

RESEARCH ARTICLE

Impact of soil salinity on mangrove restoration in a semiarid region: a case study from the Saloum Delta, Senegal

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Ongoing losses to mangrove forests globally have prompted increased interest in restoration programs that seek to restore vital ecosystem functions and services. In many cases, data on local-scale environmental tolerances of mangrove species used in reforestation efforts is lacking, and failure of restoration projects has been attributed to incorrect species selection in plantations. Here, we assess the impact of soil salinity on the early establishment success of monospecific red mangrove *Rhizophora mangle* reforestation projects in the Saloum Delta, Senegal, a region where widespread mangrove restoration efforts are ongoing. At soil salinities >60 ppt, stomatal conductance, photosystem II operating efficiency, and growth of planted *R. mangle* seedlings were severely reduced. Similarly, after 1–3 years, survival of mangrove seedlings decreased in soil salinities of >60 ppt. In contrast, we recorded naturally occurring black mangrove *Avicennia germinans* growing in exceptionally hypersaline conditions (90 ppt), representing some of the most saline vegetated ecosystems on Earth. The findings reported herein can be used to inform species choice in reforestation projects and help improve success rates of coastal wetland restoration projects in semiarid regions.

Key words: *Avicennia germinans*, mangrove reforestation, *Rhizophora mangle*, Saloum Delta, stomatal conductance, vegetated coastal ecosystems

Implications for Practice

- Mangrove restoration can be used to restore vital ecosystem functions and services provided by forested coastal wetlands.
- At the local level, identifying species tolerances to abiotic stressors such as soil salinity can inform species selection and improve restoration success.
- In situ monitoring of mangrove physiology, growth, and survival pre- and post-planting is required to enable the long-term establishment of planted mangrove forests.

Introduction

Along tropical, sub-tropical, and semiarid coastlines mangrove forests provide multiple ecosystem service benefits to local communities, including fisheries maintenance, wood production, and storm/tsunami protection (Alongi 2008; Van der Stocken et al. 2019; Xiong et al. 2019). More recently, the key role of mangrove ecosystems in the global carbon cycle has also been acknowledged; storing vast amounts of soil carbon (5–10.4 Pg globally), mangrove forests are among the most carbon-rich ecosystems on Earth (Chmura et al. 2003; Donato et al. 2011; Atwood et al. 2017). Nevertheless, the global area of mangrove forest has declined by up to one-third in the last half century

(Alongi 2002; Hamilton & Casey 2016), principally due to anthropogenic activities such as coastal development, aquaculture, and land reclamation for agriculture (Duke et al. 2007; Kamali & Hashim 2011).

In the last two decades, growing recognition of the ecological and socioeconomical importance of mangrove ecosystems has led to increasing interest in restoration programs that seek to restore vital ecosystem functions and services (Lewis III 2005; Lee et al. 2019; Yando et al. 2019). Recently, López-Portillo et al. (2017) documented 90 published accounts of mangrove restoration efforts across tropical and sub-tropical Indo-West Pacific and Atlantic East Pacific coastal regions, with information on many more projects available in “grey literature” and other publications. As well as their widespread geographic distribution, mangrove reforestation and rehabilitation programs can vary widely in focus, from emphasizing restoration of

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hydrological dynamics (Howard et al. 2017), to reducing coastal erosion (Hashim et al. 2010) and prioritizing carbon sequestration via “Blue Carbon” projects (Wylie et al. 2016).

Relative success or failure of reforestation projects is dependent on several factors, including the selection of mangrove species that are suitably adapted to local environmental conditions (Kodikara et al. 2017). For example, high seedling mortality rates of *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), and *Laguncularia racemosa* (white mangrove) at mangrove reforestation sites on the Caribbean coast of Colombia were associated with hypersalinization of the soil (Elster 2000). Similarly, widespread failure of mangrove restoration projects in the Philippines has been attributed to inappropriate planting of *Rhizophora* spp. on sandy substrates of exposed coastlines instead of natural colonizers *Avicennia marina* (grey mangrove) and *Sonneratia alba* (Primavera & Esteban 2008). Many mangrove species used in restoration projects have wide natural distribution ranges (e.g. *Rhizophora* spp. *Avicennia* spp.). While broad environmental tolerances of such species are well established (Lovelock et al. 2016), mangroves are known to demonstrate intraspecific population variability in tolerance to physiological stressors (Markley et al. 1982; Krauss et al. 2008; Proffitt & Travis 2014). Thus, background knowledge of local environmental tolerance of mangrove species is required to inform successful reforestation attempts.

With an approximate area of 1,287 km² (Feka & Ajonina 2011), mangrove ecosystems in Senegal occur along a steep climatic gradient, from tropical dry savanna in the southern Casamance region to hot desert conditions in northern Senegal (Peel et al. 2007). In the semi-arid Saloum Delta region of central coastal Senegal, mangrove ecosystems suffered major declines in spatial extent during the late 1970s and 1980s due to the Sahelian droughts (Fent et al. 2019). Mangrove loss and degradation during this period was mainly driven by hypersalinization of soils due to reduced seasonal rainfall (Conchedda et al. 2011). Since the 1990s however, mangroves have recolonized many drought affected areas of the Saloum Delta due to relative increases in regional rainfall (Conchedda et al. 2008), although mangrove cover dynamics in the region remains a subject of considerable debate (Carney et al. 2014; Andrieu et al. 2019; Fent et al. 2019). The Saloum Delta has also become a focal point for mangrove reforestation projects, implemented by a range of actors including small-scale projects initiated by local communities and regional NGOs, and large-scale reforestation campaigns operated by international NGOs (Cormier-Salem & Panfili 2016; Navarro et al. 2019). Although many restoration efforts have been successful, recent reports have expressed concern over the failure of some reforestation attempts due to the widespread use of monogeneric *Rhizophora* plantations (Cormier-Salem & Panfili 2016). As with mangrove reforestation in other regions, propagules of the widespread *Rhizophora* genus are frequently preferentially used in mangrove reforestation projects (Cormier-Salem & Panfili 2016), due to their long thin propagules that facilitate ease of planting, and their large hypocotyl nutrient storage that is thought to increase survival rates at early developmental stages (López-Portillo et al. 2017). However, relative to co-occurring *Avicennia* spp.,

Rhizophora are less tolerant of hypersaline soils (Lovelock et al. 2016). Thus, particularly in semi-arid regions where unvegetated areas proposed for mangrove afforestation are characterized by hypersaline soils, local-scale threshold responses to soil salinity can inform species choice in reforestation projects.

In this study, we assess the impact of soil salinity on the early establishment success of mangrove restoration in semi-arid West Africa. Specifically, we ask: (1) how does soil salinity affect leaf-level photosynthetic traits of *R. mangle*, namely stomatal conductance, photosystem II (PSII) operating efficiency, and relative chlorophyll content; (2) to what extent does soil salinity impact the overall growth and survival of newly planted mangroves; and (3) what is the soil salinity associated with naturally occurring *A. germinans* in these semi-arid coastal ecosystems?

Methods

Study Sites

We conducted our study at three recent mangrove reforestation sites near Bettenty, Sine-Saloum Delta, Senegal (13°41'24"N, 16°37'48"W; Fig. 1). The Sine-Saloum region straddles hot semi-arid and dry tropical savanna climate types (Peel et al. 2007). Mean annual temperature ranges from 27.2 to 30°C, total annual rainfall is 450–920 mm (Navarro et al. 2019), and mean annual relative humidity is 45.7% (Kriticos et al. 2012). The climate is characterized by a long dry season from November to June, followed by a short wet season from July to October. Mangrove reforestation efforts in the area around Bettenty involved the participation of several nongovernmental organizations and members of the local community. Sites were planted with the principal aims of reducing coastal erosion (due to storm damage and sea-level-rise) and restoring the biodiversity value of mangroves surrounding the community of Bettenty. At all sites, propagules of red mangrove *R. mangle* were collected from nearby established mature trees during June–August and planted by hand directly into unvegetated mudflats at an approximate density of 1.1 propagules/m². Site A (13°41'24.11"N, 16°38'16.25"W) was planted in 2017 in a 0.5 ha area of a small barrier island situated directly opposite the town of Bettenty. The site was previously mature mangrove habitat but was deforested following a relatively recent storm event. The site is adjacent to an older *R. mangle* restoration site that was planted in 2013, with mature naturally occurring individuals of *R. mangle*, *R. racemosa*, *A. germinans*, and *L. racemosa* also present in surrounding areas. Average pore water salinity was 47 ppt. At Site B (13°42'59"N, 16°38'12"W), *R. mangle* propagules were planted in a 0.5 ha area in 2016. Based on local information and satellite imagery, the site was previously unvegetated for at least the last 25 years. The site is situated in an open coastal location, adjacent to a 2013 *R. mangle* reforestation site, with naturally regenerating mangrove species *R. mangle*, *R. racemosa*, *A. germinans*, and scattered individuals of *L. racemosa* and *Conocarpus erectus* also occurring. Average pore water salinity at the site was 58 ppt. Site C (13°41'18.06"N, 16°36'56.33"W) was the most recent reforestation, planted in 2018 in a sheltered 0.5 ha area adjacent to a mangrove creek,

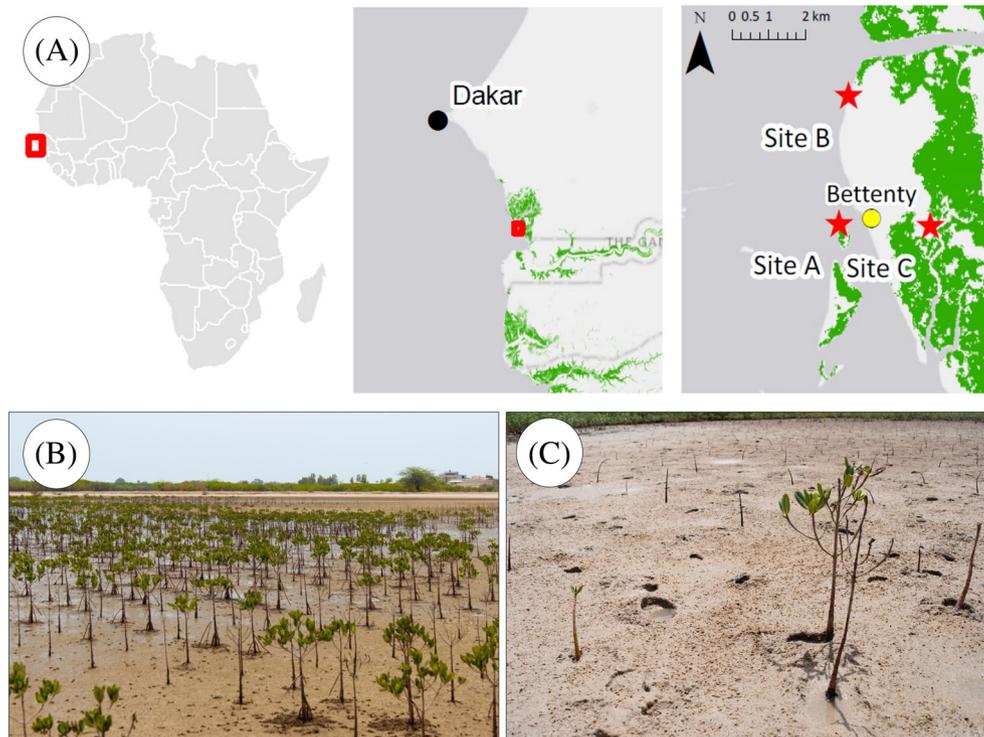


Figure 1. (A) The location of study sites in the Saloum Delta, Senegal. Sites (red stars) were located close to the town of Bettenty in the Foundiougne Department. Mangrove cover is indicated in green (Hamilton & Casey 2016). (B) Healthy *R. mangle* reforestation in the Saloum Delta and (C) widespread mortality of *R. mangle* at a hypersaline reforestation site (Site C).

1.5 km from the open coast. As with Site B, apart from some scattered naturally regenerating mangroves, Site C was previously unvegetated for at least the last 25 years. The site was hypersaline with an average salinity of 69 ppt. Mature naturally occurring *R. mangle* were present in areas fringing the river with stunted *A. germinans* individuals occurring in more inland, slightly higher elevation parts of the site. The region has a semi-diurnal tidal regime, and all sites are microtidal, ranging from 0.8 m (neap tide) to 2 m (spring tide) (Brasseur 2006).

Data Collection

Field work was conducted June–July 2019. At each site we established 10 randomly located 7 m² circular plots (radius 1.5 m). We first measured plot soil salinity by sampling pore-water at 30 cm depth in holes dug at the center of each plot. Pore-water was collected using a hand-held suction device and salinity was determined using a hand-held NaCl refractometer. Next, we counted all living and dead seedlings/propagules in each plot. Seedlings/propagules with no photosynthetic tissue (green leaves or stems) and blackened, non-pliable stems were recorded as dead. Stem elongation of all living seedlings was recorded as the height from root collar to the highest living apical bud. Root collar diameter at the soil surface was also measured using digital calipers. We measured stomatal conductance (mmol m⁻² second⁻¹) of the uppermost fully expanded leaf of seedlings using a diffusion porometer (Leaf

Porometer, model SC-1; Decagon Devices Inc., Pullman, WA, U.S.A.). PSII operating efficiency (or Φ PSII; quantum yield of PSII) and leaf relative chlorophyll content (SPAD) were also measured on the uppermost fully expanded leaf using a Multi-speQ plant phenotyping tool (Kuhlgert et al. 2016; Fernández-Calleja et al. 2020). Because of the length of time required to record physiological parameters (particularly associated with calibration of the diffusion porometer, ~5 min per measurement), and the need for relatively stable ambient environmental conditions to allow for within-site comparison, we randomly sub-sampled 3–5 individuals (when present) per plot for physiological measurements. To minimize bias caused by changing ambient environmental conditions, at each site, physiological measurements were recorded within a 2-hour period in the afternoon, on clear days, and at low tide. As well as providing information on leaf chlorophyll content and fluorescence, the Multi-speQ instrument provides simultaneous measurements of a suite of plant morphological, physiological, and ambient environmental variables, including leaf thickness, leaf temperature, ambient temperature, ambient relative humidity, and ambient photosynthetically active radiation (PAR).

Finally, to compare soil salinities of *R. mangle* reforestation areas with those associated with naturally occurring individuals of *A. germinans*, we recorded the pore-water salinity in 30 cm trenches dug directly adjacent to *A. germinans* individuals that were present within our study sites (total $n = 13$, Site A; $n = 1$, height = 0.92 m, Site B; $n = 6$, height = 1.65 ± 0.33 m, Site C;

$n = 6$, average height = 0.41 ± 0.05 m). At Site C, we also recorded stomatal conductance and Φ PSII for sampled *A. germinans* plants.

Data Analysis

We assessed the relationship between soil salinity and leaf physiological and morphological measurements using mixed-effects linear regressions (lmer in *lme4* package by Bates et al. 2014). With separate models for each site, we assessed the response of leaf stomatal conductance, Φ PSII, relative chlorophyll content, and leaf thickness to soil salinity. In each model, soil salinity was included as a continuous fixed predictor variable, with plot included as a random factor. Stomatal conductance is strongly related to leaf-to-air vapor pressure deficit (VPD). Thus, we included VPD as a covariate in our models of stomatal conductance. Leaf-to-air VPD was calculated using ambient relative humidity (%) and leaf temperature ($^{\circ}$ C) values (Allen et al. 1998) provided by the MultispeQ instrument. Similarly, Φ PSII is tightly linked to ambient light intensity. Thus, for models of Φ PSII, ambient PAR ($\text{mmol m}^{-2} \text{second}^{-1}$) was included as a covariate. We additionally assessed the cross-site relationship between VPD and stomatal conductance, and the relationship between PAR and Φ PSII for all individuals using simple linear regressions. Next, for each site, we assessed the relationship between soil salinity and mangrove stem elongation rate (RGR_s) and relative root collar diameter growth rate (RGR_d) using mixed-effects linear regressions with plot included as a random factor. Growth rates were calculated as $\ln \bar{G}_2(t)$, where $\ln \bar{G}_2$ are means of the natural logarithm transformed plant growth measurement (i.e. stem elongation or root collar diameter) and t is the time (number of months) since propagules were planted. Next, we used logistic regressions (glmer in *lme4*) to assess the effect of soil salinity on propagule survival. For each site, we assessed the binary outcome of propagule survival using soil salinity as a continuous fixed predictor variable and plot included as a random factor. For all mixed models, significance of each variable was tested using likelihood-ratio tests of reduced versus full models. Finally, across sites, we compared plot soil salinity ($n = 30$) with the salinity associated with naturally occurring *A. germinans* ($n = 13$) using one-way analysis of variance (ANOVA). We also compared averaged stomatal conductance and Φ PSII values for *A. germinans* and *R. mangle* at Site C using one-way ANOVA. All statistical analyses were conducted using R software (R Foundation for Statistical Computing).

Results

Stomatal conductance decreased as soil salinity increased at Sites A ($\chi^2 = 16.01$, $p < 0.001$) and B ($\chi^2 = 4.31$, $p = 0.037$) but not at Site C ($\chi^2 = 0.25$, $p = 0.614$; Fig. 2A). Across sites, stomatal conductance was strongly related to leaf-to-air VPD ($r^2 = 0.41$, $F = 46.51$, $p < 0.001$; Fig. S1A), with conductance being severely reduced at VPDs greater than 2.5 kPa. Over relatively lower salinity gradient at Sites A and B (average soil salinity of 47 ± 1.2 and 58 ± 0.3 ppt respectively), Φ PSII was

not significantly related to soil salinity (Site A: $\chi^2 = 4.57$, $p = 0.08$; Site B: $\chi^2 = 1.343$, $p = 0.25$; Fig. 2B). At Site C however, where soils were hypersaline (ranging from 55 to 78 ppt), Φ PSII decreased strongly with increasing soil salinity ($\chi^2 = 7.83$, $p = 0.005$; Fig. 2B). Across sites, Φ PSII decreased strongly with increasing ambient PAR ($r^2 = 0.63$, $F = 106.4$, $p < 0.001$; Fig. S1B). Neither leaf relative chlorophyll content or leaf thickness was related to soil salinity at sites (Fig. 2C & 2D respectively).

Across sites, stem elongation rate declined with increasing salinity (Fig. 3A). For example, average stem elongation of seedlings in plots with pore water salinities >60 ppt ($n = 15$) was reduced by 43% compared to seedlings growing in plots with pore water salinities of <60 ppt ($n = 12$). Within-site, however, a significant negative relationship between stem elongation and salinity was only evident across the hypersaline gradient at Site C ($\chi^2 = 5.788$, $p = 0.016$; Fig. 3A). Similarly, across sites, root collar diameter was reduced at higher soil salinities (Fig. 3B), and root collar growth declined with increasing salinity at Site C ($\chi^2 = 8.889$, $p = 0.002$; Fig. 3B).

Overall, average survival of mangrove seedlings was 61% (Site A, 67%; Site B, 62%; Site C, 53%). Seedling survival declined as plot soil salinity increased at Site A ($\chi^2 = 15.854$, $p < 0.001$; Fig. 4) and Site C ($\chi^2 = 10.439$, $p = 0.001$; Fig. 4), but not over the relatively narrow salinity gradient present at Site B ($\chi^2 = 0.048$, $p = 0.825$; Fig. 4). Proportion survival of propagules in plots with pore water soil salinities of >70 ppt were low (22%) compared to plots with salinities <70 ppt (76%).

Across sites, average soil salinity associated with naturally occurring *A. germinans* was 71 ± 4 ppt ($n = 13$), 18% higher than the equivalent value for planted *R. mangle* (60 ± 2 ppt, $F = 6.415$, $p = 0.015$; Fig. 5). At Site C, despite large differences in pore-water salinities, average stomatal conductance values were similar for both species (*A. germinans* = $212.5 \text{ mmol m}^{-2} \text{second}^{-1}$, *R. mangle* = $216.5 \text{ mmol m}^{-2} \text{second}^{-1}$, $F = 0.02$, $p = 0.88$; Fig. 6A). However, at Site C, Φ PSII of *R. mangle* was significantly reduced compared to *A. germinans* ($F = 18.82$, $p < 0.001$; Fig. 6B).

Discussion

In climate vulnerable countries, mangrove reforestation can restore vital ecosystem services such as protection from storms and flooding from sea-level rise, thus aiding climate adaptation efforts and supporting livelihoods in coastal communities (Lee et al. 2014; Primavera et al. 2016). In many cases however, quantitative data on local environmental tolerances of mangrove species used in reforestation efforts is lacking, and failure of restoration projects has been attributed to incorrect species selection in plantations. In a case study of early-stage reforestation projects in the Saloum Delta, Senegal, we identify physiological threshold responses of *R. mangle* to soil salinity. At soil salinities >60 ppt, PSII operating efficiency (Φ PSII), growth, and survival of planted *R. mangle* seedlings were severely reduced. In contrast, we recorded naturally occurring *A. germinans* growing in exceptionally hypersaline conditions (up to 90 ppt), representing some of the most saline vegetated ecosystems on Earth. The findings reported herein

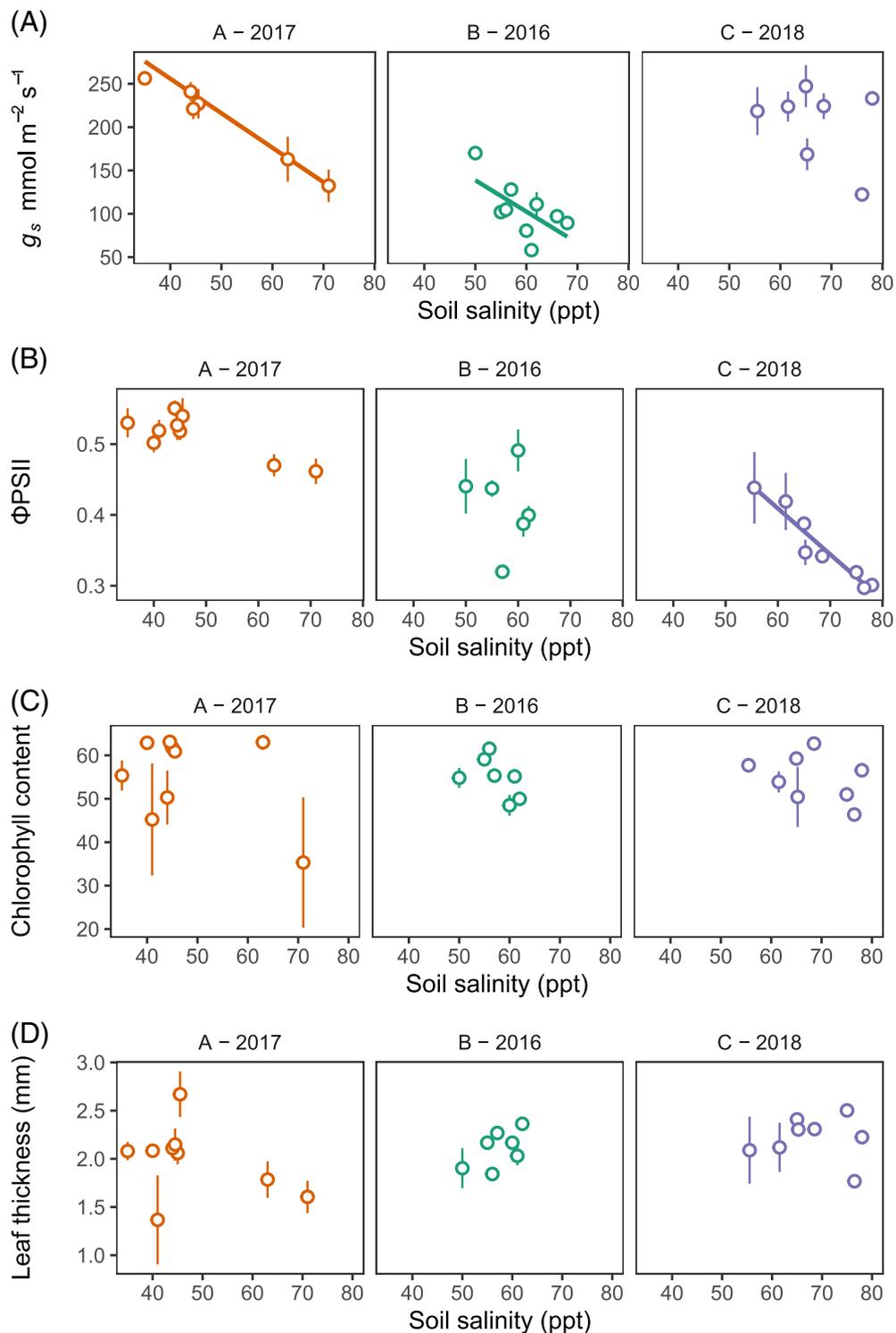


Figure 2. The relationship between soil salinity (ppt) and mean (± 1 SE) leaf stomatal conductance g_s (A), mean (± 1 SE) photosystem II operating efficiency (Φ_{PSII}) (B), mean (± 1 SE) relative chlorophyll content (SPAD) (C), and mean (± 1 SE) leaf thickness (D) of planted *R. mangle* seedlings in experimental plots at three mangrove restoration sites in the Saloum Delta, Senegal. Colors indicate reforestation sites.

can be used to inform species choice in reforestation projects and help improve success rates of coastal wetland restoration projects in semiarid West Africa.

Rhizophora spp. are a major component of mangrove ecosystems globally (Spalding et al. 2010), and generally exhibit comparatively wide tolerance to salinity stress (Lovelock et al.

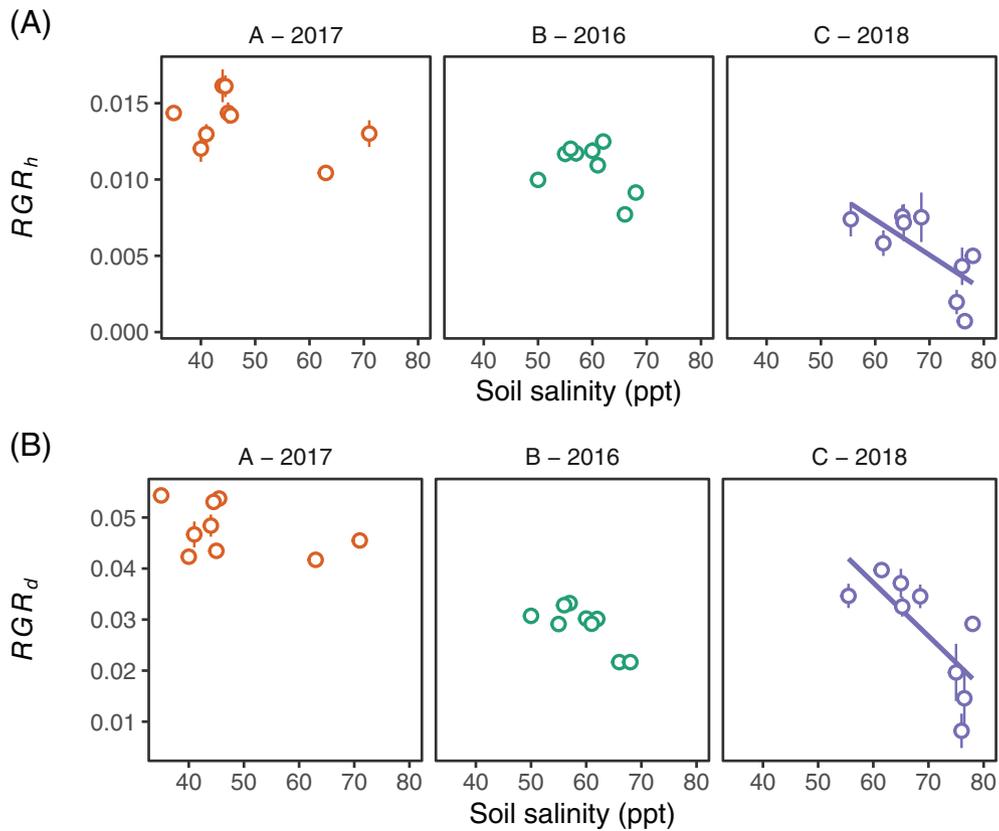


Figure 3. (A) The relationship between plot level soil salinity (ppt) and relative stem elongation rate and (B) relative root collar diameter growth rate of planted *R. mangle* seedlings at three mangrove restoration sites in the Saloum Delta, Senegal. Growth rates were calculated as $\ln \bar{G}_2 / t$, where $\ln \bar{G}_2$ are means of the natural logarithm transformed plant growth measurement (i.e. stem elongation or root collar diameter) and t is the time (number of months) since propagules were planted. Colors indicate reforestation sites.

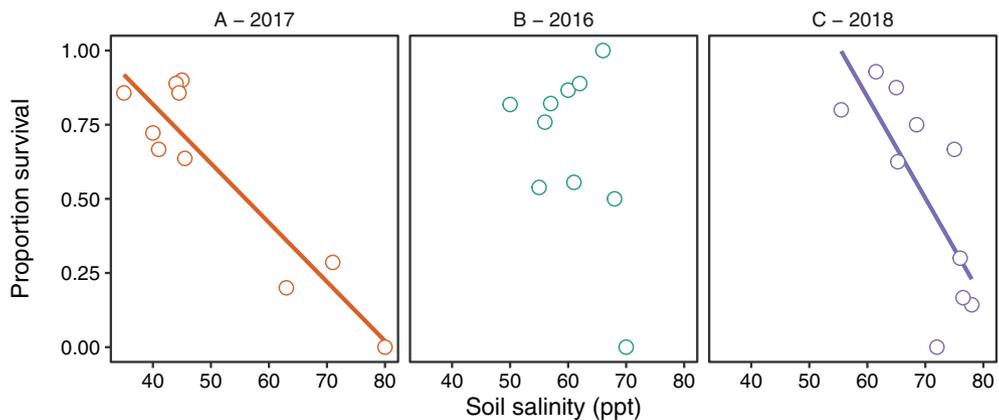


Figure 4. The relationship between plot level soil salinity (ppt) and proportion survival of planted *R. mangle* seedlings at three mangrove restoration sites in the Saloum Delta, Senegal. Colors indicate reforestation sites.

2016), one of the key factors driving the local distribution of mangrove species (Méndez-Alonzo et al. 2016). In a study of mangrove responses to salinity in Puerto Rico, although density of mature trees decreased with soil salinities of >55 ppt, *R. mangle* were present in areas of up to 80 ppt salinity (Cintron et al. 1978). In the arid conditions of coastal western

Australia, however, *Rhizophora stylosa* were restricted to soil salinities of ~50 ppt (Gordon 1988). In our study, higher soil salinities were generally associated with reduced stomatal conductance, particularly at Site A and Site B. Lower stomatal conductance resulting from increasing substrate salinity in mangroves is well established; when soil salinity is greater than

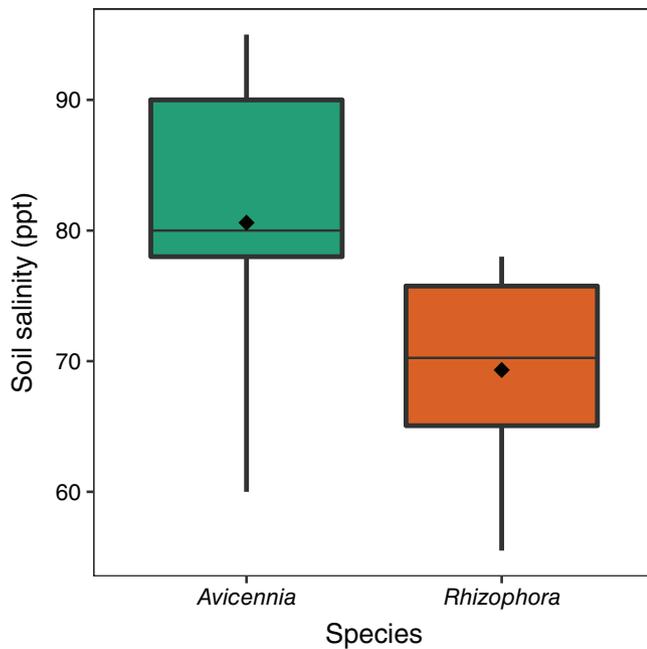


Figure 5. Average soil salinity (ppt) associated with planted *R. mangle* plots ($n = 30$) and naturally occurring *A. germinans* ($n = 13$) across all sites. Boxplots indicate the upper and lower quartiles and vertical lines indicate values within 1.5 times above the interquartile range. Horizontal lines within boxes represent median values and black diamonds indicate group means.

seawater (~ 35 ppt), whole-plant hydraulic conductance can decline due to xylem cavitation, resulting in severe limitations to photosynthesis and growth (Ball & Farquhar 1984; Melcher et al. 2001; Ewers et al. 2004; Méndez-Alonzo et al. 2016). Indeed, Méndez-Alonzo et al. (2016) demonstrated that stomatal conductance of *R. mangle* declined linearly across a substrate

salinity gradient of 0–50 ppt. In our study, although stomatal conductance declined with increasing salinity, average conductance at salinities 35–60 ppt remained relatively high (average = $204 \text{ mmol m}^{-2} \text{ second}^{-1}$), especially considering measurements were recorded during late dry season when temperatures of $>35^\circ\text{C}$ can coincide with low relative humidity. During our measurements, average ambient temperature was 36°C and average relative humidity was 50%—generating average leaf-to-air VPDs of 2.36 kPa—extremely arid conditions for mangrove growth and survival. *R. mangle* propagules used at the reforestation sites we assessed were gathered from nearby mature conspecifics, and therefore likely exhibited adaptation to localized extreme conditions, emphasizing the need for locally sourced plant material to be used in restoration activities. However, rising temperatures associated with anthropogenic climate change are continuing to increase global leaf-to-air VPDs (Grossiord et al. 2020), yet the impact of rising VPD on arid mangrove ecosystems remains underexplored (Lovelock et al. 2016). Thus, whether restored arid mangroves, often already existing close to the edge of their range limit, can persist under future climate conditions is unclear.

In hypersaline conditions at Site C, PSII operating efficiency of *R. mangle* declined sharply with increasing substrate salinity. A reduction of photosynthetic efficiency in saline soils is well established, especially for crop plants (Dionisio-Sese & Tobita 2000; Sayed 2003). For mangroves, previous work has demonstrated that photoinhibition, or the light-dependent reduction of quantum yield of photosynthesis, occurs in hypersaline conditions for a number of species (Sobrado & Ball 1999; Biber 2006; Naidoo 2006). In the hypersaline conditions (>60 ppt) of our study, reduced stomatal conductance, coupled with impaired function of PSII, likely resulted in reduced growth and survival of planted seedlings.

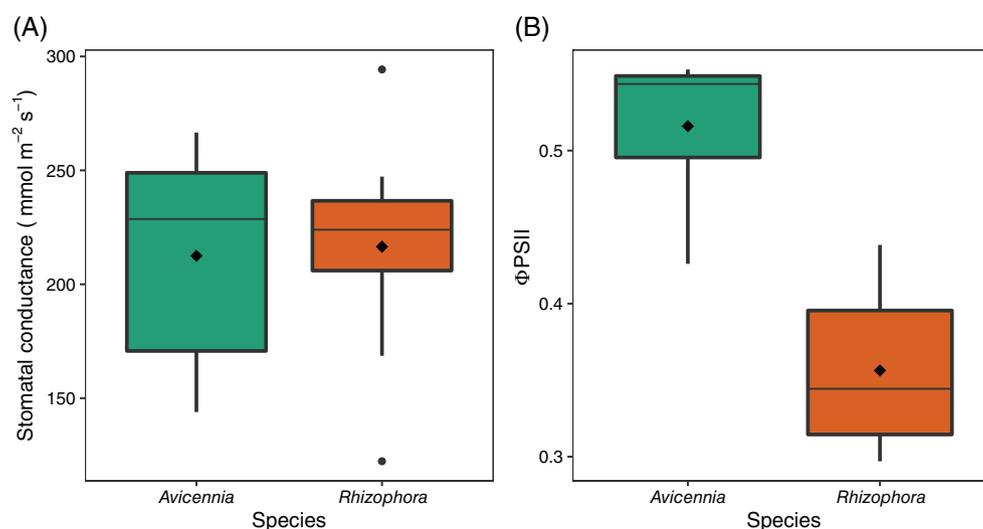


Figure 6. Average stomatal conductance g_s (A) and ΦPSII (B) associated with planted *R. mangle* ($n = 9$, values averaged per plot) and naturally occurring *A. germinans* ($n = 6$) at Site C. Boxplots indicate the upper and lower quartiles and vertical lines indicate values within 1.5 times above the interquartile range. Horizontal lines within boxes represent median values and black asterisks indicate group means.

Compared to planted *R. mangle*, naturally occurring *A. germinans* were associated with more saline substrates. High salinity tolerance of *A. germinans* is well established (Lovelock et al. 2016) and at global mangrove range limits *Avicennia* spp. often extend beyond *Rhizophora* spp. into more saline, arid environments (Quisthoudt et al. 2012). Nevertheless, survival of *A. germinans* in hypersaline conditions (up to 90 ppt) in our study represents high tolerance to soil salinity, even compared to other *Avicennia* populations in comparable semiarid mangrove ecosystems. For instance, in *A. germinans* dominated mangroves in semiarid Baja California Sur, Mexico, pore-water salinity reaches a maximum of 77 ppt during the dry season (Vovides et al. 2011). Similarly, Schile et al. (2017) reported that stunted *A. marina* stands in the Arabian Gulf reached maximum salinity levels of 67 ppt. The level of adaptation of *A. germinans* to hypersaline conditions in semiarid West Africa highlights the potential value of this species in reforestation efforts in sites that are not capable of supporting viable *R. mangle* plantations.

Notwithstanding other physiological stressors such as extreme air temperatures and tidal inundation, our study demonstrates that areas in the Saloum Delta with soil salinities of up to 60 ppt may be suitable for planting with *R. mangle* as part of mangrove reforestation and restoration projects. In areas of >60 ppt, however, *Avicennia* is likely to be more tolerant of hypersaline conditions and more likely to persist in the long term. *Rhizophora* spp. are often preferred in mangrove restoration efforts as their large, elongated propagules are comparatively easy to collect and insert directly into the substrate (Lee et al. 2019). Relative to *Rhizophora*, the initial costs of *Avicennia* plantations may be higher, generally requiring the establishment of seedling nurseries and time consuming by-hand planting of seedlings that can be prone to higher levels of failure (Cormier-Salem & Panfili 2016; Kodikara et al. 2017). Nonetheless, at hypersaline sites, initial investment in planting *Avicennia* spp. may result in higher survival rates, although experimental evidence for our region is required. Indeed, despite their broad environmental tolerance, planting *Avicennia* in unvegetated salt flats (or *tanns*) should be avoided given the hypersaline and arid conditions that persist in the region. Moreover, despite soil salinities being within their environmental tolerance, the low number of naturally regenerating *A. germinans* at restoration sites indicates that factors other than salinity, such as hydrological dynamics, may be preventing natural mangrove establishment at these sites. In several regions globally, there has been criticism of mangrove planting initiatives that have afforested sites that have not previously supported mangrove forest such as intertidal mudflats and seagrass beds (Ertfemeijer & Lewis 1999; Primavera & Esteban 2008). Such sites have sub-optimal environmental conditions for mangrove growth, often leading to reduced tree survival. We suggest that restoration efforts should focus on areas where mangroves have previously existed but have been degraded or lost due to factors such as storm damage or harvesting. On degraded and deforested mangrove sites, studies in Malaysia and elsewhere (Kamali & Hashim 2011; López-Portillo et al. 2017) have documented the potential of mangrove natural regeneration to rehabilitate degraded sites, particularly

once hydrological dynamics have been restored. Thus, passive recovery of mangroves via natural regeneration may be used as a low-cost alternative in certain cases (Ferreira et al. 2015).

Our study demonstrates that simple field-based assessments may be useful during mangrove restoration planning, implementation, and monitoring phases. Initial characterization of the soil environment prior to planting can be carried out with low-cost handheld refractometers, guiding species choice for reforestation. Across semiarid mangrove regions, soil salinity is the dominant stressor and should be characterized at sites prior to reforestation activities and used to guide species selection decisions. Moreover, chlorophyll fluorescence may be used as a tool for monitoring plant health in restoration projects (Biber 2006). Although costs of such equipment have previously been prohibitive, recent technological advances have dramatically reduced costs for hand-held chlorophyll fluorescence instruments (Kuhlgert et al. 2016). Such devices may be used in the field, both prior to planting (as a tool to guide species selection) and to monitor the long-term health of reforested areas, a process that is rarely implemented currently (Lee et al. 2019). More broadly, the widespread use of monotypic mangrove plantations has been questioned (particularly for diverse mangrove stands in the Indo-West Pacific region) and may in fact accelerate the loss of mangrove services (Lee et al. 2019). For neotropical and arid-zone mangroves, where stands often support 3–4 mangrove species or even less, single species plantations may effectively restore ecosystem function and services, but only if species environmental tolerances and site suitability are carefully considered. We echo calls from Lee et al. (2019) for evidence-based mangrove restoration policies, with prioritization of long-term establishment over short-term increases in area.

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Supporting Information

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

Figure S1. (A) Relationship between leaf-to-air vapor pressure deficit (VPD) and mean stomatal conductance (gs) of planted *Rhizophora mangle* in experimental plots, and (B) relationship between photo synthetically active radiation (PAR) and mean photo system II operating efficiency Φ PSII of planted *Rhizophora mangle* in experimental plots.

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