



# Survival, Growth, and Productivity of *Rhizophora racemosa* Transplanted in Natural Ecosystems: Implications for Mangrove Restoration

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## Abstract

Mangroves are coastal wetland ecosystems of tropical and subtropical regions. Water and substrate salinities are important drivers of their development and trajectories. Therefore, understanding how main mangrove species respond to salinity gradient when transplanted in natural environment is essential for their restoration. This study assessed the survival, growth, and productivity of *Rhizophora racemosa* seedlings in response to gradient of salinity. Seedlings were grown in nursery under low (3–5 psu) and medium (15–17 psu) water salinities for thirty days and transplanted to three mangrove sites with various salinities (4.6, 11.41, and 18.27 psu). Seedling survival and growth were monitored monthly for 6 months. At the end of month 6, total biomass was harvested and partitioned among plant parts. Results showed that growth, survival, and productivity of *R. racemosa* were mainly influenced not by the salinity under which the seedlings were raised in nursery but rather by site. Survival was higher (88.33%) at the site with the highest salinity. Total plant biomass was similar across sites, but root biomass and root weight ratio were higher on sites with higher salinity. Biomass was disproportionately higher in stems (45–54%) than in roots (28–37%), and leaves (15–18%). We suggest that restoration is done in appropriate period, ideally one month before the start of rainy season. This will not only allow seedlings to well establish their rooting system before rains start but also favour seedling growth, because of substrate salinity dilution by fresh water from rains and flows from uplands.

**Keywords** Red mangrove · Restoration · Salinity · Nursery · Growth · Biomass

## Résumé

Les mangroves sont des écosystèmes de zones humides côtières des régions tropicale et subtropicale. Les salinités de l'eau et du substrat sont des facteurs déterminants de leur développement et de leur trajectoire. Par conséquent, comprendre comment les principales espèces de mangroves réagissent au gradient de salinité lorsqu'elles sont transplantées en milieu naturel est essentiel pour la restauration des mangroves par la plantation. Cette étude a évalué la survie, la croissance et la production de biomasse des plantules de *Rhizophora racemosa* en réponse au gradient de salinité. Des plantules de *Rhizophora racemosa* ont été produites en pépinière sous des salinités d'eau faible (3–5 psu) et moyenne (15–17 psu) pendant trente jours et transplantées dans trois sites de mangroves avec différentes salinités (4,6 – 11,41 – 18,27 psu). La survie et la croissance des plantules ont été suivies mensuellement pendant 6 mois. À la fin du sixième mois, la biomasse totale a été récoltée par individu et répartie entre les parties de la plante. Les résultats ont montré que la croissance, la survie et la productivité des

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plantules de *R. racemosa* étaient principalement influencées non pas par la salinité sous laquelle les plantules étaient produites en pépinière mais plutôt par le site. La survie était plus élevée (88,33%) sur le site avec la salinité la plus élevée de l'expérience (18,27 psu). La biomasse végétale totale était similaire d'un site à l'autre, mais la biomasse racinaire et le ratio de la biomasse racinaire étaient plus élevés sur les sites à salinité plus élevée. La biomasse était disproportionnellement plus élevée dans les tiges (45–54%) que dans les racines (28–37%) et les feuilles (15–18%). Nos résultats suggèrent que la restauration par plantation soit effectuée dans un délai approprié, idéalement un mois avant le début de la saison des pluies. Cela permettra aux plantules non seulement de bien établir leur système racinaire avant le début des pluies, mais aussi favoriser leur croissance, en raison de la dilution de la salinité du substrat par l'eau douce des pluies et des écoulements des hautes terres.

## Introduction

Mangroves are peculiar wetland ecosystems, providing multiple ecosystem services. They are however increasingly being degraded, and several current actions are focused on their restoration, mostly through transplantation (López-Portillo et al. 2017). Restoration and sustainable management of mangroves require an understanding of the functioning of the ecosystem components, particularly dominant species. In addition to species auto-ecology, abiotic conditions at restoration sites are significant determinants of the success of restoration initiatives. Light, tidal fluctuations, seasonal flooding, water and substrate salinity, sediments are among others, important drivers of restoration success (Hope-Speer et al. 2011; Bompoy et al. 2014; Dangremond et al. 2015; Chen and Wang, 2017; Li et al. 2020). For example, survival and growth of *Avicennia germinans* and *Lumnitzera racemosa* are optimal at low to medium salinities at restoration site, regardless of light level – under high salinity, growth performances of the two species decrease dramatically, especially under high light conditions (Dangremond et al. 2015). Short term inundation (e.g., tidal fluctuation) is beneficial for some mangrove species (e.g., *Avicennia marina*) while long term inundation (e.g., seasonal flooding) is detrimental for others (Li et al. 2020). Furthermore, climate change and associated sea level rise are major threats to coastal mangroves, and hence to success of transplantation – mainly through shrinkages in salinity and sediment ranges (Ellison 2015). For example, in the coastal area of Benin, Sinsin et al. (2021a, b) found that under projected changes in climate, mangroves' ecological niches could experience shrinkages in salinity, dissolved oxygen, and conductivity, which are key to species survival, growth, and reproduction (López-Portillo et al. 2017).

Salinity of water and soil substrates are the most studied abiotic factors influencing functioning of mangroves, probably because of their prominent role in mangrove species survival, growth, and reproduction. The establishment and equilibrium of mangroves require optimal salinity ranges in both water and soil substrates, which differ markedly among species (Khan and Aziz 2001; Stern and Voigt 1959). While some mangrove species are facultative halophyte i.e., can survive with or without saline, others are obligate halophyte

i.e., only able to survive in habitats with high salt concentrations (Wang et al. 2011). Consequently, optimum salinity range is large (Ball and Pidsley 1995) and a uniform framework cannot be applied to all mangrove species; understanding species-specific response to salinity is therefore needed to design tailored restoration guidelines. For instance, occurrence of species from the genus *Avicennia* fits within salinity of 12–14 psu while *Ceriops decandra* (Griffith) Ding Hou requires salinity up to 27–28 psu and *Sonneratia apetala* Buch. Ham adapts to a wide range of salinity (Dasgupta et al. 2017).

West-Africa shares 10.3% of global mangroves and 55.93% of mangroves in Africa, making it a hotspot of mangroves in Africa. However, mangroves of the region have been less studied (López-Portillo et al. 2017), and most of transplantation guidelines are based on experiences elsewhere. The West African mangrove ecosystems are less species-diverse, made of only eight mangrove plant species (Saenger 1995) of which *Rhizophora racemosa* (G.) Meyer is the most widespread. Restoration of degraded mangroves are mainly based on *R. racemosa*. Usually, young plants are produced in nursery, and then transplanted in natural stands. Though *R. racemosa* is well documented (Duke and Allen 2006), its physiological response to environmental stresses is still not well studied, especially for ecotypes from West Africa. Such information is crucial for planning, monitoring, and evaluation of mangrove restoration initiatives. For e.g., careful choice of matching nursery practices (mainly salinity) and conditions at restoration sites (salinity ranges) would improve success of restoration initiatives.

The main objective of this study was to assess the survival, growth, and productivity of *R. racemosa* in response to gradient of saline conditions. Specifically, the study compared survival, growth in height, number of leaves, biomass allocation (aboveground versus belowground) and its partitioning among roots, stem, and leaves of *R. racemosa*, at three mangrove sites experiencing different natural salinity conditions. Assuming that nursery conditions, particularly watering salinity under which seedlings are grown before being transplanted in natural environments may affect their performance, the study tested the effect of salinity (of water used to raise seedlings in nursery) on their survival, growth, and productivity. Based on previous reports that *Rhizophora*

spp are less salt tolerant (Duke and Allen 2006), the study examined the hypothesis that survival, growth, and productivity of *R. racemosa* negatively correlate with salinity. Furthermore, according to the optimal partitioning theory, plants allocate more biomass to the organ capturing the most limiting resource (Kobe et al. 2010), implying that relationship between above and belowground biomass may change in stress conditions (e.g., high salinity). Yet, regarding biomass partitioning between above- and below- ground, Enquist and Niklas (2002) proposed that juveniles have an isometric relationship between above and belowground biomass (i.e., slope = 1). Considering that the difference in salinity conditions in nursery and salinity conditions at transplantation sites are potential sources of stress to the transplanted seedlings (i.e., osmotic shock), we also predicted a shift from the isometric relationship between above and belowground biomass at sites with higher salinities, and for individuals raised under higher water salinities.

## Material and Methods

### Study Sites

The study was conducted in Benin, at three sites, namely Azizakouè, Djègbamé, and Lanhou along lagoon of Grand Popo (Fig. 1). The climate is equatorial, with an average rainfall of 1360 mm/year across the three sites. However, there are differences in physico-chemical features, especially with regards to salinity (Table 1). The sites are all islands located at latitude N: 6.31 and longitude E: 1.97 (Azizakouè), latitude N: 6.32 and longitude E: 1.97

**Table 1** Physico-chemical characteristics (mean  $\pm$  standard error) of experiment sites

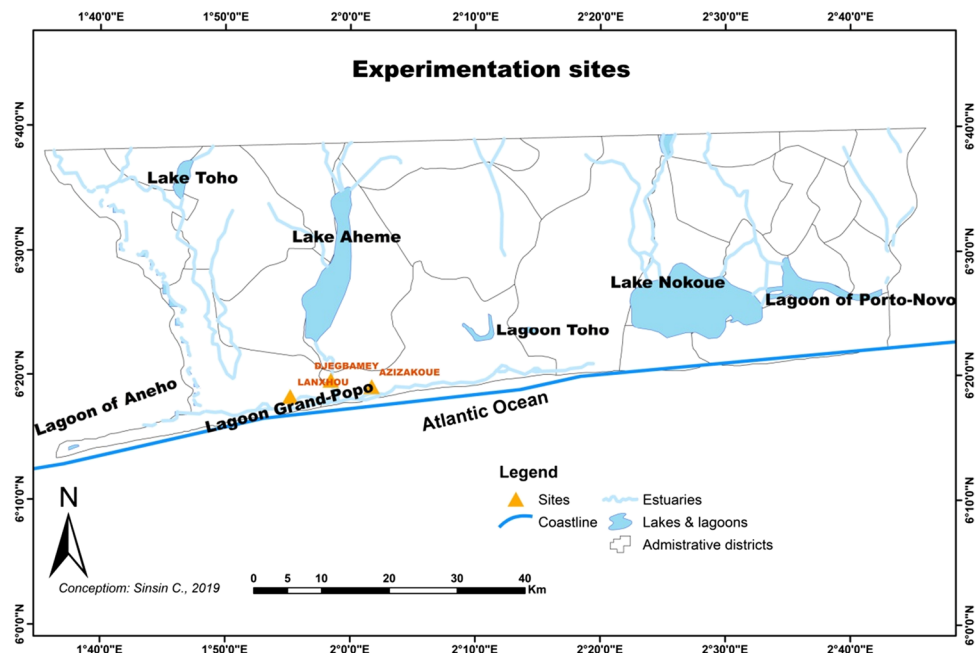
Parameters	Azizakouè	Djègbamè	Lanhou
Salinity (psu)	18.16 $\pm$ 0.46	11.60 $\pm$ 1.14	4.60 $\pm$ 1.78
pH	6.90 $\pm$ 0.21	6.90 $\pm$ 0.14	7.00 $\pm$ 0.78
Temperature ( $^{\circ}$ C)	31.30 $\pm$ 0.87	31.50 $\pm$ 1.15	31.60 $\pm$ 0.26
Conductivity (ms/cm)	29.20 $\pm$ 0.62	29.60 $\pm$ 1.78	29.20 $\pm$ 0.60
Dissolved oxygen (%)	2.40 $\pm$ 0.26	2.30 $\pm$ 0.26	2.50 $\pm$ 0.15
Oxygen rate (%)	35.40 $\pm$ 4.28	35.20 $\pm$ 3.86	35.90 $\pm$ 1.47
Atmospheric pressure (PSI)	14.90 $\pm$ 0.07	14.90 $\pm$ 0.02	14.90 $\pm$ 0.01
Rate of dissolved solids (ppt)	14.77 $\pm$ 0.30	14.50 $\pm$ 0.23	14.20 $\pm$ 0.14
Orthophosphate	66.51 $\pm$ 14.27	66.25 $\pm$ 7.96	67.00 $\pm$ 4.40

(Djègbamé), and latitude N: 6.31 and longitude E: 1.92 (Lanhou). The experiment sites were all in natural mangrove stands characterized by clay-muddy soil flooded in period of high tides: July to December. Along the lagoon of Grand Popo, the predominant oceanic winds are from the South-West (64%), the West-South-West (16%) and the South-South-West (14%) (ACL Consultant 2016); and generate semi-waves and micro-semi-diurnal tides ranging between 0.8 and 1.8 m for neap and spring tides (Ondo et al. 2017).

### Experiment Setting

One-month old seedlings of *R. racemosa* were first produced in nursery (nylon bag filled with substrate) at Kpèko (latitude N: 6.32 and longitude E: 1.91) but watered with either

**Fig. 1** Map showing the experimentation sites



low (3–5 psu) or medium (15–17 psu) water salinity. At this stage, seedlings raised under low salinity were relatively taller (height of the seedlings was considered as the length of the epicotyls,  $6.07 \text{ cm} \pm 0.38$ ) compared to seedlings raised under medium salinity ( $5.69 \text{ cm} \pm 0.38$ ). Similarly, the number of leaves was significantly higher for seedlings raised under low salinity ( $2.42 \pm 0.08$ ) than for seedlings raised under medium salinity ( $1.82 \pm 0.07$ ) (Sinsin et al. 2021a).

For the experiment of transplantation into natural ecosystems, 45 seedlings of *R. racemosa* were considered for each treatment (level of watering salinity) on each site; which made 45 seedlings  $\times$  2 levels of watering salinity  $\times$  3 sites = 270 seedlings. At each site, the 90 seedlings were arranged in a randomized complete block design with 3 replicates. The experimental unit was a plot consisting of 3 rows, each row receiving five seedlings planted at 1 m (between two seedlings)  $\times$  1 m (between two rows) spacing, with a sowing depth of 15 cm. Nylon bags were torn and removed before transplantation. Seedlings did not receive any post sowing maintenance; they were left to face constraints from their new environment as usually practiced in mangrove restoration projects.

## Data Collection

### Survival and Growth

After experiment was settled, each month, for 6 months (from June 2019 to November 2019), seedlings' survival (yes or no) was monitored. Data on growth parameters namely total height and number of leaves were also collected monthly, on each seedling.

### Biomass Estimation

At the end of the experiment (6<sup>th</sup> month), five seedlings were randomly selected and harvested from each block (3 blocks per site) per level of "salinity of water in nursery" (hereafter "salinity"); making a total of 30 seedlings per site. Hypocotyl length, total stem length (= epicotyl + hypocotyl), and taproot length (from the base of the stem until the taproot had approximately 5 mm diameter (see Cuni Sanchez et al. 2011); the remaining roots were considered fine roots) were measured with a graduated ruler. Stem and taproot diameters were measured at the collar. Thereafter, the first three leaves from the top of each sampled plant were collected, packed separately, and measured for their total length and width. To measure the specific leaf area, the widest possible section was extracted (using a blade) for each of the first three leaves; length and width of each section was measured, the sections were oven-dried at 80 °C up to constant weight (at the laboratory), and SLA was estimated following Gbeffe et al. (2017). For the estimation of biomass component, each

selected seedling was up-rooted and separated into different parts including epicotyl (from the top to the node from which starts the hypocotyl), hypocotyl (from the node from which the epicotyl ends up to the stem base), taproot, fine roots, other leaves, and branches. Sectioned samples from each part were weighted in the field (using an electronic scale) and later dried in an oven at 80°C up to constant weights.

## Data Processing and Statistical Analysis

### Survival and Growth

Survival at time  $t$ ,  $S(t)$  of transplanted individuals in relationship to site and salinity, was estimated using the non-parametric Kaplan-Mayer method (Onofri et al. 2010). The estimator of the survival  $S(t)$ , that is the probability that life is longer than  $t$ , is given for a time  $t_i$  by:

$$\hat{S}(t) = \prod_{i: t_i \leq t} \left( 1 - \frac{d_i}{n_i} \right)$$

In this equation  $d_i$  is the number of seedlings that did not survive in the interval of time  $i$ ,  $n_i$  is the number of seedlings known to have survived up to time  $t_i$ , and  $\prod$  stands for products. The estimation of the survival function was done in the package "survival" (Therneau and Grambsch 2000).

Linear mixed model (LMM) on longitudinal data with a normal distribution for errors was used to assess variation in time of plant total height in relationships to the fixed effects of "sites" and "salinity" and the random effect of "block". The models were run with the packages "nlme" (Pinheiro et al. 2021). Similarly, generalized linear mixed model (GLMM) on longitudinal data was applied on the number of leaves using the Poisson error distribution. GLMM was run using package "MASS" (Venables and Ripley 2002). The function *anova* was used to test the overall significance of fixed effects. The random effect of block was assessed through the Intra Class correlation (ICC) by fitting unconditional means models (Singer and Willett 2003).

### Biomass Productivity

Productivity indices such as Total Plant Biomass (TPB), Aerial Biomass (AB), Root Biomass (RB), Taproot Ratio (TPR), Shoot Root Ratio (SRR), Leaf Weight Ratio (LWR), Stem Weight Ratio (SWR), Root Weight Ratio (RWR), Top Weight Ratio (TWR), Leave Morphology Index (LMI), Specific Leaf Area (SLA), Leaf Water Content (LWC), Stem Water Content (SWC), and Root Water Content (RWC) were calculated per seedling. Table 2 summarizes each index, its formula, and its importance to the description or estimation of growth and productivity. Linear mixed effect model (LMM) was also performed to

assess the influence of salinity and sites on each index. In these models, salinity and sites were considered as fixed whereas block was random. The models were run with the *lmer* function of the package “lmerTest” (Kuznetsova et al. 2017). To test the prediction of a shift from the isometric relationship between above and below-ground biomass at sites with higher salinities and for individuals raised with higher salinities (non-parallelism of slopes), we fitted a linear model, particularly an analysis of covariance (ANCOVA) with above-ground biomass (leaves plus stems) as a function of below-ground biomass (roots), including interactions of below-ground with salinity on one hand and with site on the other hand.

Total weight was separated into biomass content (%) and water content (%) for each individual, and each plant part (leaves, roots, and stem). Similarly, the total biomass was separated into stem (%), leaves (%), and roots (%). Log-linear analysis was applied on these data to test (i) the effect of “site”, “salinity”, and “plant part”, on the component (biomass *versus* water content) of the plant total weight, and (ii) the effect of “site”, and “salinity” on the repartition of the total plant biomass among plant parts (leaves, stem, and roots) (see supplementary information). All statistical analyses were implemented in R software version 3.5.1 (R Core Team 2018), except the log-linear analyses which were implemented in SAS Studio online for Academics ([https://www.sas.com/en\\_us/software/on-demand-for-academics.html](https://www.sas.com/en_us/software/on-demand-for-academics.html), accessed on May, 28<sup>th</sup>, 2022).

## Results

### Survival

After the 5<sup>th</sup> month, due to an unexpected management to take place at the site of Djègbamè, we were no longer able to collect data on this site. Only site had a significant effect ( $P < 0.001$ ) on the survival rate of seedlings. Salinity under which the propagules emerged did affect ( $P > 0.05$ ) survival neither as main factor nor in the interaction (Table 3). At the end of the month five, survival rates were 75.30% and 75.50% for individuals raised under low and medium salinities, respectively. With regards to sites, survival rate was relatively higher at sites of Azizakouè (87.50%) and Djègbamè (77.30%) as compared to Lanhou (62.40%) (Fig. 2).

### Growth

To be able to compare all three sites, estimation of growth trends considered data until the end of the 5<sup>th</sup> month (Fig. 3). On average, the total height was  $60.54 \text{ cm} \pm 1.53$  and  $61.05 \text{ cm} \pm 1.64$  for individuals raised under low and

medium salinities, respectively. Regarding sites, average total height was  $63.00 \text{ cm} \pm 1.59$ ,  $58.29 \text{ cm} \pm 1.37$ , and  $64.57 \text{ cm} \pm 2.73$  for Azizakouè, Djègbamè, and Lanhou, respectively. There was significant effect of the interactions of time with salinity ( $p = 0.017$ ) and site ( $P = 0.045$ ) on the plant total height, indicating that growth trends in total height across time differed among salinity levels and sites. However, the main effect of salinity was not significant contrary to that of time and site ( $P > 0.05$ ) (Table 4). Growth speed was lower with seedlings raised under medium salinity (estimate =  $-5.12$ , se =  $2.15$ ,  $t = -2.38$ , df = 791,  $P = 0.017$ ) compared to seedlings raised under low salinity. The lowest total height of seedlings was recorded on Lanhou site (estimate =  $-16.87$ , se =  $7.06$ ,  $t = -2.39$ , df = 791,  $P = 0.017$ ) while statistically similar for Djègbamè and Azizakouè sites (Fig. 3). Nevertheless, growth speed was relatively lower at the Djègbamè site (estimate =  $-4.33$ , se =  $2.19$ ,  $t = -1.98$ , df = 791,  $P = 0.048$ ) compared to Azizakouè.

At the end of the 5<sup>th</sup> month, the total number of leaves were  $24.02 \pm 0.47$  and  $25.57 \pm 0.62$  for individuals raised under low and medium salinities, respectively. With regards to sites, average numbers of leaves were  $24.93 \pm 0.59$ ,  $24.46 \pm 0.66$ , and  $25.09 \pm 0.85$  for the sites of Lanhou, Djègbamè, and Azizakouè, respectively. Significant interaction ( $P = 0.003$ ) was detected between time, salinity, and site; indicating that the evolution of leaves production across time differed among sites and salinity levels. In general, the number of leaves was significantly higher for individuals raised under medium salinity levels (estimate =  $12.00$ , se =  $1.96$ , df = 791, chisq =  $6.12$ ,  $P < 0.001$ ). Though not significant, the number of leaves was highest at Azizakouè, the more saline site (Fig. 4). Further analyses conducted per site due to the significant interaction of the three factors showed that neither the main effect of salinity nor its interaction with time were significant ( $P > 0.05$ ) at Djègbamè and Lanhou sites. On the contrary, at Azizakouè, the trend of the number of leaves was comparatively lower for seedlings raised under medium salinity (estimate =  $-2.34$ , se =  $0.80$ , df = 273, chisq =  $-2.92$ ,  $P = 0.004$ ) (Fig. 4).

### Biomass

Only sites of Azizakouè and Lanhou were considered for biomass estimation due to restriction of access to the site of Djègbamè at the end of the experiment. Table 5 summarizes variation of structural parameters and productivity indices in relationships to watering salinity in nursery and sites at the end of month six.

Salinity treatment received by the propagules at the emergence stage had significant effect ( $P < 0.05$ ) on weight ratio indices, namely shoot root ratio, stem weight ratio, root weight ratio, and top weight ratio. Site had significant

**Table 2** Growth/productivity indices: formula, description, and relevance

Growth parameters	Symbol	Unit	Formula for calculation	Description of formula	Relevance of the parameter/ index for this study	References
Plant total height	Ht	Cm	$\sum_{i=1}^n H_{t_i}/n$	$H_{t_i}$ is the length of the sapling at the day of biomass collection (six months); It was measured from the base of the stem until the apex of the sapling's terminal bud. $n$ is the total number of seedlings considered	Structural indicator of growth	
Hypocotyl height	Hh	Cm	$\sum_{i=1}^n H_{h_i}/n$	$H_{h_i}$ is the length of the hypocotyl at the day of biomass collection (six months); It was measured from the base of the stem until the base of the epicotyl. $n$ is the total number of seedlings considered	Structural indicator of growth	
Basal circumference	Cb	Cm	$\sum_{i=1}^n Cb_i/n$	$Cb_i$ is the circumference of sapling $i$ at the day of biomass collection (6 months); It was measure with tailor meter. $n$ is the total number of seedlings considered	Structural indicator of growth	
Total Plant Biomass	TPB	G	$\sum AB + RB$	Sum of the dry weight of all parts of the sapling	It informs on the species productivity at juvenile stage as a response to salt gradient and sites	Cuni Sanchez et al. (2011)
Aerial Biomass	AB	G	$\sum DW_{leaves} + DW_{branches} + DW_{stem}$	Sum of dry weights (DW) of all parts of the sapling that are aboveground	Indicator of growth and productivity, it informs on the species investment in aboveground parts at juvenile stage for different salinity and sites	Cuni Sanchez et al. (2011)
Root Biomass	RB	G	$\sum DW_{aproot} + DW_{otherroots}$	Sum of dry weights (DW) of all parts of the sapling that are belowground	Indicator of growth and productivity, it informs on the species investment in belowground parts at juvenile stage for different salinity and sites	Cuni Sanchez et al. (2011)
Top Weight Ratio	TWR	—	$\frac{AB}{TPB}$	The ratio of above ground dry weight over the total plant biomass	The contribution of aboveground part to the species biomass at six months (sapling) as response to different salinity and sites	Cuni Sanchez et al. (2011)
Shoot Root Ratio	SRR	—	$\frac{AB}{RB}$	The ratio of aboveground biomass over the belowground biomass	It gives an idea of the contribution of leaves and stem to the species biomass at six months (sapling) as response to different salinity and sites	Cuni Sanchez et al. (2011)
Stem Weight Ratio	SWR	—	$\frac{Dryweight_{stem}}{TPB}$	The ratio of stem dry weight over the total plant biomass	The contribution of stem to the species biomass at six months (sapling)	Cuni Sanchez et al. (2011)
Root Weight Ratio	RWR	—	$\frac{Dryweight_{roots}}{TPB}$	The ratio of total roots dry weight over the total plant biomass	The contribution of roots to the species biomass at six months (sapling) as response to different salinity and sites	Cuni Sanchez et al. (2011)

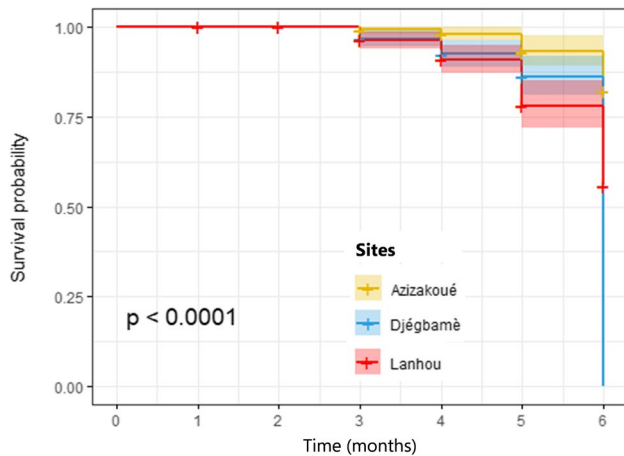
**Table 2** (continued)

Growth parameters	Symbol	Unit	Formula for calculation	Description of formula	Relevance of the parameter/ index for this study	References
Taproot Ratio	TPR	—	$\frac{\text{Taproot length}}{Cb}$	The ratio taproot length divided its basal diameter	It informs not only on the shape of the taproot but also on the response of the former to different salinity and sites	Cuni Sanchez et al. (2011)
Leaf Weight Ratio	LWR	—	$\frac{\text{Dryweight}_{\text{leaves}}}{\text{TPB}}$	The ratio of total leaf dry weight over the total plant biomass	The contribution of leaves to the species biomass at six months (sapling) as response of seedlings to different salinity and sites	Cuni Sanchez et al. (2011)
Leaf water content	LWC	%	$\text{Freshweight}_{\text{leaves}} - \text{Dryweight}_{\text{leaves}}$	The percent water content of stem defined by its wet weight minus its dry weight	It informs on water uptake ability of leaves	Kodikara et al. 2018
Stem Water Content	SWC	%	$\text{Freshweight}_{\text{stem}} - \text{Dryweight}_{\text{stem}}$	The percent water content of stem defined by its wet weight minus its dry weight	It informs on water uptake ability of stem	Kodikara et al. 2018
Root Water Content	RWC	%	$\text{Freshweight}_{\text{roots}} - \text{Dryweight}_{\text{roots}}$	The percent water content of all roots defined by its wet weight minus its dry weight	It informs on the water uptake ability of roots	Kodikara et al. 2018
Leave Morphology Index	LMI	—	$(\sum_{i=1}^3 \frac{\text{Length}_i}{\text{width}_i})/3$	The ratio of length over width of each of the first three leaves of each sapling	It informs on the shape of the species leave at the sapling stage. If LMI = 1, then leaves are said round; when LMI < 1, leaves are considered ovoid; and when LMI > 1, leaves are described as lanceolate	Houunkpevi (2016)
Specific Leaf Area	SLA	—	$(\sum_{i=1}^3 \frac{\text{Surface}_{\text{section}_i}}{\text{Dryweight}_{\text{section}_i}})/3$	The ratio of the widest section surface (first three leaves) by the dry weight of the section	It informs on the efficiency of the use of environmental resources by species, and on site and salinity influence on nutrient uptake, productivity (mass-based light-saturated photosynthetic rate), leaves resilience to stressors (longevity), and carbon investment in secondary dry mass (tannin, lignin, etc.). The higher it is, the lower is the species performance (adaptation to stressors and efficient use of resources)	Gbeffe et al. (2017)

**Table 3** Effects of salinity and site on the survival seedlings: results of the survival model based on the Kaplan-Mayer method

Source of variation	Df	Chisq	<i>P</i>
Site	2	13.83	<0.001
Salinity	1	1.23	0.268
Site: Salinity	2	4.95	0.084

*Df* degree of freedom; *Chisq*  $\chi^2$  statistic; *P* probability of significance

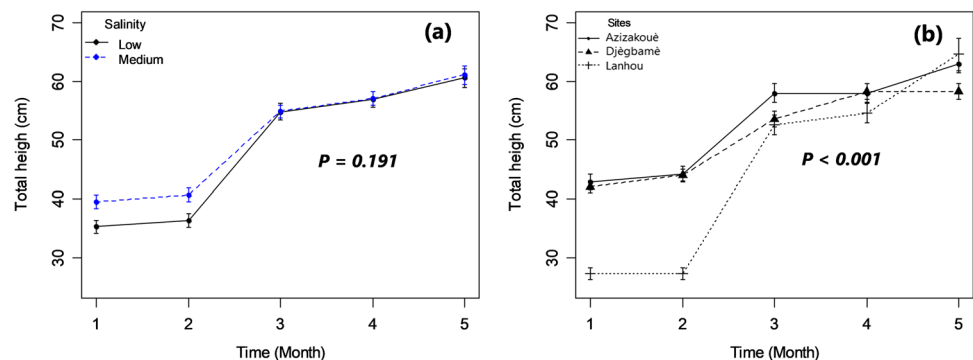
**Fig. 2** Survival patterns of *R. racemosa* seedlings across sites

effect ( $P < 0.05$ ) on structural parameters — total height and hypocotyls height, but also productivity indices — root biomass, shoot root ratio, stem weight ratio, and root weight ratio. The interaction between salinity and site was significant only for root weight ratio (RWR,  $P < 0.024$ ) and top weight ratio (TWR,  $P < 0.021$ ), indicating that the difference between salinity levels for these ratios was not similar between the two sites. The other parameters and indices did not vary neither with salinity nor with sites (Table 5).

The total plant biomass and the aerial biomass were on average  $36.27 \text{ g} \pm 12.62 \text{ g}$  and  $24.89 \text{ g} \pm 1.31$ , respectively. The root biomass was on average  $11.37 \text{ g} \pm 0.76$  and was 1.3 times higher at Azizakoué than at Lanhou. The top weight ratio was

on average  $0.19 \pm 0.01$  and was higher for seedlings raised with low salinity. Shoot Root Ratio (SRR) and Stem Weight Ratio (SWR) were on average  $2.37 \pm 0.77$  and  $0.52 \pm 0.02$  respectively and were higher for seedlings raised with low water salinity and at the site of Lanhou. SRR values greater than 1 for both sites indicate that from seedling to sapling stages, *R. racemosa* invest more in the development of aerial biomass. Higher value of SRR at Lanhou ( $2.69 \pm 0.14$ ) indicates that saplings of this site invested more in aerial biomass than in roots contrary to saplings of Azizakoué ( $2.05 \pm 0.14$ ) which invested relatively more in the development of their root system. The mean value of SRR also indicates that from seedling to sapling stages, individuals of *R. racemosa* invest 2 times more in aboveground biomass production than in below ground biomass. The root weight ratio (RWR) was on average  $0.31 \pm 0.01$  and was higher for seedlings raised with low water salinity and at the site of Azizakoué, confirming that seedlings of Azizakoué invested more in the development of their root systems than those of Lanhou. The taproot ratio (TRR) and the leaf weight ratio (LWR) were on average  $9.23 \pm 2.66$  and  $0.17 \pm 0.01$ . The value of the taproot ratio ( $> 1$ ) indicates that at this stage of life cycle, roots of *R. racemosa* are already very deep in the substrate.

There was a significant positive relationship between above and below ground biomasses ( $F = 63.16$ ,  $df = 1$ ,  $P < 0.001$ , Table 6). The interaction of below-ground biomass with site was significant ( $F = 7.56$ ,  $df = 1$ ,  $p = 0.008$ ) contrary to the interaction with salinity that was not significant ( $F = 0.68$ ,  $df = 1$ ,  $P = 0.413$ ), indicating shifting pattern of biomass allocation between above- and below- ground across sites, but not salinities. Specifically, the Lanhou site had a significantly higher slope compared to Azizakoué site ( $p = 0.008$ , Table 6 and Fig. 5). The equations established per site showed that the slope was 0.94 ( $CI = [0.47; 1.41]$ ) for Azizakoué site (Above-ground biomass =  $12.48 + 0.94$  Below-ground biomass,  $R^2 = 0.38$ ) and 1.86 ( $CI = [1.39; 2.41]$ ) for Lanhou site (Above-ground biomass =  $6.41 + 1.86$  Below-ground biomass;  $R^2 = 0.67$ ) (Fig. 5). Confidence intervals showed that the slope for Azizakoué site was statistically not different from one whereas the slope at Lanhou site was greater than one

**Fig. 3** Evolution trend of growth in total height (length of epicotyl) of *R. racemosa* in relationships to salinity and sites. *P* is the p-value of the interaction of “Salinity” and “Time”, testing whether growth in total height across time varies between salinity levels



**Table 4** Effects of salinity and site on plant total height and number of leaves of *R. racemosa*: results of LMM and GLMM on longitudinal data

Source of variation	Df	Plant total height		Number of leaves	
		Chisq	P	Chisq	P
Time	1	35.39	<0.001	0.00	0.979
Salinity	1	3.51	0.061	37.48	<0.001
Site	2	11.25	0.004	3.48	0.175
Time: Salinity	1	5.68	0.017	14.68	<0.001
Time: Site	2	6.19	0.045	1.82	0.402
Salinity: Site	2	2.16	0.338	23.82	<0.001
Time: Salinity: Site	2	4.35	0.114	11.68	0.003
ICC Bloc (%)			<b>5.40</b>		<b>15.18</b>

Df degree of freedom; Chisq  $\chi^2$  statistic; P probability of significance; ICC Intra Class correlation

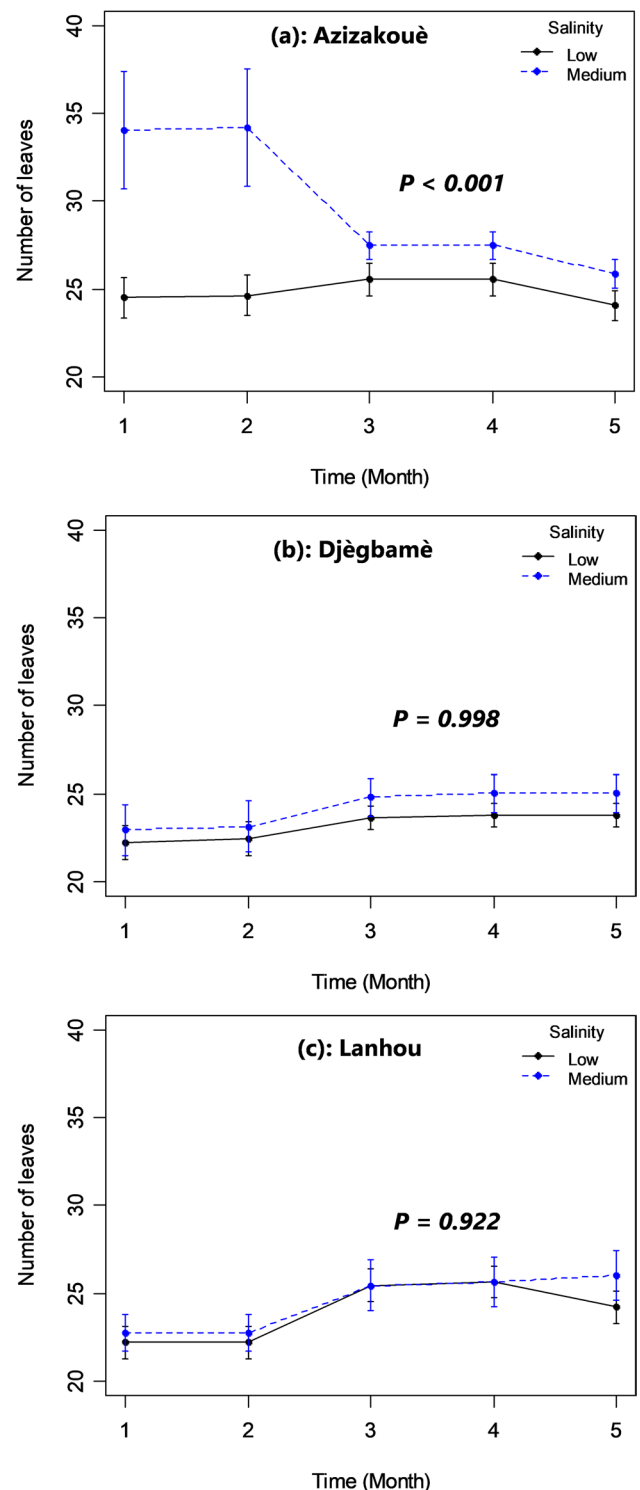
indicating isometric relationship at Azizakouè site and non-isometric relationship at Lanhou site.

Up to six months after emergence, the water content of *R. racemosa* individuals was higher than its accumulated biomass (Fig. 6). For the whole plant, water content percentage is about 2/3 of the total plant weight in Lanhou (on average  $66.92 \pm 0.15\%$ , Fig. 6b) and much higher at Azizakouè site (on average  $72.41 \pm 2.71\%$ , Fig. 6a). The distribution of the total weight of the individuals between water content and biomass content was not affected by neither site, plant part, nor watering salinity (Table S1, Supplementary information). On average,  $30.49 \pm 1.15\%$  of the total weight is biomass while the remaining ( $69.50 \pm 1.15\%$ ) is water (see Fig. 6). Results on biomass partitioning among leaves, stem, and roots, indicated that about half of the total biomass (45 – 54%, on average  $51.36 \pm 2.03$ ) is stored in the stem, followed by roots (28 – 37%, on average  $31.32 \pm 2.03\%$ ), and lastly leaves (15 – 18%, on average  $17.32 \pm 0.61\%$ ) (Fig. 7). The individual distribution of the total biomass among plant parts was also not affected neither by site, nor by watering salinity (Table S2, Supplementary information).

Leaf Morphology Index (LMI) was on average  $3.93 \pm 2.46$  and was greater than 1 (Table 5) indicating that leaves of *R. racemosa* are lanceolate. The Specific Leaf Area (SLA) was on average  $63.33 \pm 14.91 \text{ cm}^2/\text{g}$  indicating that about  $63 \text{ cm}^2$  of leaves of *R. racemosa* correspond to 1 g of dry biomass at this stage.

## Discussion

Abiotic factors such as light, slope, substrates physical structure and chemical composition are determinant for the emergence, growth, distribution, and survival of mangrove species (Dasgupta et al. 2017; Khan and Aziz 2001).



**Fig. 4** Evolution trend of number of leaves of *R. racemosa* in relationships to salinity. P is the p-value of the interaction of “Salinity” and “Time”, testing whether trend of number of leaves across time varies between salinity levels

Several studies have also reported site salinity as a key factor influencing the survival, establishment, growth, and productivity of mangrove species (Amores et al. 2013;

**Table 5** Variation of productivity indices in relationships to watering salinity in nursery and sites: mean (m)±standard error (se) of indices, p-values from mixed effects models (p) and intra-class correlation due to bloc effect (ICC<sub>Bloc</sub>)

Growth and productivity indices	Salinity of watering in nursery			Sites (salinity level)			P <sub>Salinity: Site</sub>	ICC Bloc
	Low	Medium	P	Azizakouè (High)	Lanhou (Low)	P		
	m±se	m±se		m±se	m±se			
Plant total height: Ht (cm)	75.72a±1.79	75.74a±2.35	0.272	72.33b±1.64	79.13a±2.29	<b>0.007</b>	0.125	0.00
Hypocotyl height: Hh (cm)	29.24a±1.50	31.10a±2.00	0.305	34.61a±2.00	25.72b±0.97	<b>0.017</b>	0.542	7.81
Basal circumference: Cb (cm)	5.70a±0.12	5.95a±0.15	0.160	5.97a±0.14	5.68a±0.13	0.542	0.501	1.06
Total Plant Biomass: TPB (g)	34.84a±1.21	37.69a±3.59	0.494	37.36a±2.54	35.17a±2.87	0.598	0.993	0.00
Aerial Biomass: AB (g)	23.42a±0.87	26.36a±2.44	0.307	24.54a±1.77	25.24a±2.10	0.808	0.307	0.00
Root Biomass: RB (g)	11.42a±0.95	11.33a±1.28	0.942	12.82a±0.94	9.93b±0.90	<b>0.023</b>	0.588	21.71
Top Weight Ratio: TWR	0.21a±0.01	0.17b±0.00	<b>0.001</b>	0.20a±0.02	0.18a±0.01	0.067	<b>0.021</b>	7.50
Shoot Root Ratio: SRR	2.18b±0.23	2.56a±0.12	<b>0.004</b>	2.05b±0.14	2.69a±0.14	<b>0.001</b>	0.127	33.41
Stem Weight Ratio: SWR	0.49b±0.02	0.55a±0.01	<b>0.004</b>	0.46b±0.02	0.54a±0.02	<b>0.036</b>	0.159	3.33
Root Weight Ratio: RWR	0.33a±0.02	0.29b±0.00	<b>0.001</b>	0.34a±0.02	0.28b±0.01	<b>0.001</b>	<b>0.024</b>	17.86
Taproot Ratio: TRR	9.18a±0.58	9.28a±0.72	0.903	8.90a±0.67	9.57a±0.61	0.448	0.110	0.00
Leaf Weight Ratio: LWR	0.18a±0.01	0.16a±0.01	0.155	0.16a±0.01	0.18a±0.01	0.434	0.775	0.00
Leaf Water Content: LWC (%)	65.75a±2.28	64.36a±3.36	0.736	66.14a±3.59	63.98a±1.83	0.603	0.245	0.00
Stem Water Content/ SWC (%)	65.83a±1.58	62.65a±1.27	0.062	65.61a±1.45	62.87a±1.50	0.106	0.384	26.34
Root Water Content: RWC (%)	71.38a±1.09	72.20a±1.94	0.737	71.23a±2.01	72.36a±0.91	0.646	0.858	0.00
Leaf Morphology Index: LMI	3.86a±0.14	3.74a±0.27	0.695	3.86a±0.23	3.74a±0.20	0.695	0.184	0.00
Specific Leaf Area: SLA	64.88a±5.15	61.19a±2.68	0.498	67.70a±5.03	58.37a±1.00	0.086	0.510	0.00

Only two sites (Azizakouè and Lanhou) are considered for growth and productivity (instead of 3 as shown by Figs. 1 and 2) because after the 5<sup>th</sup> month, due to an unexpected management to take place at the Djégbamè site, we were no longer able to collect data on this site

**Table 6** Variation of the relationships between above- and below-ground biomass across salinities and sites: results of the linear models (R<sup>2</sup>=0.58, F=14.98, Df=5 on 54, P=3.26e-09)

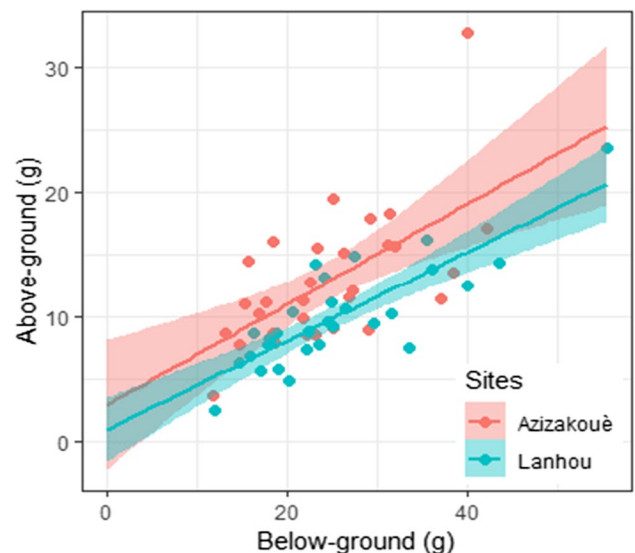
Sources of variation	Estimate	se	CI	t-value	P
Intercept	13.83	4.71	[4.39; 23.28]	2.935	0.005
Below-ground	0.72	0.36	[-0.01; 1.44]	1.976	0.053
Site <sup>†</sup> —Lanhou	-6.20	4.15	[-14.52; 2.11]	-1.496	0.140
Salinity <sup>††</sup> —Medium	-0.73	4.49	[-9.74; 8.28]	-0.162	0.872
Below-ground: Site—Lanhou	0.94	0.34	[0.25; 1.62]	2.75	0.008
Below-ground: Salinity—Medium	0.30	0.37	[-0.44; 1.05]	0.825	0.413

<sup>†</sup> Azizakouè is taken as the reference level

<sup>††</sup> Low is taken as the reference level

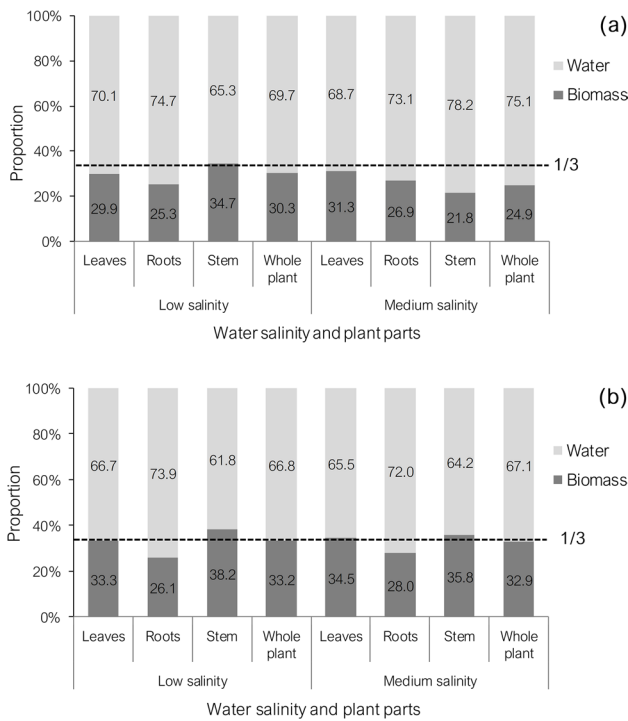
R<sup>2</sup>=R-square of the model, F=Fisher statistics, Df=Degree of freedom, P=Probability of the test

Ball and Pidsley 1995; Vovides et al. 2018; and Lambs et al. 2008). Other studies have demonstrated that salinity of water in nursery greatly influences emergence and early growth of mangrove species (Chen and Ye 2014; Saha et al. 2014). However, we still know little on the effects of salinity (salinity under which propagules emerged in nursery) on survival and productivity performances after transplantation of seedlings, particularly

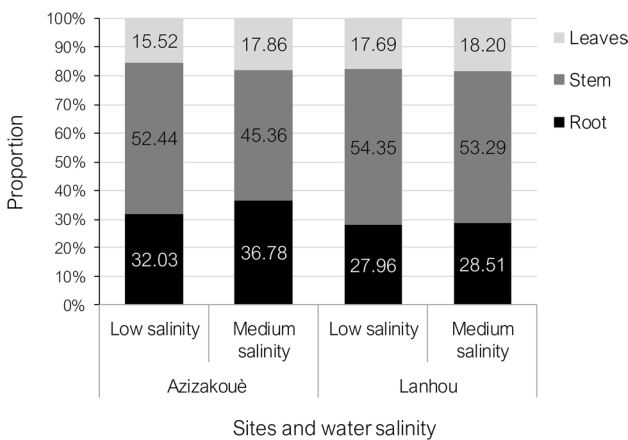


**Fig. 5** Relationships between above-ground and below-ground biomass across the two sites

for mangrove species from West-Africa. This study is to our knowledge, the first one to report on this in a less studied mangrove zone such as West-Africa. The study used the case study of *R. racemosa* which is one of the most common true mangrove species in the region.



**Fig. 6** Biomass allocation and water uptake patterns in *R. racemosa* at sapling stage at (a) Azizakouè and (b) Lanhou



**Fig. 7** Biomass repartition among plant parts

Survival of seedlings after transplantation was not influenced by salinity in nursery but rather by site, the survival rate being higher in sites with higher salinities (87.50%, 77.30%, and 62.40% for sites with mean salinity values of  $18.16 \pm 0.46$  psu,  $11.60 \pm 1.14$  psu, and  $4.60 \pm 1.78$ , respectively). This implies that salinity of transplantation site overrules salinity under which seedlings were raised in nursery, as far as seedling survival is concerned. Thus, corroborating previous findings that transplantation salinity is key for the survival of transplanted seedlings. Some authors further consider that survival

of mangroves' seedlings/saplings depend only on tidal/wave action (e.g., Clarke and Allaway 1993) while others argue that survival could depend on many factors including species tolerance (Dangremond et al. 2015), salinity and water level fluctuation (Hope-Speer et al. 2011), fluctuation of salinities (Bompy et al. 2014), tidal inundation patterns (Chen and Wang 2017; Li et al. 2020; Wang et al. 2022). For example, Bompy et al. (2014) found that fluctuating salinities affect mangrove species *Avicennia germinans* and *Laguncularia racemosa* different than constant salinities. The non-significance of water salinity used in nursery (3–5 versus 15–17 psu) on seedling survival after transplantation may suggest a lack of salinity shock vis-à-vis salinity of transplantation sites and that prior acclimation of seedlings from nursery is not necessary in such conditions. Raising seedling of *Xylocarpus granatum* J. König (Meliaceae), one of the most valuable mangrove tree species of the Sundarbans with plain water and transplanting in polyethylene bag with various water salinity, Siddique et al. (2017) rather found negative correlation of salinity (range: 0 – 35 psu) and survival rate. The positive correlation we found can be due to the combined effect of raising seedlings with non-hypersaline water i.e., 3–5 and 15–17 psu that might have prepared seedlings to cope with the salinity in transplantation site which can also be considered medium (< 20 psu). We might have observed decreased survival if the study included sites with hypersaline condition up to or even higher than 35 psu (seawater salinity). Considering higher values of salinity will certainly provide additional insights into effect of salinity at transplantation site on seedlings survival. The difference with findings of Siddique et al. (2017) might also be due to species-specific response. In fact, although it has been suggested that optimum salinity for growth of mangrove species generally ranges from 5 to 50% seawater (Ball 1988), there is a large variation in species response to salinity; while some are facultative halophyte, others are obligate halophyte (Wang et al. 2011). It might however also be plausible that other environmental factors (e.g., nutrients availability) that differ among the sites interfere with the effect of site salinity.

Concerning growth parameters, the site with the lowest salinity had the lowest growth in height, especially, during the first three months, suggesting that sites of medium salinity favour growth in height of *R. racemosa* seedlings after transplantation. On the opposite, variation in the number of leaves was not influenced by salinity of transplantation site. We rather found that while salinity in the nursery had no significant influence on Lanhou and Djègbamè sites (low to medium saline sites), seedlings raised with medium water salinity in nursery had higher number of leaves than seedlings raised with low water salinity in the more saline site of Azizakouè. Therefore, depending on the salinity of the transplantation site, salinity in nursery may result into differential growth performance. Similar results were reported for the survival patterns after transplantations for *Rhizophora*

*mangrove* seedlings (from two different ranges of salinity: 0–20 PSU and 20–70 PSU) (Sanchez et al. 2021). The low performance of seedlings raised with low salinity in this site could be linked to the difference with salinity of the transplantation site, and thus highlights that in case of a greater gap between salinity in nursery and that of transplantation site, seedlings might not perform well, and hence require a sufficient acclimation period before.

Although our study suggests positive correlation between site salinity and growth of mangrove species, some authors found negative correlation between salinity and growth of mangrove species. For instance, salinity of 25 psu in nursery conditions was found to be lethal for the growth of *Xylocarpus granatum* (Siddique et al. 2017). Since salt tolerance is species specific (Ye et al. 2005) and age dependent (Kodikara et al. 2018), divergence of correlation trends may be linked to species identity and life stage of individuals considered in experiments. Beyond salinity, site nutrient composition is a possible cause of the differing growth patterns among sites (Chen and Ye 2014). Also, flood events (which occurred just three days after transplantation) could explain the low growth performance at Lanhou. As a response to the sudden water logging, individuals of *R. racemosa* might have invested in root strengthening (instead of aerial growth) as to increase their likelihood to survive whereas rapid growth in height and number of leaves following water recessed could be the expression of efficient extraction of nutrients brought to the soil by the tides. Besides, transplantation period could justify the observed low growth and survival rates as it was done at the end of the dry season/beginning of the longest rainy season. Seedlings might not have enough time to well establish their roots before rains start and might have easily been uprooted by inundation of substrates and strong water flow (e.g., Lanhou site). Relating transplantation period to growth and survival rates, we could recommend restoration through plantation of seedlings from nursery not to be done on the eve of rainy season even if Kodikara et al. (2018) suggested eve of rainy season to favour the establishment of seedlings and to be suitable for restoration from nursery. We argue that while restoration on the eve of rainy season may help controlling the salinity through dilution, and thus favour seedling growth, it is equally important that seedlings have strong rooting system to thrive high water currents due to rainy season. In our study area, we observed higher growth in total height, but no clear trend for the change in the number of leaves for individuals of *R. racemosa* at the most saline site (Azizakouè). This pattern may be because sixty days after planting, the leaves were attacked by *Phytophagus sp* (caterpillar, Fig. 8) which caused massive loss of leaves. With this parasitic attack, plants might have slackened their growth rate in order to develop resistance mechanism and possibly invest more in renewing lost leaves (Ellison and Farnsworth 1993).

Characteristics of transplantation site, including salinity lead nutrient uptake, conductance through the xylem can affect productivity of the plants (Biber, 2006; Chen and Ye

2014). As salinity increases, many mangrove species reduce the intake of salt, and consequently, of water and nutrients, and require greater allocation of biomass to root growth, thus contributing to a higher root/shoot ratio in more saline environments (Naidoo 2016). In this study, although total biomass and aerial biomass did vary neither with water salinity in nursery nor with sites, our finding of higher root biomass and root weight ratio in the site with highest water salinity (Azizakouè) does supports the point that mangrove species tend to allocate more biomass to root to adapt to higher salinity conditions. These results therefore imply that salinity represents a stressor which affects biomass partitioning of *R. racemosa* at juvenile stage. Water represents approximately 2/3 of the total plant weight and seems to be slightly higher in Lanhou site (less saline site) compared to Azizakouè (more saline site). Moreover, stem, root, and leaves in this order stored more biomass confirming the assumption of the existence of trade-offs in biomass allocation to roots, leaves, and stem functions as suggested by the optimal partitioning theory (Mccarthy and Enquist 2007).

These findings suggest that *R. racemosa* first solidifies its root system in the substrate followed by investment in growth (height, leaves). This is consistent with the description of *Rhizophora* spp by Duke and Allen (2006).

Overall, site salinity is found to influence *R. racemosa* seedlings' survival, growth, and productivity. In natural mangroves ecosystems, site salinity includes water and substrate salinities both which relate to other abiotic factors such as temperature, tidal movements, freshwater flow (Robinson



**Fig. 8** Caterpillar (*Phytophagus sp*): predator of leaves of *R. racemosa*

et al. 2007; Nguyen and Kawanisi 2021). On top of these common abiotic factors, salinity, the main brackish water induced factor (Biber 2006), is influenced by climate change which represents a major threat to mangroves (Ellison 2015). Temperature-rise coupled with rise of sea level increase salinity in coastal systems like mangroves (Gilman et al. 2008). Similarly, aridity due to the rise in temperature and prolonged drought spells lift evapotranspiration, and thereby, increase in salinity (Snedaker 1995). Unlikely, increase in precipitation induces decrease in salinity via direct dilution and additional run off from upland systems (Des et al. 2021). As results, mangroves ecosystems and composite species will experience climate change-induced shrinkages measurable through species acclimation rates to variations in physico-chemical covariates. For example, salinity, dissolved oxygen, and conductivity are predicted to significantly increase in mangroves niche (lakes and lagoons) in Benin (Sinsin et al. 2021b); which will affect species diversity, population density, and niche occupancy patterns to the advantage of most salt tolerant species. Subsequently, the less salt tolerant *Rhizophora racemosa* (Duke and Allen 2006) may struggle to survive. It is thus important that further studies are conducted on the combined effects of dissolved oxygen, conductivity, and salinity (inclusive of tidal fluctuations) on the survival, growth, and productivity of *R. racemosa*. In these future studies, an additional experimental control as nursing propagules at each site and transplant the saplings locally would provide an ideal null control. This will allow among others to test whether nursing propagules locally has an advantage over nursing propagules elsewhere.

## Conclusion

Survival, growth, and productivity of transplanted *R. racemosa* from nursery are not mainly influenced by salinity treatment received by propagules, but rather by site and the interaction of the two factors. Salinity treatment received at nursery should then be carefully chosen with consideration of salinity conditions of restoration sites. It is recommended that restoration activities are planned in appropriate period, ideally one month before the beginning of rainy season not only to allow seedling to well solidify their rooting system in the substrate before rains start, but also to favour seedlings growth, because of substrate salinity dilution by fresh water from rains and flow from uplands. Repeating our experiment with a larger range of salinity and inclusion of tidal fluctuation would provide additional insights for successful restoration through transplantation.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s13157-022-01583-1>.

**Author Contributions** SCBL and SKV conceived and designed the study with advice from GKR. SCBL collected the data with the support of SKV. SCBL, TRJ and SKV processed the data and performed the statistical analyses. SCBL and SKV wrote the initial draft of the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Data Availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Ethics Approval** Not applicable.

**Consent for Publication** Not applicable.

**Competing Interests** The authors have no relevant financial or non-financial interests to disclose.

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