sesuvium portulacastrum* in these areas. (C) Subsequent natural recruitment of *Rhizophora racemosa* occurring in these non-planted areas, with both species progressively increasing in coverage.

Effective interventions must account for the local ecology, seasonality, and specific environmental conditions of the mangrove systems being restored. Implementing these strategies at the local level, supported by national governments and aligned with international agreements on mangrove protection and restoration, is crucial (Romañach et al. 2018). This study highlights the success of combining site-specific hydrological repair, micro-topographic adjustments, with high-density propagule planting to address local challenges, such as invasive species and degraded interstitial water quality, while fostering conditions suitable for mangrove survival and growth.

Managing invasive species requires an integrated approach, including physical, mechanical, chemical, and biological measures (Augusthy et al. 2024). Additionally, interactions between plants and their environment can play a key role in curbing invasions, as demonstrated by the suppression of *Paspalum vaginatum* through hydrological repair and high-density planting of *Rhizophora racemosa*. These findings align with broader principles of mangrove ecosystem management (Augusthy et al. 2024).

At the restoration site, hydrological disruptions and nutrient loading had significantly degraded interstitial water quality, resulting in high ammonium concentrations, reduced oxygen levels, and conditions unsuitable for natural mangrove recovery. The invasive grass *P. vaginatum* exacerbated degradation by thriving under prolonged water residence times, high salinity, and nutrient-enriched conditions, spreading rapidly and altering sediment dynamics (Saluzzo et al. 2015).

Hydrological repair through channel excavation and micro-topographic adjustments successfully restored tidal flow, reduced water residence times, and improved key physicochemical parameters, such as salinity and redox potential, within

24 months. These changes directly suppressed *P. vaginatum* growth and supported the survival of planted *R. racemosa* propagules.

High-density planting further demonstrated its effectiveness in controlling *P. vaginatum* by reducing competition for light, space, and resources. This approach aligns with previous findings that dense planting suppresses invasive grasses and facilitates mangrove establishment (Primavera & Esteban 2008).

Although complete eradication of *P. vaginatum* remains unlikely given it is still common in surrounding areas, its observed decline highlights the potential of this management strategy. Continued monitoring will determine whether additional interventions, such as thinning, are necessary as the mangroves mature.

The role of the pioneer species *Sesuvium portulacastrum* was also critical in facilitating restoration success. As *S. portulacastrum* colonized sediment-stabilized areas, it suppressed *P. vaginatum* and created conditions favorable for mangrove survival and growth. Its dense vegetative cover reduced erosion, protected propagules from desiccation, and enhanced sediment nutrient retention, contributing to improved conditions for mangrove establishment (Zedler & Kercher 2005; McKee et al. 2007; Villavicencio et al. 2024). Moreover, in the 10 ha not planted due to unsuitable micro-topography, natural recruitment of *R. racemosa* occurred primarily in areas initially colonized by *S. portulacastrum*. This natural recruitment highlights the effectiveness of hydrological repair combined with pioneer species establishment, underscoring the potential for integrated approaches that promote both active planting and passive ecological recovery in mangrove restoration efforts (Donnelly & Walters 2014).

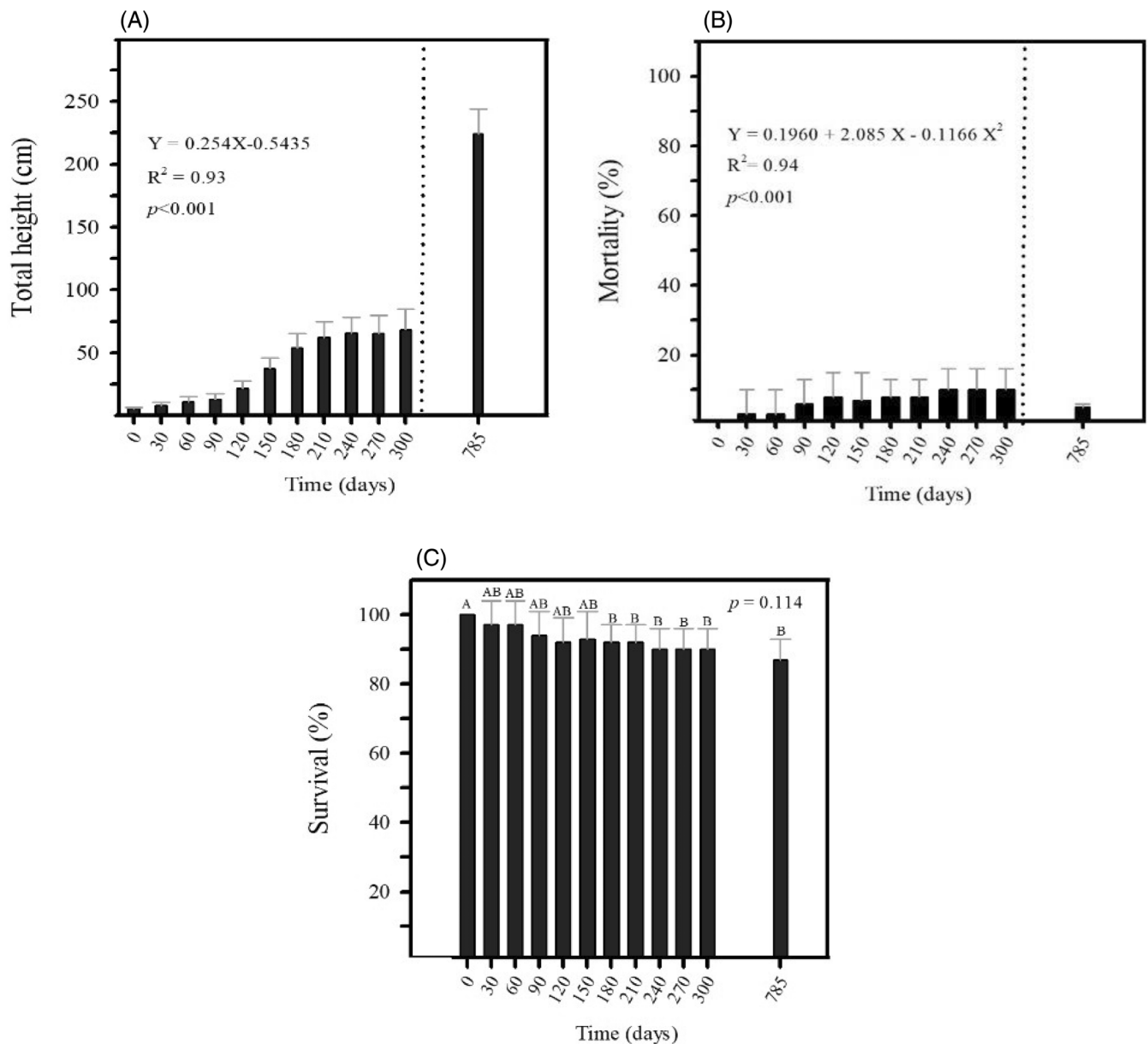


Figure 3. Height growth (A), mortality (B), and survival percentage (C) of *Rhizophora racemosa* propagules planted across 20 ha following hydrological repair in the municipality of Ouidah, Benin, Africa. Black bars represent the mean of each variable, while error bars indicate the standard error of the mean. In (C), bars that do not share the same letter differ significantly from each other ($p < 0.05$).

Beyond vegetation recovery, ecological benefits extended to fauna. Migratory bird species, crabs, and fish—absent before restoration—returned to the site, including species such as Fiddler crab (*Uca* sp.), Roseate spoonbill (*Ajaia ajaja*), and Brown pelican (*Pelecanus occidentalis*). These observations indicate the reestablishment of habitat functionality and biodiversity, reinforcing the broader ecological impact of restoration efforts.

The project also proved cost-effective, with a total cost of \$1394.3 USD per hectare, including hydrological repair and high-density planting, including a planting density of 250,000 propagules per hectare at planting. Compared to international averages, which range from \$1140 to \$6545 USD per hectare

depending on techniques and materials (Bayraktarov et al. 2016), this approach offers a scalable and affordable model. By involving local communities in propagule collection and planting, costs were reduced by involving local communities, making this approach both socially inclusive and replicable. Direct planting with propagules, as conducted in this study, is a less expensive alternative compared to other restoration methods. Nursery-grown seedlings can cost up to \$216,000 USD per hectare (Reyes Chargooy & Tovilla Hernández 2016; Su et al. 2021).

This study underscores the critical importance of integrating hydrological repair with a thorough consideration of the

micro-topographic distribution range of the restoration site, as well as the natural distribution range of mangrove species in the reference forest. These measures, combined with high-density reforestation, emphasize the need for incorporating comprehensive physical, chemical, and biological assessments. This integrated approach not only aids in controlling invasive species but also enhances the survival rates of reforested areas by leveraging plant-environment interactions as a foundation for ecological restoration success. Community participation emerged as a key element for successfully initiating the recovery of degraded mangrove ecosystems. While the results represent the early stages of restoration, with propagules transitioning to saplings, this project establishes a solid foundation for the long-term and large-scale development of mangrove forests. The success of this approach demonstrates its potential applicability to other degraded systems facing similar challenges, offering a scalable and cost-effective model for mangrove restoration.

Acknowledgments

This manuscript was significantly improved by two anonymous reviewers and S. Davis. We thank the French Global Environment Facility (FFEM) for funding the restoration project. Likewise, we extend our gratitude to the community of Ouidah for their excellent work during the restoration activities. The authors also wish to acknowledge the dedicated efforts of the government, field, and technical personnel from the Autonomous University of Campeche; the support provided by the Wetlands Program of SINAC; and the administrative work of Fundación Neotrópica and Fundación Corcovado.

LITERATURE CITED

- Agoungbome SMD, Gbenontin E, Thiam M (2020) Mangroves under demographic pressure and salt production threats in the municipality of Ouidah (Benin). Pages 105–118. In: Thorn JPR, Gueye A, Hejnowicz AP (eds) Innovations and interdisciplinary solutions for underserved areas. Springer International Publishing, Cham, Switzerland. https://doi.org/10.1007/978-3-030-51051-0_8
- Agraz Hernández CM (2024) Guide méthodologique pour la restauration des mangroves. Editions du FFEM, Paris, France
- Agraz Hernández CM, García Zaragoza C, Iriarte-Vivar S, Flores-Verdugo FJ, Moreno Casasola P (2011) Forest structure, productivity and species phenology of mangroves in the La Mancha lagoon in the Atlantic coast of Mexico. *Wetlands Ecology and Management* 19:273–293. <https://doi.org/10.1007/s11273-011-9216-4>
- Agraz-Hernández CM, Chan-Keb CA, Muñiz-Salazar R, Pérez-Balan RA, Vanegas GP, Manzanilla HG, Osti-Sáenz J, del Río Rodríguez R (2022) Pore water chemical variability and its effect on phenological production in three mangrove species under drought conditions in southeastern Mexico. *Diversity* 14:668. <https://doi.org/10.3390/d14080668>
- Agraz-Hernández C, Del Río-Rodríguez R, Chan-Keb C, Osti-Saenz J, Muñiz-Salazar R (2018) Nutrient removal efficiency of *Rhizophora mangle* (L.) seedlings exposed to experimental dumping of municipal waters. *Diversity* 10:16. <https://doi.org/10.3390/d10010016>
- Ahouangninou C (2013) Using *Aedes aegypti* larvae to assess pesticide contamination of soil, groundwater and vegetables. *British Biotechnology Journal* 3:143–157. <https://doi.org/10.9734/BBJ/2013/2161>
- Akodekou D (2022) Ecophysiological response of *Avicennia germinans* (L.) L. and *Rhizophora racemosa* (G. Mey.) to the variation in groundwater salinity in Ouidah, Benin. Master dissertation, University of Abomey-Calavi, Abomey-Calavi, Benin.
- Andrieu J, Cormier-Salem M-C, Descroix L, Sané T, Diéye EHB, Ndour N (2019) Correctly assessing forest change in a priority west African mangrove ecosystem: 1986–2010 an answer to Carney et al. (2014) paper “assessing forest change in a priority west African mangrove ecosystem: 1986–2010”. *Remote Sensing Applications: Society and Environment* 13: 337–347. <https://doi.org/10.1016/j.rsase.2018.12.001>
- Augusthy S, Nizam A, Kumar A (2024) The diversity, drivers, consequences and management of plant invasions in the mangrove ecosystems. *Science of the Total Environment* 945:173851. <https://doi.org/10.1016/j.scitotenv.2024.173851>
- Bayraktarov E, Saunders MI, Abdullah S, Mills M, Beher J, Possingham HP, Mumby PJ, Lovelock CE (2016) The cost and feasibility of marine coastal restoration. *Ecological Applications* 26:1055–1074. <https://doi.org/10.1890/15-1077>
- Biswas SR, Biswas PL, Limon SH, Yan E-R, Xu M-S, Khan MSI (2018) Plant invasion in mangrove forests worldwide. *Forest Ecology and Management* 429:480–492. <https://doi.org/10.1016/j.foreco.2018.07.046>
- Borrini-Feyerabend G, Hill R (2015) Governance for the conservation of nature. Pages 169–206. In: Worboys GL, Lockwood M, Kothari A, Feary S, Pulsford I (eds) Protected area governance and management. ANU Press, Canberra, Australia
- Corcoran E, Ravilious C, Skuja M (2007) Mangroves of western and Central Africa. UNEP World Conservation Monitoring Centre: UNEP, Regional Seas Programme, Cambridge, United Kingdom
- Donnelly M, Walters L (2014) Trapping of *Rhizophora mangle* propagules by coexisting early successional species. *Estuaries and Coasts* 37:1562–1571. <https://doi.org/10.1007/s12237-014-9789-2>
- Duke NC, Pinzón ZS (1992) Aging *Rhizophora* seedlings from leaf scar nodes: a technique for studying recruitment and growth in mangrove forests. *Biotropica* 24:173. <https://doi.org/10.2307/2388671>
- Duncan RR, Carrow RN (1999) Seashore paspalum: the environmental turfgrass. Wiley, Hoboken, New Jersey
- FAO (Food and Agriculture Organization of the United Nations) (2007) The world's mangroves, 1980–2005: a thematic study in the framework of the global forest resources assessment 2005. Food and Agriculture Organization of the United Nations, Rome, Italy
- Feller IC, Friess DA, Krauss KW, Lewis RR (2017) The state of the world's mangroves in the 21st century under climate change. *Hydrobiologia* 803:1–12. <https://doi.org/10.1007/s10750-017-3331-z>
- Flores-Verdugo F, Moreno-Casasola P, Agraz-Hernández CM, López-Rosas H, Benítez-Pardo D, Travieso-Bello AC (2007) La topografía y el hidropérido: dos factores que condicionan la restauración de los humedales costeros. *Boletín de la Sociedad Botánica de México* 80:33–47. <https://doi.org/10.17129/botsci.1755>
- Hounvou SF, Guedje KF, Koubeagbede H, Adechinan J, Houngninou E, Houeto A (2023) Spatiotemporal variability of extreme rainfall in southern Benin in the context of global warming. *Advances in Meteorology* 2023:1–11. <https://doi.org/10.1155/2023/9902326>
- INSAE (Institut national de la statistique et de l'analyse économique) (2016) Effectifs de la population des villages et quartiers de ville du Bénin (RGPH-4, 2013), République du Bénin: Institut national de la statistique et de l'analyse économique, Cotonou, Bénin.
- Lewis RR (2005) Ecological engineering for successful management and restoration of mangrove forests. *Ecological Engineering* 24:403–418. <https://doi.org/10.1016/j.ecoleng.2004.10.003>
- McKee KL, Rooth JE, Feller IC (2007) Mangrove recruitment after forest disturbance is facilitated by herbaceous species in the Caribbean. *Ecological Applications* 17:1678–1693. <https://doi.org/10.1890/06-1614.1>
- Obada E, Alamou EA, Biao EI, Zandagba EBJ (2021) Interannual variability and trends of extreme rainfall indices over Benin. *Climate* 9:160. <https://doi.org/10.3390/cli9110160>
- Primavera JH, Esteban JMA (2008) A review of mangrove rehabilitation in the Philippines: successes, failures and future prospects. *Wetlands Ecology and Management* 16:345–358. <https://doi.org/10.1007/s11273-008-9101-y>

- Reyes Chargoy MA, Tovilla Hernández C (2016) Restauración de áreas alteradas de manglar con *Rhizophora mangle* en la Costa de Chiapas. Madera y Bosques 8:103–114. <https://doi.org/10.21829/myb.2002.801294>
- Romañach SS, DeAngelis DL, Koh HL, Li Y, Teh SY, Raja Barizan RS, Zhai L (2018) Conservation and restoration of mangroves: global status, perspectives, and prognosis. Ocean & Coastal Management 154:72–82. <https://doi.org/10.1016/j.ocecoaman.2018.01.009>
- Saluzzo H, Reinoso P, Martínez V (2015) Caracterización y evaluación del crecimiento como césped de *Paspalum alnum*, *Paspalum denticulatum* y *Paspalum vaginatum*. Phytion 84:51–55
- Su J, Friess DA, Gasparatos A (2021) A meta-analysis of the ecological and economic outcomes of mangrove restoration. Nature Communications 12: 5050. <https://doi.org/10.1038/s41467-021-25349-1>
- Teka O, Houessou LG, Djossa BA, Bachmann Y, Oumorou M, Sinsin B (2019) Mangroves in Benin, West Africa: threats, uses and conservation opportunities. Environment, Development and Sustainability 21:1153–1169. <https://doi.org/10.1007/s10668-017-0075-x>
- Tide Table (n.d.) Tidal data for Cotonou, Benin. <https://es.tideschart.com/Benin/Atlantique/Ouidah/> (accessed 21 Feb 2025)
- Villavicencio CB, Ferreira AC, Costa RCD, Machado JV, Freitas CVC, Moro MF, Bezerra LEA (2024) Facilitation in mangrove ecosystem: the role of herbaceous species in seedling recruitment and growth patterns of *Avicennia germinans* in a recovering mangrove in northeastern Brazil. Acta Botanica Brasiliica 38:e20220283. <https://doi.org/10.1590/1677-941x-abb-2022-0283>
- Zanvo MGS, Barima YSS, Salako KV, Koua KAN, Kolawole MA, Assogbadjo AE, Glèlè Kakaï R (2022) Mapping spatio-temporal changes in mangroves cover and projection in 2050 of their future state in Benin. Bois et Forêts des Tropiques 350:29–42. <https://doi.org/10.19182/bft2021.350.a36828>
- Zedler JB, Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30:39–74. <https://doi.org/10.1146/annurev.energy.30.050504.144248>
- Zhang P, Li B, Wu J, Hu S (2019) Invasive plants differentially affect soil biota through litter and rhizosphere pathways: a meta-analysis. Ecology Letters 22:200–210. <https://doi.org/10.1111/ele.13181>
- Zheng X, Javed Z, Liu B, Zhong S, Cheng Z, Rehman A, Du D, Li J (2023) Impact of *Spartina alterniflora* invasion in coastal wetlands of China: boon or bane? Biology 12:1057. <https://doi.org/10.3390/biology12081057>

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Mangrove restoration locality in the Djegbadji district, Ouidah, Benin, Africa.

Figure S2. Manual removal of *Paspalum vaginatum* using the tool of the community of Ouidah, Benin (a), Africa, known in Fon as “Alín” (b).

Figure S3. *Rhizophora racemosa* propagules planted at a density of 25 propagules/m² in the restoration area: (a) Planting process, (b, c) Growth monitoring, and (d) Heights measured 300 days after planting, along with the growth velocity curve shown in the graph.

Figure S4. Physicochemical parameters of the interstitial water from April 2019 to December 2021 (after hydrological rehabilitation) at the restoration site located in the Djegbadji district in Ouidah, Benin, Africa. mV: redox potential, °C: temperature, UPS: salinity. The vertical lines on the values of the physicochemical parameters represent the standard error of the mean.

Figure S5. Physicochemical parameters of the interstitial water from April 2019 to December 2021 (after hydrological rehabilitation) at the *Rhizophora racemosa* forest of the reference site located in the Djegbadji district in Ouidah, Benin, Africa. mV: redox potential, °C: temperature, PSU: salinity. The vertical lines on the values of the physicochemical parameters represent the standard error of the mean.

Figure S6. Nutrient concentration in the interstitial water from February 2018 to March 2019 (before hydrological rehabilitation) at the *Rhizophora racemosa* forest of the reference site located in the Djegbadji district in Ouidah, Benin, Africa. The vertical lines on the chemical parameter values represent the standard error of the mean.

Figure S7. Nutrient concentration in the interstitial water from February 2018 to March 2019 (before hydrological rehabilitation) at the *Rhizophora racemosa* forest of the restoration site located in the Djegbadji district in Ouidah, Benin, Africa. The vertical lines on the chemical parameter values represent the standard error of the mean.

Table S1. Environmental parameters measured at different sites and years. The table includes data on pH, redox potential (mV), salinity (PSU), temperature (°C), and concentrations of nitrite (NO₂⁻), nitrate (NO₃⁻), ammonium (NH₄⁺), phosphate (PO₄⁻³), and sulfate (SO₄⁻²) in mg L⁻¹. Each parameter is presented with its mean value and associated uncertainty (± standard deviation). Measurements were taken at a reference site in 2018 and 2019, before restoration in 2018 and 2019, and after restoration in 2019.

Coordinating Editor: Stephen Davis

Received: 4 January, 2024; First decision: 4 May, 2024; Revised: 21 April, 2025; Accepted: 21 April, 2025