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Adrien Jacotot, Cyril Marchand, Michel Allenbach. Increase in Growth and Alteration of C:N Ratios of *Avicennia marina* and *Rhizophora stylosa* Subject to Elevated CO₂ Concentrations and Longer Tidal Flooding Duration. *Frontiers in Ecology and Evolution*, 2019, 7, pp.98. 10.3389/fevo.2019.00098 . insu-02139096

HAL Id: insu-02139096

<https://insu.hal.science/insu-02139096v1>

Submitted on 26 Aug 2019

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Increase in Growth and Alteration of C:N Ratios of *Avicennia marina* and *Rhizophora stylosa* Subject to Elevated CO₂ Concentrations and Longer Tidal Flooding Duration

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Specialty section:

This article was submitted to
Conservation,
a section of the journal
Frontiers in Ecology and Evolution

Received: 04 November 2018

Accepted: 11 March 2019

Published: 10 April 2019

Citation:

Jacotot A, Marchand C and
Allenbach M (2019) Increase in
Growth and Alteration of C:N Ratios of
Avicennia marina and *Rhizophora*
stylosa Subject to Elevated CO₂
Concentrations and Longer Tidal
Flooding Duration.
Front. Ecol. Evol. 7:98.
doi: 10.3389/fevo.2019.00098

We investigated the effects of elevated CO₂ concentrations and longer tidal flooding duration on two-year-old *Avicennia marina* and *Rhizophora stylosa* seedlings for a full year. The seedlings were grown in greenhouses for ambient CO₂ (400 ppm) and in enclosed CO₂-controlled chambers, which were installed inside the greenhouses for elevated CO₂ (800 ppm). The tidal flooding duration was set-up according to the species distribution in the intertidal zone in New Caledonia for the controlled treatment and was increased by 1 h 45 min for the experimental treatment. A total of 400 *A. marina* and 720 *R. stylosa* were monitored during this experiment. We measured heights and basal diameters of all seedlings every 90 days, and we determined the above and below ground biomass at the end of the experiment. Our results showed that elevated CO₂ increased the growth rates of both *A. marina* and *R. stylosa*, for which the final biomass was, respectively, 46 and 32% higher than in the ambient CO₂ treatment. We suggest that this increase was driven by a stimulation of photosynthesis under elevated CO₂, as demonstrated in a previous study. Considering the tidal flooding duration treatment, we observed a contrasted effect between the species. Longer tidal flooding increased the growth of *A. marina*, whereas it reduced the growth of *R. stylosa* in comparison to the controlled treatment. This result may be related to the specific ecosystem zonation in this semi-arid climate, which limits water inputs into the *Avicennia* zone that increases the salt concentration in the soil, whereas *Rhizophora* is regularly submerged by tides due to its lower position in the intertidal zone. As a result, the combination of both treatments had a positive cumulative effect on the growth of *A. marina*. Although it was not the case for *R. stylosa*, the negative effect of longer tidal flooding on this species did not suppress the enhancement of growth resulting from elevated CO₂ concentrations. At the end of the experiment, elevated CO₂ increased the C:N ratios of the seedlings, thereby producing a more refractory organic matter, which will potentially result in lower decomposition rates

and thus may increase carbon accumulation in mangrove soils. These results suggest that future climate changes may enhance the productivity of mangrove seedlings by increasing their growth, which may in turn increase the carbon storage potential of mangroves in their biomass.

Keywords: mangrove, elevated CO₂, sea-level rise, growth, biomass, climate changes

INTRODUCTION

The steady increase in anthropogenic greenhouse gas emissions since the preindustrial age resulted in a substantial atmospheric CO₂ concentrations augmentation, from 280 ppm to over 400 ppm currently (Betts et al., 2016). This increase is strongly inducing global warming (Cook et al., 2016), which, in turn, leads to an augmentation of the global mean sea-level. Projections agree that atmospheric CO₂ concentrations will continue to rise in the future, and are predicted to range from 794 to 1,150 ppm by the end of the 21st, depending on simulation models (Collins et al., 2014). As a result, the global mean sea-level is expected to increase from 0.26 to 0.98 m by 2,100 (Church et al., 2013).

Mangroves are forested ecosystem that develop along tropical and subtropical coastlines and are mainly composed of halophytic C3 trees. Due to their high primary productivity (average of 218 ± 72 Tg C yr⁻¹) (Bouillon et al., 2008), mangroves are considered as major ecosystems in the coastal carbon cycle, and have therefore been recently named “blue carbon” sinks (McLeod et al., 2011). Many studies have investigated the response of C3 terrestrial plants to elevated CO₂ concentrations, which mainly results in photosynthesis stimulation and higher productivity (Norby et al., 2005; Prior et al., 2011). However, only a few studies have focused on the response of mangroves to elevated CO₂ concentrations. These studies showed that that the response of mangroves plants is similar to other C3 plants with an increase in photosynthesis and productivity (Farnsworth et al., 1996; Ball et al., 1997; McKee and Rooth, 2008; Luo et al., 2010; Reef et al., 2016; Jacotot et al., 2018), highlighting their valuable role in climate change mitigation. However, the effects of elevated CO₂ concentrations may be strongly dependent of other biotic and abiotic factors such as temperature, nutrient availability, or flooding (Alongi, 2015).

Due to their position at the interface between land and sea, increase in global mean sea-level may be a major threat to mangroves (Ellison, 2015; Ward et al., 2016). Mangrove ecosystems have the ability to cope with sea-level rise through surface elevation change processes (Krauss et al., 2014), however, this capacity is influenced by several factors (Ward et al., 2016) and may be specific to each mangrove forest. In fact, (Lovelock et al., 2015) reported that 69% of mangroves surveyed in the Indo-Pacific region were not building surface elevation at rates that equal or exceed sea-level rise and, consequently, will experience major changes in their tidal flooding duration if their landward migration is prevented by human activities (Gilman et al., 2008).

A handful studies have examined the response of mangroves plants with climate changes and they mainly focused on elevated CO₂ in interaction with salinity (Reef et al., 2015), nutrient availability (McKee and Rooth, 2008; Reef et al., 2016), or species competition (McKee and Rooth, 2008). However, to our knowledge, no studies have focused on the effects of elevated CO₂ in interaction with an increase in tidal flooding duration on mangrove seedlings before, thus, the present study is the first to have investigated this interaction.

During one complete year, between 2016 and 2017, we conducted, in New Caledonia, a greenhouses experiment in which 720 *R. stylosa* and 400 *A. marina* were grown at two CO₂ concentrations (400 vs. 800 ppm) over two tidal flooding durations (one typical of Neo Caledonian mangroves, and a longer one). In a previous paper concerning this experiment (Jacotot et al., 2018), we were mainly interested in the variability of leaf-gas exchange parameters of both species, and our main results were: (i) elevated CO₂ concentrations affected seedlings physiology, notably by increasing photosynthesis by more than 37 and 45% for *A. marina* and *R. stylosa*, respectively, (ii) higher mean temperature during the warm season further enhanced this photosynthesis increase, and (iii) longer tidal flooding duration slightly reduced photosynthesis but not enough to offset the carbon gain induced by the elevated CO₂ concentrations. In the present complementary study, we now focus on seedlings growth and tissues quality (using C:N ratio as a proxy). Measurements presented herein were conducted at the same time, and thus, on the same seedlings as in Jacotot et al. (2018). In the present study, the questions we wanted to answer were: (i) does atmospheric CO₂ enrichment, which increased photosynthesis, lead to a stimulation of growth and biomass? (ii) is the growth response to tidal flooding duration reduced due to waterlogging variations? (iii) what will be the effects of these two parameters on the plant tissues quality, and notably on C:N ratios?

MATERIALS AND METHODS

Greenhouses and Closed Chambers Experiments

Description of the Facility

The study was conducted in New Caledonia (22°13'49"S, 166°31'09"E) from June 2016 to May 2017, a period encompassing the two main seasons (i.e., the cool season from June to November, and the warm season from November to June). Experiments were realized in three semi-open greenhouses (Figure 1a) (12 × 6 m, 6 m height, 72 m² each), following a split-plot design with CO₂ atmospheric concentrations as the whole-plot (Ambient, 400 ppm vs. Elevated, 800 ppm) and

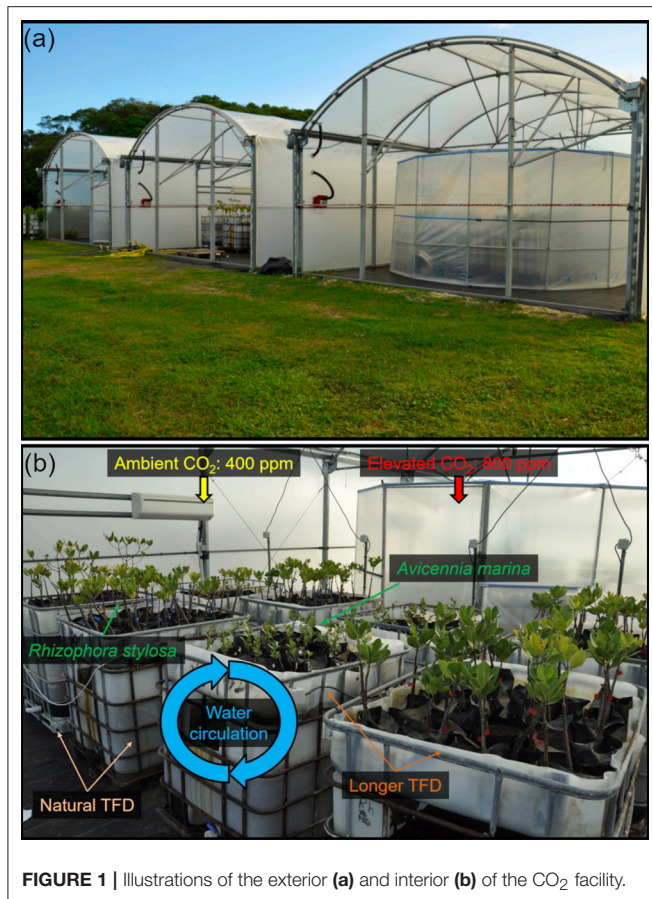


FIGURE 1 | Illustrations of the exterior (a) and interior (b) of the CO₂ facility.

tidal flooding duration (TFD) as the split-plot nested within CO₂ (Natural vs. Longer). Inside each greenhouse, a circular closed chamber of 36 m² (2.4 m height) was constructed to maintain elevated atmospheric CO₂ concentrations (Figure 1b). To control the tidal duration treatment, custom-designed tidal tables were built (Figure 1b). The tidal tables consisted of a 700 liters polypropylene tank (1 m² area over 0.7 m height) serving as a water reserve, surmounted by a 300 liters planting tray (1 m² area over 0.3 m height). Each tidal table worked as an individual unit. Every 2 weeks throughout the studied period, the water reserves were renewed with fresh seawater pumped into the adjacent lagoon (20 m). To simulate high tide periods, an aquarium pump placed in each tank sent the water to the planting trays. During low tide periods, a siphon pipe allowed the planting tray to drain the water back into the reserve. To control the tidal treatment assigned to each tank, the aquarium pumps were connected to three custom-build current controllers (one per greenhouse). The controllers were built from open source Arduino plans freely available under public licenses and were programmed according to the needs of the experiment. Water quality (pH, salinity, DO) in the tanks was checked periodically using YSI probes.

Air temperature and humidity were recorded every 5 min inside the greenhouses and the closed chambers with HOBO sensors (Onset, Cape Cod, Massachusetts, USA). The temperature and humidity could fluctuate naturally inside the

greenhouses, however, air cooling units have been installed in the closed chambers to prevent large temperature fluctuations. During the experimental period, average temperatures were, for inside the greenhouses and the closed chambers respectively, 23.1 ± 2.6 and $22.3 \pm 3.0^\circ\text{C}$ during the cool season and 26.4 ± 3.2 and $26.7 \pm 3.5^\circ\text{C}$ during the warm season. The relative humidity was, for inside the greenhouses and the closed chambers respectively, 85.8 ± 12.6 and $78.4 \pm 12.2\%$ during the cool season and 80.7 ± 14.2 and $80.8 \pm 12.8\%$ during the warm season.

Plant Materials

A total of 720 *R. stylosa* and 400 *A. marina* propagules were collected from multiple trees in the pristine mangrove of Oundjo, in New Caledonia ($21^\circ 4' 8''\text{S}$, $164^\circ 42' 51''\text{E}$). They were collected between February and March 2014, during the optimal fruiting period. They were then individually planted in 2.5-liters polyethylene bags in a 1:1 mixture of mangrove peat and sand and grown for two complete years before being used in the experiment.

The mangrove seedlings were randomly allocated between the tidal tables, with 25 *A. marina* or 30 *R. stylosa* on each tidal table, resulting in 100 *A. marina* (4 tidal tables) and 180 *R. stylosa* (6 tidal tables) for each of the four treatments (Figure 1b). The tidal tables were then distributed between the three greenhouses as true experimental replicates, and then either inside or outside the closed chambers according to their CO₂ treatment. During the experiment, mangrove seedlings were regularly rotated within each tidal table and were rotated three times between the greenhouses to minimize positional effect.

CO₂ Enrichment

Pure CO₂ was supplied into each of the three closed chambers between 5:00 a.m. to 7:00 p.m. and the concentrations were maintained between 780 and 820 ppm throughout this period. The CO₂ concentrations inside the chambers were continuously monitored using CO₂ probes connected to a central unit that controlled the entire system (MAXICLIM NG 08/3Z, Anjou Automation). In addition, CO₂ concentrations were periodically checked using two different infrared portable CO₂ analyzers (a G2131-*i* CRDS analyzer from Picarro Inc., Santa Clara, USA; and a Li-8100A from LI-COR Biosciences, Lincoln, USA).

Tidal Flooding Duration Treatment

The natural tidal flooding duration (TFD) was set up according to the average flooding duration measured in New Caledonian mangroves for both species (unpublished data). These tidal durations may be different and variable according to the geographical position of the studied mangrove (e.g., Van Loon et al., 2007). In New Caledonia, mangroves develop in semi-arid conditions with a specific zonation of the vegetative species: *Rhizophora* spp. colonizes the sea side, while *Avicennia marina* develops at higher elevations. Previous studies have suggested that the main factor controlling this distribution of mangrove species in New Caledonia is soil salinity, which in turn is controlled by the duration of tidal inundation, and thus, by the soil elevation (Marchand et al., 2011b, 2012). As a result, the flooding duration for *Rhizophora* trees is higher than for

Avicennia. Consequently, in the experiment, natural TFD was 3 h 15 min for *A. marina* and 6 h 00 min for *R. stylosa* for each high tide. Simulated tidal cycles were semi-diurnal, meaning that there were two high tides each day, separated by a low tide period of 8 h 30 min and 5 h 45 min for *A. marina* and *R. stylosa*, respectively.

We hypothesized that an increase in mean sea-level would similarly affect the flooding duration of both species; thus, in the experiment, longer TFD was simulated by increasing the natural times by 1 h 45 min, which corresponded to a high tide of 5 h 00 min and 7 h 45 min for *A. marina* and *R. stylosa*, respectively. Consequently, low tides periods were reduced to 6 h 45min and 4 h for *A. marina* and *R. stylosa*, respectively. This increase in flooding duration has been randomly defined but remains realistic given the projected sea-level rise at the end of the century. Although we have chosen a similar increase in flooding duration for both species, we are aware that this may be not the case, and that the flooding duration may increase differently in both stands in the natural system. Nevertheless, an increase of 1 h 45 min of tidal duration will have different implications for both species, as it corresponds to an increase of 45% of the natural tidal duration of *A. marina*, whereas it is only 25% for *R. stylosa*. During high tide, the water level in the planting trays was identical for all tidal tables, 5 cm above sediment surface to completely submerge the root system.

Measurements

Growth and Biomass

All mangrove seedlings were measured for their height and basal diameter. Height measurements were made along the main axis, from the soil for *A. marina*, and from the top of the hypocotyl for *R. stylosa*. Basal diameters were taken at 0.5 cm above these two limitations. The measurements were realized five times during the experimental period: at the beginning, after 90, 180, 260 days, and at the end of the experiment, when the seedlings were three-years old.

Biomass was measured at the beginning and at the end of the experiment. For each species and treatment, 30 seedlings were randomly selected and separated into below (root system) and above (leaves and stems) ground parts. All plant components were then thoroughly washed with deionized water. Then, all plant materials were dried at 60°C during 72 h before being weighted for dry mass (g). Relative growth rates (RGR) were calculated as the difference between final and initial mass over the duration of the experiment. In addition, the leaf mass area (LMA, g cm⁻²) was calculated as the inverse of the surface leaf area (SLA), which was previously determined on the same trees and during the same experiment (Jacotot et al., 2018).

Carbon and Nitrogen Content

Carbon and nitrogen contents were measured at the end of the experiment. For each species and treatment, 30 individuals were randomly selected and separated in three batches of 10 individuals. Within each batch, all seedlings were separated into leaves, stems and roots. All plants materials were then dried at 60°C for 72 h, and then ground using a ball mill, to finally obtain three batches of leaves, stems and roots for each species and treatment, each one constituted by 10 individuals. Three

subsamples (~2 mg) of each lot of leaves, stems and roots were then analyzed for total carbon (C) and nitrogen (N) contents (%) using an elemental analyzer (Integra2, Sercon, UK). All the analyses were performed at the French National Institute for Sustainable Development (IRD) of Noumea, New Caledonia (France). The analytical precision of the analyzer was checked using IAEA-600 caffeine standard (IAEA Nucleus) and was less than 0.3% for C and 0.15% for N. All C:N ratios in this study were calculated on the mass basis.

Statistical Analysis

Final heights, basal diameters, final above and below ground biomasses, below to above ground ratios and C:N ratios were analyzed for significant differences ($p < 0.05$) between the four treatments. Both species were analyzed independently. We used a Linear Mixed-Effects model (LMER) in which we set the CO₂ treatment (whole-plot) and the TFD treatment (subplot) as fixed effects. Multiple pairwise comparisons were then realized using a Tukey test for above and below ground biomasses, below to above ground ratios and C:N ratios, and a Scheffe *post-hoc* test was used for heights and basal diameters. All statistical analyzes were performed using R software version 3.5.1 (R Development Core Team, 2008). All results in the manuscript are reported by their mean ± standard error (SEM).

RESULTS

Basal Diameters and Heights

Changes in basal diameters and heights of *A. marina* and *R. stylosa* subjected to the four different treatments along the year of experiment are presented in **Figure 2**. The CO₂ enrichment resulted in a strong stimulation of seedlings growth from the start of the experiment (**Figure 2**); however, this effect was significant only 6 months after the beginning of the enrichment. For *A. marina*, final basal diameters and heights were significantly higher at elevated CO₂ than at ambient CO₂ concentrations (**Figures 2A,C** and **Table 1**), either with normal or longer tidal flooding duration (TFD). In addition, within each CO₂ treatment, the longer TFD significantly increased final basal diameters and heights (**Figures 2A,C** and **Table 1**). For *R. stylosa*, elevated CO₂ significantly increased final basal diameters and heights for both natural and longer TFD treatments (**Figures 2B,D** and **Table 1**); however, no significant effect was observed for longer TFD within each CO₂ treatment (**Table 1**).

Biomass, Below to Above Ground Ratios and Relative Growth Rates

Results of final above and below ground biomass are presented in **Figure 3**. For *A. marina*, elevated CO₂ significantly increased final above and below ground biomass, either under natural or longer TFD (**Figure 2A** and **Table 1**). However, the increase of the above ground biomass was higher (140 and 126% for natural and longer TFD) than the augmentation of the below ground biomass (78 and 74% for natural and longer TFD), which resulted in a significant decrease of the below to above ground ratio (**Figure 2C**). In addition, no significant effect of the TFD treatment was observed within each CO₂ treatment (**Figure 2A**

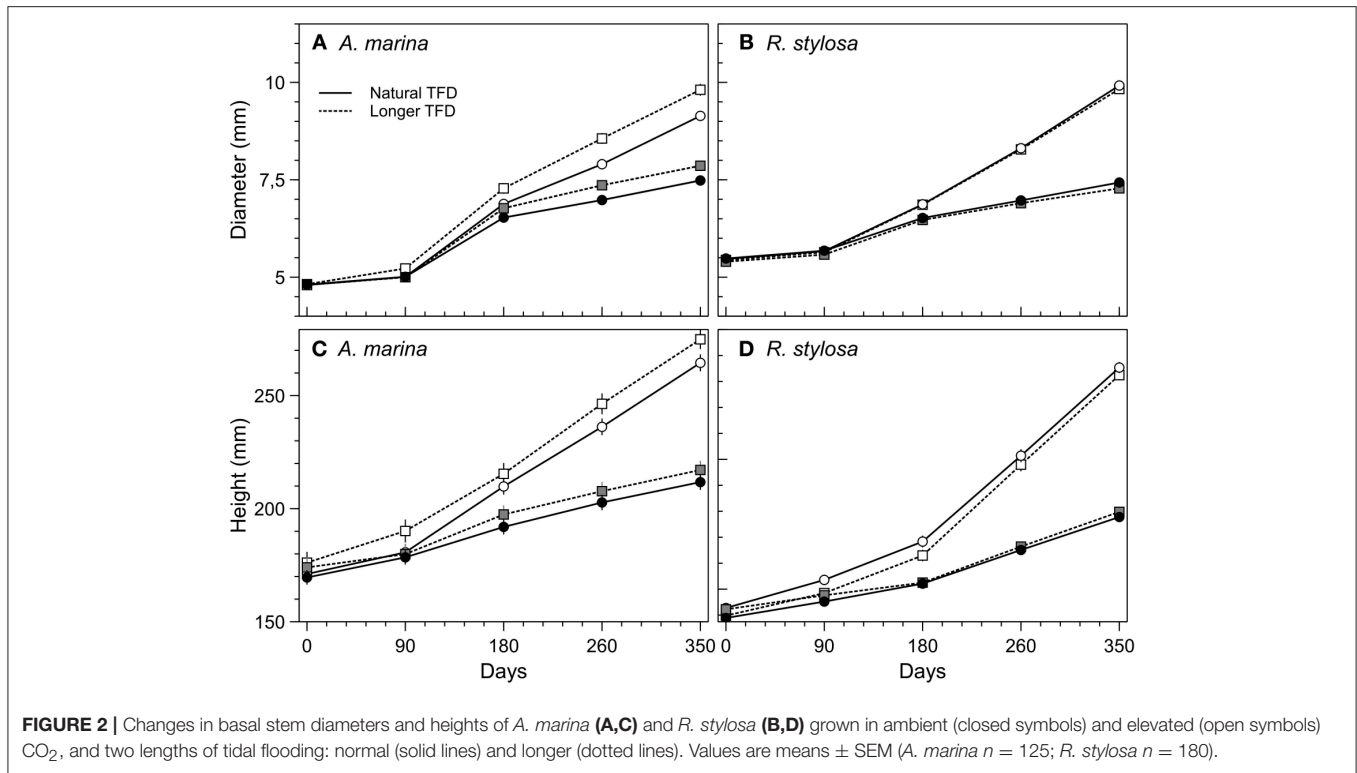


FIGURE 2 | Changes in basal stem diameters and heights of *A. marina* (A,C) and *R. stylosa* (B,D) grown in ambient (closed symbols) and elevated (open symbols) CO₂, and two lengths of tidal flooding: normal (solid lines) and longer (dotted lines). Values are means ± SEM (*A. marina* n = 125; *R. stylosa* n = 180).

TABLE 1 | Significance values reported after a Linear Mixed-Effects model.

| | <i>Avicennia marina</i> | | | <i>Rhizophora stylosa</i> | | |
|----------------|-------------------------|---------------------|----------------------|---------------------------|---------------------|----------------------|
| | CO ₂ | TFD | Interaction | CO ₂ | TFD | Interaction |
| Height | 2.015* | 4.124* | 0.422 ^{NS} | 117.178*** | 0.040 ^{NS} | 2.376 ^{NS} |
| Diameter | 204.141*** | 17.151*** | 1.303 ^{NS} | 23.877*** | 3.841 ^{NS} | 0.289 ^{NS} |
| BIOMASS | | | | | | |
| Above ground | 376.099*** | 0.825 ^{NS} | 0.0596 ^{NS} | 298.433*** | 6.961** | 3.044 ^{NS} |
| Below ground | 112.676*** | 4.695* | 0.168 ^{NS} | 75.337*** | 4.653* | 0.062 ^{NS} |
| BG/AG ratio | 44.228*** | 1.584 ^{NS} | 0.149 ^{NS} | 54.142*** | 0.332 ^{NS} | 3.221 ^{NS} |
| C:N | | | | | | |
| Leaves | 2.434* | 0.007 ^{NS} | 0.446 ^{NS} | 3.727 ^{NS} | 10.806* | 14.352** |
| Stems | 4.161 ^{NS} | 22.057** | 4.033 ^{NS} | 26.955*** | 4.288 ^{NS} | 0.896 ^{NS} |
| Roots | 22.418** | 3.243 ^{NS} | 6.096* | 1.371*** | 0.281 ^{NS} | 0.0744 ^{NS} |

***, **, * indicates significant effects at p < 0.001, 0.01, and 0.05, respectively. NS, non-significant.

and Table 1). For *R. stylosa*, elevated CO₂ concentrations also significantly increased the final above and below ground biomass (Figure 3B and Table 1). As for *A. marina*, the increase was higher for the above ground biomass (84 and 78% for natural and longer TFD) in comparison to the below ground biomass (37 and 50% for natural and longer TFD), which resulted in a significant decrease of the below to above ground ratio (Figure 3D). Concerning TFD, a significant reduction was observed for the above ground biomass under elevated CO₂ (Figure 3B).

Concerning the whole period of the experiment, relative growth rates (RGR) of *A. marina* were, under ambient CO₂ concentrations 18.19 ± 1.33 and 20.36 ± 0.96 g yr⁻¹, and under elevated CO₂ concentrations 35.56 ± 0.69 and 38.38 ± 1.46 g yr⁻¹, for natural and longer TFD, respectively. For *R. stylosa*,

RGR were 42.87 ± 1.89 and 37.39 ± 1.33 g yr⁻¹ under ambient CO₂ concentrations, and 63.23 ± 1.85 and 58.44 ± 1.99 g yr⁻¹ under elevated CO₂ concentrations, for natural and longer TFD, respectively.

C:N Ratios

Results of C:N ratios in the leaves, stems and roots of *A. marina* and *R. stylosa* at the end of the experiment are presented in Table 2. Elevated CO₂ concentrations significantly increased the C:N ratios in the leaves and roots of *A. marina*, as well as in the stems and roots of *R. stylosa* (Tables 1, 2). In addition, TFD significantly decreased the C:N ratios in the stems of both species (Tables 1, 2).

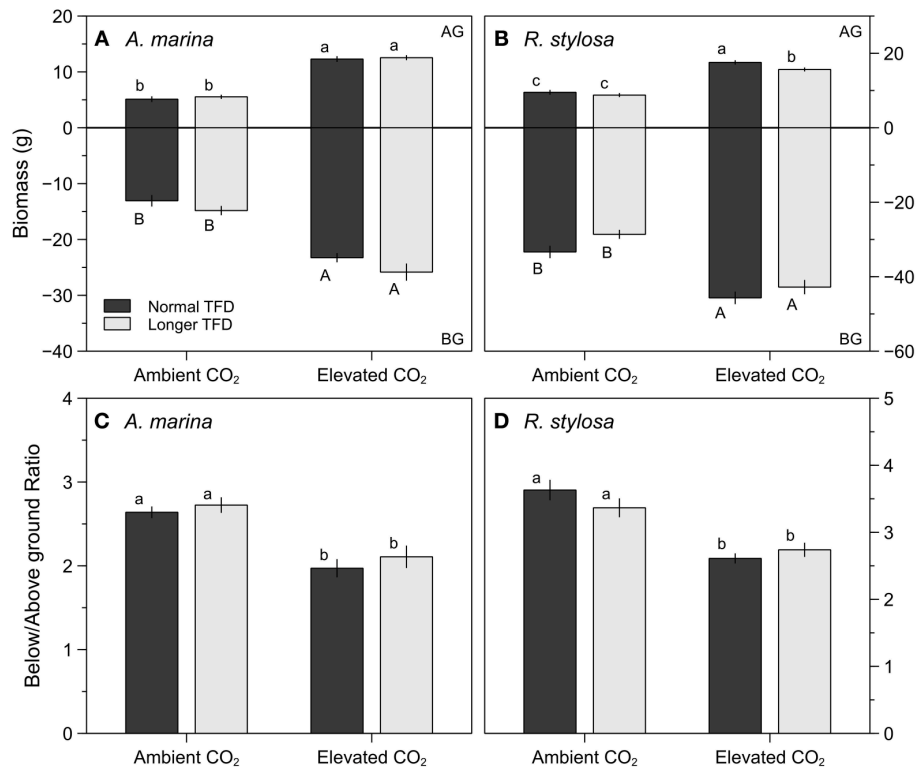


FIGURE 3 | Final above ground (AG) and below ground (BG) biomass (g), and below/above ground biomass ratios of *A. marina* (A,C) and *R. stylosa* (B,D) grown in ambient or elevated CO₂, and under normal (dark-gray bars) and longer TFD (gray bars), for 12 months. Values are means ± SEM (n = 30). Different letters indicate significant differences (p < 0.05).

TABLE 2 | C:N ratios in leaves, stems and roots of *A. marina* and *R. stylosa* grown in ambient and elevated CO₂, and under natural (N) and longer (L) TFD, for 12 months.

| C:N | Ambient CO ₂ (400 ppm) | | Elevated CO ₂ (800 ppm) | |
|----------------------------------|-----------------------------------|---------------|------------------------------------|----------------|
| | N TFD | L TFD | N TFD | L TFD |
| <i>Avicennia marina</i> | | | | |
| Leaves | 36.53 ± 1.89 | 35.41 ± 2.05 | 41.30 ± 1.02 | 42.18 ± 0.33 |
| Stems | 76.10 ± 0.30 | 71.27 ± 0.42 | 72.45 ± 2.13 | 62.02 ± 2.12 |
| Roots | 52.56 ± 0.39 | 53.20 ± 0.75 | 61.22 ± 0.87 | 57.14 ± 1.48 |
| <i>Rhizophora stylosa</i> | | | | |
| Leaves | 61.75 ± 0.56 | 69.94 ± 1.05 | 70.06 ± 0.92 | 69.47 ± 1.76 |
| Stems | 132.20 ± 0.39 | 119.26 ± 2.84 | 172.26 ± 7.47 | 167.61 ± 2.06 |
| Roots | 101.57 ± 2.06 | 100.02 ± 4.20 | 159.64 ± 3.39 | 154.80 ± 10.58 |

Values are means ± SEM. (n = 3).

DISCUSSION

Elevated CO₂ Will Enhance Mangrove Productivity, Carbon Storage, and Seedlings Establishment

Our results clearly confirmed that rise in atmospheric CO₂ concentrations would affect the growth of mangrove seedlings. In this experiment, doubling CO₂ concentrations for one year

resulted in an increase of RGR of more than 89 and 47% for *A. marina* and *R. stylosa*, respectively. These strong raises in RGR may be partly related to an increase in the photosynthetic activity of both species under elevated CO₂ concentrations. Indeed, the present study was performed concomitantly with another one that focused on the photosynthetic response of the seedlings (Jacotot et al., 2018), and both were conducted during the same time period and on the same seedlings. In this related study, we observed that CO₂ enrichment enhanced the mean photosynthetic response of both species (Jacotot et al., 2018). However, a 89% increase in RGR for *A. marina* and 47% for *R. stylosa* was surprising as it was much higher than the increase of photosynthesis that rose by more than 37% for *A. marina* (from 6.25 ± 2.24 to 10.52 ± 3.24 μmol m⁻² s⁻¹) and by more than 45% for *R. stylosa* (from 6.247 ± 1.63 to 11.35 ± 2.91 μmol m⁻² s⁻¹). In fact, Kirschbaum (2011) reported a RGR augmentation of 10% for a 30% increase in photosynthesis, which is a reverse ratio in comparison to our study and we should have expected a lower increase in RGR, but no clear explanation was found to clarify this result. However, Kirschbaum (2011) suggested that excess carbohydrates produced by the enhancement of photosynthesis might not be converted into plant tissues due to other resource limitations. In this case, carbohydrates may accumulate in leaves as sugars and starches, resulting in an increase in the leaf mass area ratio (Poorter and Navas, 2003). In fact, a decrease in the leaf mass per area was observed for both species under elevated CO₂

concentrations (Jacotot et al., 2018), by more than 33 and 21% for *A. marina* and *R. stylosa*, respectively (Figures 5C,D). This development of seedlings leaves suggests that they have not been affected by nutrient limitations during the experiment, which have been sufficiently provided by the frequent water renewal that was operated in the greenhouses.

RGRs were higher during the last 180 days of the experiment than during the first 180 days (Figure 2), i.e., during the warm season rather than during the cool season. Inside the greenhouses, the mean monthly temperature raised from 22.3 to 26.7°C during the warm season. This raise in temperature is thought to be responsible for the increase in productivity of both species. In fact, photosynthetic activity of *A. marina* and *R. stylosa* under elevated CO₂ increased by 40 and 45% during the warm season, whereas it was only enhanced by 32 and 38%, respectively, during the cool season (Figure 4) (Jacotot et al., 2018), which confirms our hypothesis. Photosynthesis of tropical C3 species, such as *A. marina* and *R. stylosa*, can operate between 15 and 45°C, however, there is a temperature optimum for which photosynthesis is maximal. Gilman et al. (2008) reported a temperature optimum for photosynthesis of 28–32°C for mangroves species, but lower temperatures were reported for specific species, such as 24.5°C for *Avicennia germinans* (Reef et al., 2016), or 26.8°C for *A. marina* in New Caledonia (Leopold et al., 2016). The temperature reached during the warm season in our study was closer to the temperature optimum for photosynthesis than the one reached during the cold season, therefore, we suggested that seasonal variations in temperature drove the RGRs throughout the year of experiment. With future climate change, the global temperatures are expected to rise by 0.3–4.8°C (Stocker et al., 2013), and our results suggest that elevated CO₂ concentrations and increased temperatures could further promote productivity, and thus carbon storage, at least in biomass, of mangrove forests.

Elevated CO₂ reduced the below to above ground ratio due to a higher increase of the above ground biomass than of the below ground biomass (Figures 3C,D). This allocation of carbon under elevated CO₂ with more carbon invested in the above ground parts has previously been observed for *A. germinans* by Reef et al. (2016). This newly acquired carbon investment reveals a strategy of light capture and photosynthesis optimization that suggests a lack of limitations of the availability of soil resources. This result was consistent with our previous study (Jacotot et al., 2018), in which we observed, for both species, an increase in the specific leaf area with elevated CO₂ (Figure 5), which leads to a higher potential for light interception. Although more carbon was invested in above ground parts, a significant increase in the below ground biomass was also observed for both species (Figures 3A,B). This result may lead to several beneficial implications in the response of mangroves ecosystems to climate change: (i) the soil carbon storage potential of the ecosystem may increase, (ii) the increase in root development may facilitate seedlings establishment in intertidal sediments (Balke et al., 2011), which could in turn promote ecosystem expansion, and (iii) the capacity of mangrove ecosystems to face sea-level rise could be improved, as higher root density will increase soil volume and soil organic matter content, two important factors contributing to the vertical accretion of

mangrove soils (Cahoon et al., 2006; McKee et al., 2007; McKee, 2011; Krauss et al., 2014, 2017).

In addition to increases in growth and biomass, we also observed a significant change in plant composition, and notably an increase in the C:N ratios in roots and leaves of *A. marina* and in stems and roots of *R. stylosa* under elevated CO₂ (Tables 1, 2). The effects of elevated CO₂ on C:N ratios have been extensively examined in natural ecosystems, however, the available literature shows contrasting results (e.g., Gifford et al., 2000; Luo et al., 2006). C:N ratios may increase, decrease or be unaffected under elevated CO₂ but, in general, a 15% of increase is observed (Gifford et al., 2000). In our study, the increase in C:N ratios was mainly due to a decrease in nitrogen content (N) in plant tissues. Such a decrease of N with elevated CO₂ has often been observed in terrestrial plants (Cotrufo et al., 1998; Yin, 2002; Ainsworth and Long, 2005; de Graaff et al., 2006), including mangroves (McKee and Rooth, 2008), but remains poorly understood (Taub and Wang, 2008; Lotfiomran et al., 2016). Some authors have shown a general decrease in the specific N uptake rates by the roots under elevated CO₂ (McDonald et al., 2002; Taub and Wang, 2008; Lotfiomran et al., 2016). These authors have suggested that this decrease results from both a decrease in N demand by shoots and from a reduction of the soil-root system ability to supply N. They also suggested that the best-supported mechanism for decreased N supply is a decrease in transpiration-driven mass flow of N in soils due to decreased stomatal conductance at elevated CO₂. In fact, such a decrease in stomatal conductance has effectively been observed for *A. marina* and *R. stylosa* grown under elevated CO₂ (Jacotot et al., 2018), which adds to this last hypothesis. Higher C:N ratios may have an important implication, as it may be negatively correlated with lower rates of organic matter decomposition in soils (Hättenschwiler and Gasser, 2005; Zhang et al., 2008; Zimmermann et al., 2009; Jacob et al., 2010), which may lead to a reduction in the greenhouse gas production, and, in turn, to a higher carbon storage capacity. However, this reasoning must be nuanced considering that OM quality is not the only driver of GHG production and emissions in mangrove soils, other parameters influence these biogeochemical processes and will also vary with climate changes and must be taken into account. For example, the increase in soil organic matter decomposition rates with increasing temperature has been widely described in the literature for different ecosystems (Segers, 1998; Fang and Moncrieff, 2001; Fierer et al., 2005; Davidson and Janssens, 2006; Conant et al., 2011; Inglett et al., 2012), including mangroves (Mackey and Smail, 1996; Barroso Matos et al., 2012). Conversely, the increase in tidal flooding duration may lead to a lower renewable of the electron acceptors pool within the soil and to a more anoxic environment, which may limit the organic matter decomposition processes.

Contrasting Effects of the Increase in Tidal Flooding Duration Between *A. marina* and *R. stylosa*

According to our initial hypothesis, growth and biomass of *R. stylosa* were reduced under longer tidal flooding duration (Figures 2B,D, 3B) although this effect was not significant

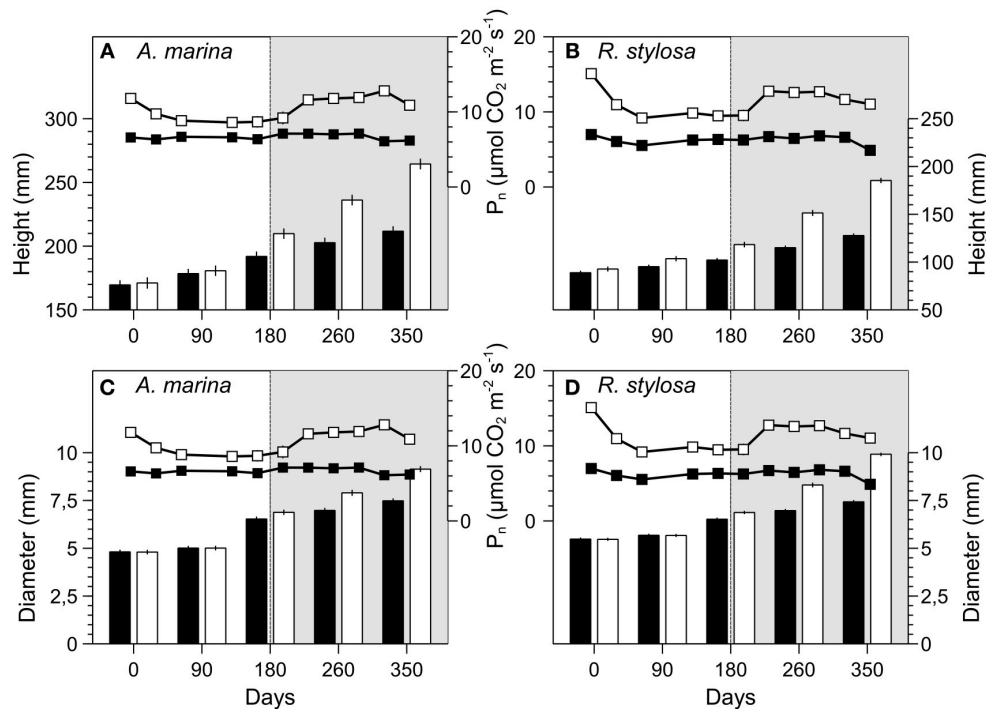
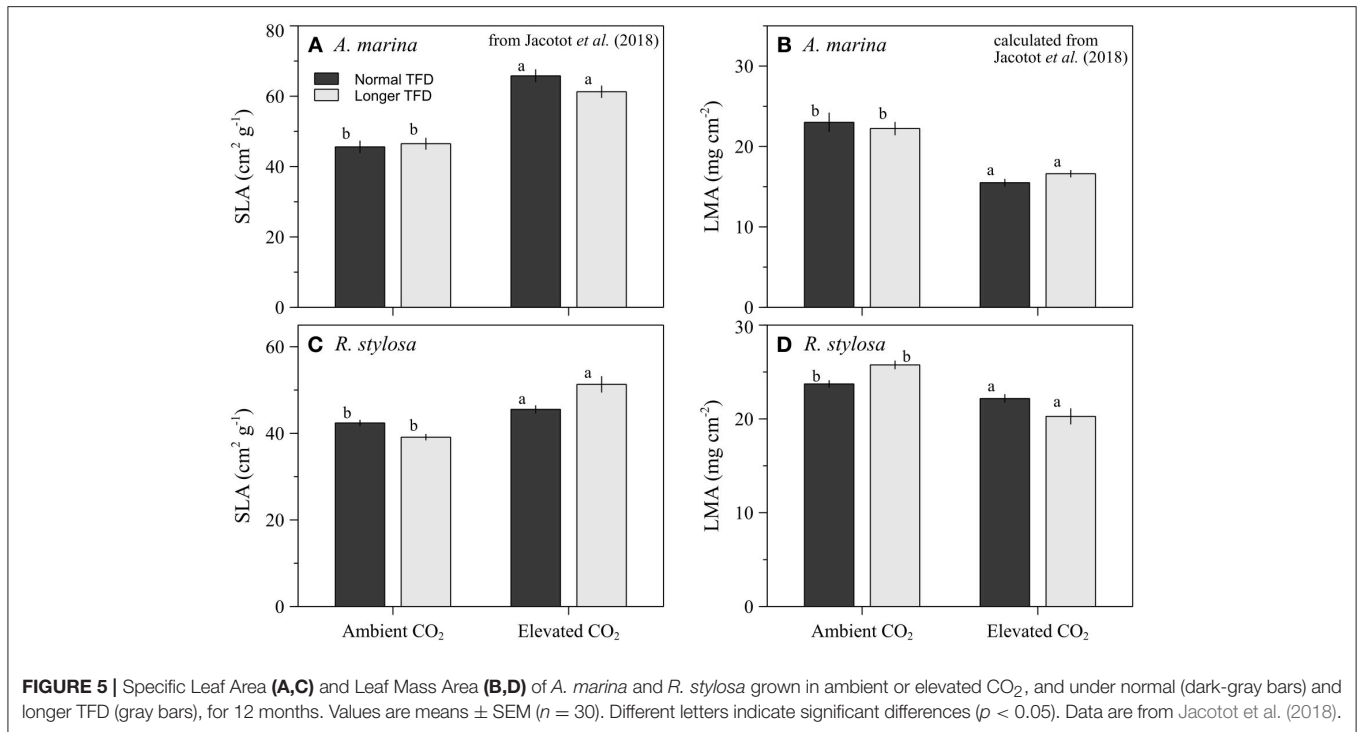


FIGURE 4 | Heights (mm), diameters (mm) and photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of *A. marina* (A,C) and *R. stylosa* (B,D) grown in ambient (black bars and markers) or elevated CO_2 (white bars and markers) for 12 months. Values are means \pm SEM (Heights and diameters: *A. marina* $n=125$; *R. stylosa* $n=180$; photosynthesis: $n=30$). The white and shaded area correspond respectively to the cool and the warm seasons. Photosynthesis data are from Jacotot et al. (2018).

(Table 1). Under longer TFD, basal diameters decreased by 13 and by 5%, and seedlings heights decreased by 6 and 11% for ambient and elevated CO_2 , respectively. Consequently, final biomass of *R. stylosa* was reduced by 11 and 4% for ambient and elevated CO_2 , respectively, in comparison to the controlled TFD treatment. Although we agree that the effect of longer TFD was not significant, we suggest that the reduction in the seedlings growth should not be ignored. We also suggest that the lack of significance in the present work may be due to the limited duration of the experiment and that a longer study could highlight a significant effect of increased TFD on mangrove seedlings. This result may be explained by the 3% reduction in photosynthesis that we observed for *R. stylosa* seedlings growing under longer tidal duration (Jacotot et al., 2018). However, this slight decrease might be related to other factors. For instance, longer tidal flooding will have probably induced a deficit in oxygen in the soil due to roots and micro-organisms respiration, as well as a reduction of air penetration in the soil from the atmosphere (Naidoo et al., 1997). Although no oxygen measurements have been performed in our experiment, we can expect such a decrease after the longer tidal flooding applied, as it was previously reported in similar experiments (Hovenden et al., 1995; Skelton and Allaway, 1996). In anoxic mangrove sediments, rich in organic matter and in sulfates brought at each tide, organic matter may be oxidized through sulfate reducing processes, leading to sulfide production (Kristensen et al., 2008; Balk et al., 2016). Sulfide compounds, including H_2S , are highly toxic to plants (Lamers et al., 2013), and inhibit the growth of

mangrove seedlings (Holguin et al., 2001; Lyimo and Mushi, 2005; Reef et al., 2010). The presence of sulfide in the longer TFD treatment was assumed due to the dark color of the sediment and because of the strong rotten egg odor typical of H_2S , therefore, we suggest that sulfides were possibly responsible for the seedlings growth inhibition.

In contrast to *R. stylosa*, final biomass of *A. marina* increased with longer TFD by 11 and 8% under ambient and elevated CO_2 concentrations, respectively (Figures 2A,C, 3A). Natural TFD were based on our field observations and measurements (unpublished data) and were therefore representative of the natural conditions, in which both species develop along the intertidal gradient in New Caledonia, with *A. marina* growing at a higher elevation than *R. stylosa*. This position in the intertidal area, combined to the semi-arid climate of New Caledonia, implies *A. marina* suffer from elevated salt concentrations due to high evaporation processes, low freshwater inputs either by rains or river discharges and low frequency of tidal submersions (Marchand et al., 2011a, 2012). We suggest that longer tidal flooding in our experiment increased water availability that in turn decreased soil salinity, which are two stressing factors affecting growth and biomass, and therefore promoted the growth of *A. marina* seedlings. With climate changes, due to its positive response to both longer TFD to elevated CO_2 concentrations, we can expect that colonization abilities and productivity of *A. marina* seedlings will be enhanced in the future in this context of a semi-arid climate, where *A. marina* develops behind *Rhizophora* spp.



Eventually, to fully understand the response of *A. marina* and *R. stylosa* to future climate changes, other parameters should be taken into account such as competition between species (McKee and Rooth, 2008). In New Caledonia, the mangrove ecotone is composed of a succession of different mangrove species, including a saltmarsh C4 grass, *Sarcocornia quinqueflora*, which competes for suitable spaces for expansion, and future climate may change their specific distribution.

CONCLUSION

Our results suggest that future climate changes, and specifically the increase in atmospheric CO₂ concentrations and tidal flooding duration, will affect *A. marina* and *R. stylosa* seedlings physiology. Elevated CO₂ concentrations enhanced growth and biomass, with an increase of the relative growth rates of 89% for *A. marina* and of 47% for *R. stylosa*, for a 100% increase of atmospheric CO₂ concentrations. These results are suggested to be related to photosynthesis enhancement, measured for the same seedlings in a previous study. Elevated CO₂ concentrations also increased below-ground biomass, which can lead to soil vertical accretion, thus helping mangroves to face sea-level rise. The increase in below-ground biomass could also favor seedling establishment and mangrove colonization of new available spaces resulting from sea-level rise. Future increase in surface temperature will further stimulate trees development, as seasons affected seedlings productivity with higher relative growth rates during the warmer period. Additionally, C:N ratios of seedlings tissues were increased under elevated CO₂, which may lower organic matter degradation in mangrove soils, and thus reduce greenhouse gas emissions while increasing carbon sequestration.

When increasing tidal flooding duration, the growth of *R. stylosa* was slightly reduced, but this effect did not significantly affect the initial enhancement of growth and biomass resulting from elevated CO₂ concentrations. Conversely, growth of *A. marina* was further enhanced by 8% under longer tidal flooding duration in comparison to the control treatment. This result suggests that this species develops in a constraining position along the intertidal gradient in New Caledonia, probably suffering from the lack of water and from high salt concentrations in the soil pore waters. Therefore, the future rise in mean sea level will promote the development of *A. marina* by a favorable modification of the conditions in the intertidal area under semi-arid climate, which will also affect the recruitment of seedlings and the expansion of mangroves. This study provides complementary information about the productivity of mangrove seedlings with future climate changes. We now suggest that research efforts focus on the impact of climate change on the mineralization processes in mangrove soils to better understand the role of mangroves in climate change mitigation.

AUTHOR CONTRIBUTIONS

CM, AJ, and MA performed the experimental design. AJ performed data collection and statistical analyses. AJ and CM performed the data interpretation. AJ, CM, and MA wrote the paper.

ACKNOWLEDGMENTS

This study was funded by the Province Sud of New Caledonia, the City of Mont Dore, KNS Koniambo Nickel SAS and

Vale NC. We are very grateful to the IFRECOR Committee for having attributed to this study the IFRECOR Palme National Distinction. We thank Eric Gay, the mayor of the city of Mont-Dore, for his continuous support during the

study. We also thank Jacky Mermoud and Diana Burns for their help in managing the facilities. Eventually, we are thankful to Tracy Rolland and Inès Gayral for their help in fieldwork.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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