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ORIGINAL ARTICLE

Effects of elevated atmospheric CO_2 and increased tidal flooding on leaf gas-exchange parameters of two common mangrove species: *Avicennia marina* and *Rhizophora stylosa*

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Abstract
In this study, we examined interactive effects of elevated atmospheric CO_2, concentrations, and increased tidal flooding on two mangroves species, Avicennia marina and Rhizophora stylosa. Leaf gas-exchange parameters (photosynthesis, transpiration rates, water-use efficiency, stomatal conductance, and dark respiration rates) were measured monthly on more than 1000 two-year-old seedlings grown in greenhouses for 1 year. In addition, stomatal density and light curve responses were determined at the end of the experiment. Under elevated CO_2 concentrations (800 ppm), the net photosynthetic rates were enhanced by more than 37% for A. marina and 45% for R. stylosa. This effect was more pronounced during the warm season, suggesting that an increase in global temperatures would further enhance the photosynthetic response of the considered species. Transpiration rates decreased by more than 15 and 8% for *A. marina* and *R. stylosa*, respectively. Consequently, water-use efficiency increased by 76% and 98% for *A. marina* and *R. stylosa*, respectively, for both species, which will improve drought resistance. These responses to elevated CO_2 were minimized (by 5%) with longer flooding duration. Consequently, future increases of atmospheric CO_2 may have a strong and positive effect on juveniles of *A. marina* and *R. stylosa* during the next century, which may not be suppressed by the augmentation of tidal flooding duration induced by sea-level rise. It is possible that this effect will enhance seedling dynamic by increasing photosynthesis, and therefore will facilitate their settlements in new area, extending the role of mangrove ecosystems in carbon sequestration and climate change mitigation.

Keywords Mangrove · CO_2 enrichment · Photosynthetic activity · Stomatal density · Climate change · Sea-level rise

Introduction

Mangroves are considered to be major ecosystems involved in the carbon cycle along tropical and subtropical coastlines. Due to their high ability to fix and store CO_2 (Donato et al. 2011; Alongi 2014), they are among the most efficient blue carbon sinks (Kauffman et al. 2011). Besides providing many ecosystem services (Lee et al. 2014), mangroves are characterized by a limited number of plant species because of a stressful environment (e.g., salinity, anoxia, soil instability). In addition, future climate change could affect the functioning of mangrove ecosystems, such as their productivity and carbon sequestration capacities, or even their ability to conquer new available spaces. Sea-level rise will probably induce an even more stressful environment for mangrove plants, while temperature and atmospheric CO_2 increases would favor their growth.

Atmospheric CO_2 concentrations have been rising continuously from 280 ppm at the preindustrial age to more than 400 ppm currently (Betts et al. 2016). By the end of the twenty-first century, atmospheric CO_2 concentrations could range from 794 to 1150 ppm, with the uncertainty depending on which model is consulted (Collins et al. 2014). The effects of elevated atmospheric CO_2 concentrations on temperate plant species are well documented, usually an enhancement of photosynthesis and water-use efficiency is observed (Urban 2003; Karnosky 2003; Ainsworth and Long 2005). Photosynthesis responses of tropical plants, especially mangroves, are less well studied, although stimulation

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of photosynthesis and net primary productivity has been reported (Farnsworth et al. 1996; Reef et al. 2015).

Climate change is not a single parameter but a combination of numerous ones, which may have opposing effects on mangrove plants. Sea-level rise is considered to be the major climate change threat to mangrove ecosystems because of their development in the intertidal areas (Ellison 2015). Global mean sea level increased over recent decades and is predicted to increase from 0.26 to 0.98 m by 2100 (Church et al. 2013). All mangroves may not be able to keep pace with sea level and will have to migrate landward to maintain their preferred hydroperiod (Gilman et al. 2008). However, both natural and artificial barriers will strongly limit the inland migration of mangroves (Mcleod et al. 2011; Lovelock et al. 2015). If mangroves cannot migrate or keep pace with sea-level rise, they will be subjected to greater depth and duration of tidal flooding. When grown outside their optimum flood duration, mangrove trees respond by a decrease in photosynthetic activity and in net primary productivity (Krauss et al. 2008).

Major advances in the comprehension of the evolution of the ecosystem have been made recently by studying the effects of elevated atmospheric CO_2 in combination with other environmental parameters such as 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, although the interactive effect of elevated CO_2 and tidal flooding duration was tested on brackish marshes (Cherry et al. 2009), no study tested these effects on mangrove physiology and specifically on photosynthesis.

Within this context, the main objective of this study was to evaluate the long-term effects of elevated CO_2 and tidal flooding duration on the leaf gas-exchange parameters (assimilation, transpiration, dark respiration, stomatal conductance, water-use efficiency) of seedlings of *Avicennia marina* and *Rhizophora stylosa*, the most widespread mangrove species throughout the Indo-Pacific region (Buchmann et al. 2008; Ellison et al. 2008). We were also interested in the seasonal variations of leaf net photosynthetic rates. Our main hypotheses were (i) atmospheric CO_2 enrichment will lead to a stimulation of photosynthetic activity, (ii) tidal flooding duration will reduce the photosynthesis response due to waterlogging stress. To reach our goals, we used a closed chamber experiment, where more than 1000 two-year-old mangrove seedlings were grown at two CO_2 concentrations (400 vs. 800 ppm), over two semi-diurnal tidal flooding durations (3h15 vs. 4h45 for *A. marina*, 6h00 vs. 7h45 for *R. stylosa*), during one complete year. Leaf gas-exchange parameters were measured monthly during the whole year of experiment, and chlorophyll fluorescence was determined only for the last 6 months. Light curve responses, stomatal density, and specific leaf area were assessed at the end of the experiment.

Materials and methods

Description of the facility

The experiment was conducted in the City of Mont-Dore in New Caledonia (22°13′49″S, 166°31′09″E) from June 2016 to May 2017. The facility consists of three semi-open greenhouses of 72 m^2 each (12 m × 6 m, 6 m height). Inside each greenhouse, a circular closed chamber of 36 m^2 (2.4 m height) was built to maintain elevated atmospheric CO_2 concentrations. The atmospheric CO_2 concentrations in each of the three closed chambers were continuously monitored during the experiment using CO_2 probes connected to a CO_2 central unit, which controlled the entire system (MAXICLIM NG 08/3Z, Anjou Automation). Pure CO_2 gas was supplied from 5:00 a.m. to 7:00 p.m. at the top of the chambers by brief pulses from a high-pressure cylinder.

HOBO temperature and humidity sensors (Onset, Cape Cod, Massachusetts, USA) were installed inside the greenhouse and the closed chamber. Air temperature and humidity were recorded every 5 min. Temperature and humidity were allowed to fluctuate naturally inside the greenhouses, however, air cooling units were installed in the closed chambers to prevent high variations of temperatures. Mean temperatures and relative humidity for the experiment period are given in Table 1.

Mangrove seedlings were placed on custom-built tidal tables, each working individually. Each tidal table included a 700-l polypropylene tank (1 m^2 area over 0.7 m height), surmounted by a 300-l planting tray (1 m^2 area over 0.3 m

Table 1 Mean annual and seasonal temperatures (°C) and relative humidity (%) ± standard deviations (SD) inside the greenhouses and the closed chambers

Parameters (means ± SD)	Annual	Cool season (June–November)	Warm season (December–May)
Greenhouse temperature (°C)	25.1 ± 2.9	23.1 ± 2.6	26.4 ± 3.2
Chamber temperature (°C)	25.0 ± 3.3	22.3 ± 3.0	26.7 ± 3.5
Greenhouse relative humidity (%)	82.6 ± 13.6	85.8 ± 12.6	80.7 ± 14.2
Chamber relative humidity (%)	79.9 ± 12.6	78.4 ± 12.2	80.8 ± 12.8

height). Fresh seawater was pumped from the adjacent lagoon (20 m) and stored in the tanks, which was replaced twice a month during the entire study. To simulate high tide periods, an aquarium pump, placed in each tank, sent the water to the planting tray. A siphon pipe allowed the planting tray to completely drain the water back to the reserve to reproduce low tide periods. To control the tidal treatment attributed to each tank, the aquarium pumps were connected to three custom-built current controllers (one per greenhouse). Controllers were constructed from Arduino open source plans available for free under public licenses and were programed according to the needs of the experiment. Water quality (pH, salinity, DO) in the reservoir was checked periodically using YSI probes.

Plant material

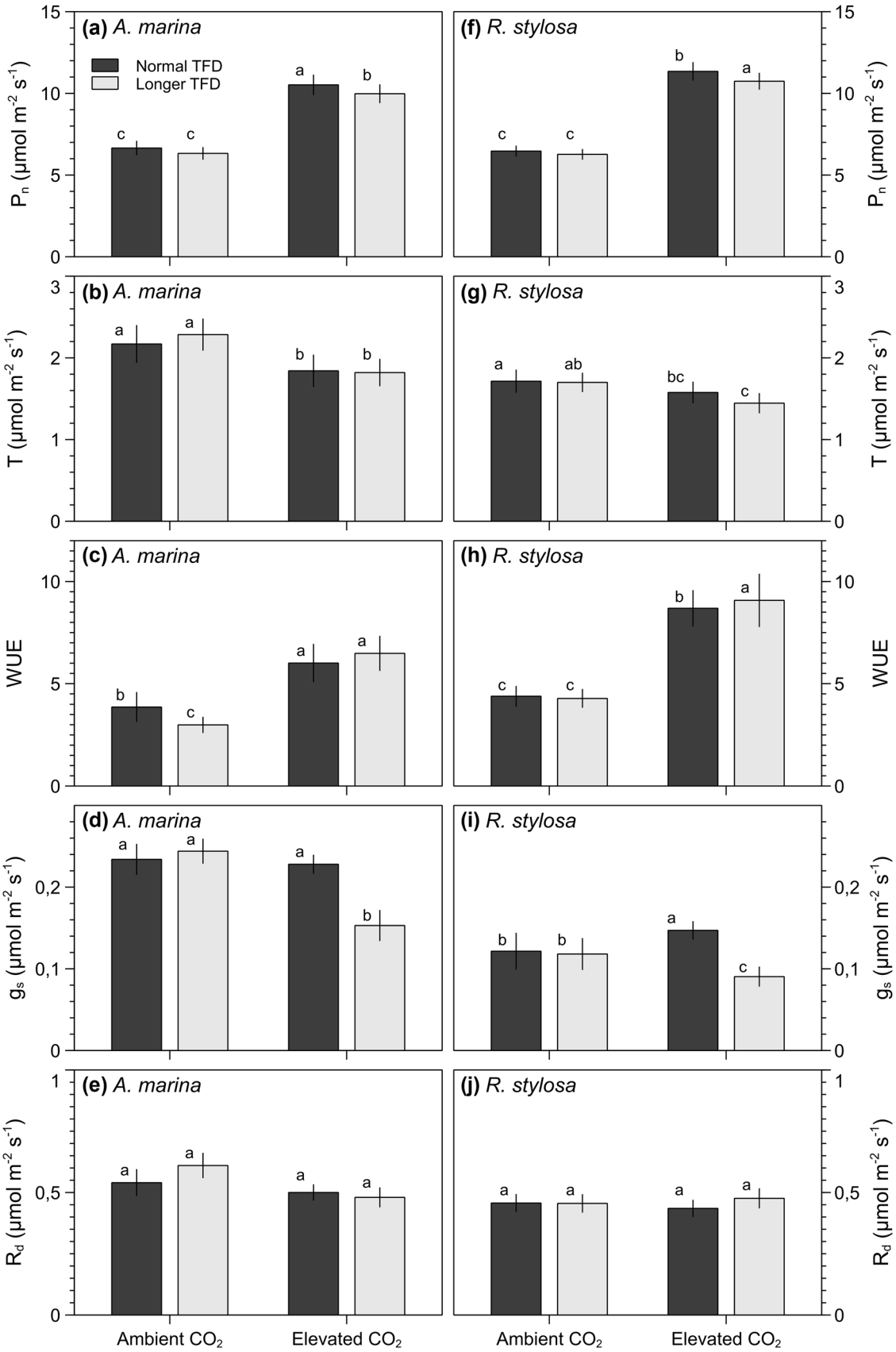
Mature propagules of *Avicennia marina* and *Rhizophora stylosa* were collected from the natural mangrove of Oundjo, in New Caledonia (21°4′8″S, 164°42′51″E). The propagules were collected from multiple trees, between February and March 2014, during the optimum fruiting period. They were then planted in 2.5-l polyethylene bags in a 1:1 hand mixed mangrove peat and sand. During the 2 years preceding the experiment, the seedling mortality was high, resulting in a different number of seedlings used for the experiment. This high mortality may be explained by a lack of water during the first stages of development of the juveniles. Indeed, the semi-arid climate of New Caledonia induces a stressful and constraining environment for the development of juveniles due to high heat and reduced rainfalls. After their installation within the greenhouses, the tidal system was fully operational and was maintained until the end of the experiment. A total of 720 and 400 two-year-old *R. stylosa* and *A. marina*, respectively, were followed for this study. During the year of experiment, the mortality dropped to less than 1%. Prior to the experiment, mean heights were 172.4 ± 40.17 and 90.91 ± 23.33 mm, and mean basal diameters 4.81 ± 0.98 mm and 5.54 ± 0.65 mm for *A. marina* and *R. stylosa*, respectively. For all seedlings, 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.

Experimental design

The experiment was setup as a split-plot design with CO_2 atmospheric concentrations as the whole-plot (Ambient, 400 ppm vs. Elevated, 800 ppm) and tidal flooding duration (TFD) as the split-plot nested within CO_2 (Natural vs Longer). Elevated atmospheric CO_2 concentrations were maintained between 780 and 820 ppm CO_2. CO_2 concentrations were periodically checked using two different portable infra-red CO_2 analyzers (a G2131-*i* CRDS analyzer from Picarro Inc., Santa Clara, USA; and a Li-8100A from LI-COR Biosciences, Lincoln, USA). Natural TFD were setup according to the average flooding duration observed in New Caledonian mangroves for both species (unpublished data). These tidal duration 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 ecosystem: *Rhizophora* spp. colonizes the seaward side, while *Avicennia marina* develops at higher elevations. Previous studies suggested that the main factor controlling the distribution of mangrove species in New Caledonia was soil salinity, which in turn was controlled by the duration of tidal inundation and thus by the soil elevation (Marchand et al. 2011, 2012). As a result, the flooding duration for *Rhizophora* trees is higher than for *Avicennia*. Consequently, in the experiment, natural TFD was 3h15 for *A. marina* and 6h00 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 8h30 and 5h45 for *A. marina* and *R. stylosa*, respectively.

We hypothesized that an increase in mean sea level will similarly affect the flooding duration of both species; thus, in the experiment, longer TFD was simulated by increasing the natural times by 1h45, which corresponds to a high tide of 5h00 and 7h45 for *A. marina* and *R. stylosa*, respectively. Consequently, low tides periods were reduced to 6h45 and 4h00 for *A. marina* and *R. stylosa*, respectively. This increase in flooding duration has been randomly defined but, however, remains realistic given the expected sea-level rise at the end of the century. Although we chose 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 within the natural system. Nevertheless, an increase of 1h45 of tidal duration will have different implication 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 submerge the root system.

The mangrove seedlings were allocated randomly 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. 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 CO_2 treatment. During the experiment, the mangrove seedlings were regularly rotated within each


(a) A. marina
Normal TFD
Longer TFD
(f) R. stylosa
Pn (µmol m-2 s-1)
(b) A. marina
(g) R. stylosa
T (µmol m-2 s-1)
(c) A. marina
(h) R. stylosa
WUE
(d) A. marina
(i) R. stylosa
gs (µmol m-2 s-1)
(e) A. marina
(j) R. stylosa
Rd (µmol m-2 s-1)
Ambient CO2
Elevated CO2

◂**Fig. 1** Mean values ± SEM ($n = 360$) of leaf gas-exchange parameters for *A. marina* and *R. stylosa* grown in ambient (400 ppm) or elevated (800 ppm) CO_2, and under normal (dark-gray bars) and longer TFD (gray bars), for 12 months. **a, f** photosynthetic rates (μmol m^{-2} s^{-1}), **b, g** transpiration rates (μmol m^{-2} s^{-1}), **c, h** water-use efficiency, **d, i** stomatal conductance (μmol m^{-2} s^{-1}), and **e, j** dark respiration rates (μmol m^{-2} s^{-1}). Analyses were realized between species by an ANOVA. Different letters indicate significant differences ($p < 0.05$)

tidal table and were rotated three times between the greenhouses to minimize the greenhouse effect.

Leaf gas-exchange measurements

Gas-exchange parameters were performed during low tides using a semi-open gas-exchange analyzer (CO-650, Qubit Systems, Canada). In this system, CO_2 is pulled from ambient air, which serves as a baseline for measurements. Prior to each measuring periods, air samples with either 400 or 800 ppm of CO_2 at 15–20% of relative humidity (RH) were prepared. These air samples were then stored in specific gas plastic bags (from Qubit Systems) and maintained at a temperature of ~ 25 °C. They were then connected to the inlet of the CO-650, which allowed to have a similar air baseline all along the year of measurements. Assimilation (P_n) and transpiration (T) rates, as well as the stomatal conductance (g_s), were determined every month from June 2016 to May 2017. Measurements were performed in the morning (8:00–12:00 a.m.), on 30 different fully expanded leaves for the two species and the four treatments with a Photosynthetic Photon Flux Density (PPFD) of 1200 μmol m^{-2} s^{-1}. The instantaneous water-use efficiency (WUE) was then calculated as $WUE = P_n/T$. Dark respiration (D_r) measurements were made at night (8:00–10:00 p.m.) on three different seedlings for each species and treatment. No dark respiration measurements were made in July and September 2016.

Light curve responses ($P_n/PPFD$ curves) were generated at the end of the experiment on three leaves per species and per treatment. Eight PPFD intensities of 1200, 800, 400, 200, 100, 50, 25, and 0 μmol m^{-2} s^{-1} were chosen. Transitions between PPFD levels were made once photosynthesis was stable and lasted between 4 and 10 min. CO_2 concentrations were maintained at 400 ppm or 800 ppm, depending of the CO_2 treatment, with a relative humidity ranging from 15 to 20%. Air temperature was maintained to 25 °C. Curve fitting was resolved using the solver function of *Microsoft Excel* (Lobo et al. 2013, 2014), and the best fitting was chosen according to the lower sum of the squares of the errors. The model, which best fitted with our data, was the rectangular hyperbola Michaelis–Menten based model (Kaipiainen 2009).

Specific leaf area

At the end of the experiment, 30 mature and fully expanded leaves per species and treatment were scanned and analyzed for leaf area (SLA) using ImageJ (Schneider et al. 2012). Then, all leaves were dried at 60 °C for 72 h before being weighed for dry mass (g). SLA (cm^2 g^{-1}) was calculated as the ratio of leaf area to the corresponding leaf dried mass.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence was measured using a portable chlorophyll fluorometer (FluorPen FP 100, Photon Systems Instruments, Czech Republic). The maximum quantum efficiency of PSII photochemistry (F_v/F_m) was measured on the abaxial leaf surface at night from 8:00 p.m. to 10:00 p.m., using a PPFD of 3000 μmol m^{-2} s^{-1} as saturating flash for a duration of 1 s. Measurements were done only for the warm season, from November 2016 to May 2017 on 30 young fully expanded leaves of both species and each of the four treatments.

Stomatal density

Five fully expanded leaves for each species and treatment were randomly collected to determine the stomatal density. For *A. marina*, because of a dense layer of trichomes obscuring stomata, the leaves were macerated in a 5:1 solution of hydrogen peroxide and glacial acetic acid for 1 h at 70 °C. Then, the abaxial epidermis was peeled and stained with Safranin O. The number of stomata was counted from the interior surface of the epidermis (Nguyen et al. 2015). For *R. stylosa*, nail varnish imprints of the abaxial side of the leaves were taken. The number of stomata was then counted under a light microscope (Leica DM500B, Leica Microsystems, Wetzlar, Germany) on three fields of view per leaf at a ×200 magnification.

Statistical analysis

Normality and equality of variance were analyzed using Shapiro and Levene tests, respectively. Following results, a two-way analysis of variance (ANOVA), followed by a Tukey's HSD test was applied to identify significant differences ($p \leq 0.05$), between treatments of gas-exchange parameters, SLA, F_v/F_m, and stomatal density. In addition, significant differences between real and estimated values of dark respiration were analyzed using Student's t test after verification of normality and equality of variance using Shapiro and Fisher tests. Both species were

analyzed independently. All statistical analyses were performed using XLSTAT version 2016.3.

Results

Leaf gas-exchange response to elevated CO_2 and flooding

The results of leaf-gas exchanges for *A. marina* and *R. stylosa* are presented in Fig. 1. For *A. marina*, mean annual net photosynthesis rate (P_n) was significantly higher under elevated CO_2 than under ambient CO_2 concentrations (Table 2), either with normal or longer TFD. Within each CO_2 treatment, longer TFD slightly decreased P_n, however, this effect is only significant under elevated CO_2 (Fig. 1a; Table 2). Furthermore, transpiration rates (T_r) were significantly reduced under elevated CO_2 in comparison to the ambient CO_2 treatment (Fig. 1b; Table 2). Consequently, elevated CO_2 significantly increased water-use efficiency (WUE) for both TFD treatments. Under elevated CO_2, WUE was significantly lower with longer TFD than with normal TFD (Fig. 1c; Table 2). In addition, only the longer TFD treatment in combination with elevated CO_2 had a significant effect on stomatal conductance (g_s) with lower values than for the others treatments (Fig. 1d; Table 2). No significant differences (Table 2) were observed for dark respiration rates (R_d) with CO_2 or TDF treatments (Fig. 1e).

For *R. stylosa*, elevated CO_2 significantly increased P_n for both natural and longer TFD treatments (Fig. 1f; Table 2); however, longer TFD significantly reduced P_n only under elevated CO_2. Furthermore, within each TFD treatments, transpiration rates were significantly reduced under elevated CO_2, while within each CO_2 treatment, TFD had no significant effect (Fig. 1g; Table 2). As a result, WUE for *R. stylosa* was significantly higher for trees grown under elevated than under ambient CO_2 concentrations. In addition, longer TFD significantly increased WUE in trees grown under elevated CO_2 (Fig. 1h; Table 2). Stomatal conductance was significantly increased under elevated CO_2 and normal TFD, however, it was significantly reduced under elevated CO2 and longer TFD (Fig. 1i; Table 2). No significant differences (Table 2) were observed for dark respiration rates (R_d) between treatments (Fig. 1j).

Seasonal response of the net photosynthetic rates

Different seasonal responses of net photosynthetic rates were observed between the cool season and the warm season (Fig. 2). From June to November, mean temperature was 22.3 °C, whereas from November to May, it was 26.7 °C (Table 1). For *A. marina*, elevated CO_2 enhanced P_n by 32 and 33% for natural and longer TFD during the cool season, whereas during the warm season, P_n was enhanced by 40 and 39% for natural and longer TFD, respectively (Fig. 2a). For *R. stylosa*, a similar response as for *A. marina* was observed. During the cool season, an increase in P_n of 40 and 37% was observed for natural and longer TFD, whereas an increase of P_n of 45% was observed during the warm season, for both TFD treatments (Fig. 2b).

Specific leaf area after 12 months of enrichment

Specific leaf area (SLA) was significantly higher for both species under elevated CO_2, either with natural or longer TFD (Fig. 3a, b; Table 2). Within each CO_2 treatment, no significant effects of longer TFD on SLA were observed, either for *A. marina* and for *R. stylosa* (Fig. 3a, b; Table 2).

Net photosynthesis light curve responses (Pn/PPFD)

The net photosynthesis response to light was similar for both species (Fig. 4a, b). From 0 to 100 µmol photon m^{-2} s^{-1}, P_n showed no difference between all the four treatments either for *A. marina* or *R. stylosa*. For PPFD values higher than 100 µmol photon m^{-2} s^{-1}, both

Table 2 Significance values reported by two-way analysis of variance (ANOVA), followed by a Scheffe post hoc test or a Kruskal–Wallis test

	Avicennia marina			*Rhizophora stylosa*		
	CO_2	TFD	Interaction	CO_2	TFD	Interaction
P_n	667.70***	8.86**	0.55^{NS}	1401.48**	10.37***	2.63^{NS}
T_r	45.78***	0.718^{NS}	1.304^{NS}	28.33***	3.919*	2.511^{NS}
WUE	155.64***	0.76^{NS}	8.75**	285.17***	8.17**	10.63***
g_s	16.01***	7.46**	12.25***	0.001^{NS}	25.07***	19.54***
D_r	0.05^{NS}	0.01^{NS}	0.07^{NS}	1.77^{NS}	0.017^{NS}	0.241^{NS}
SLA	114.49***	1.260^{NS}	2.75^{NS}	51.61***	1.35^{NS}	18.00^{NS}
F_v/F_m	3.96*	9.26**	7.45**	25.04***	2.32^{NS}	4.50*
SD	94.97***	0.426^{NS}	0.05^{NS}	83.06***	0.535^{NS}	0.05^{NS}

NS non-significant

***, **, * indicates significant effects at $p < 0.001$, 0.01, and 0.05, respectively

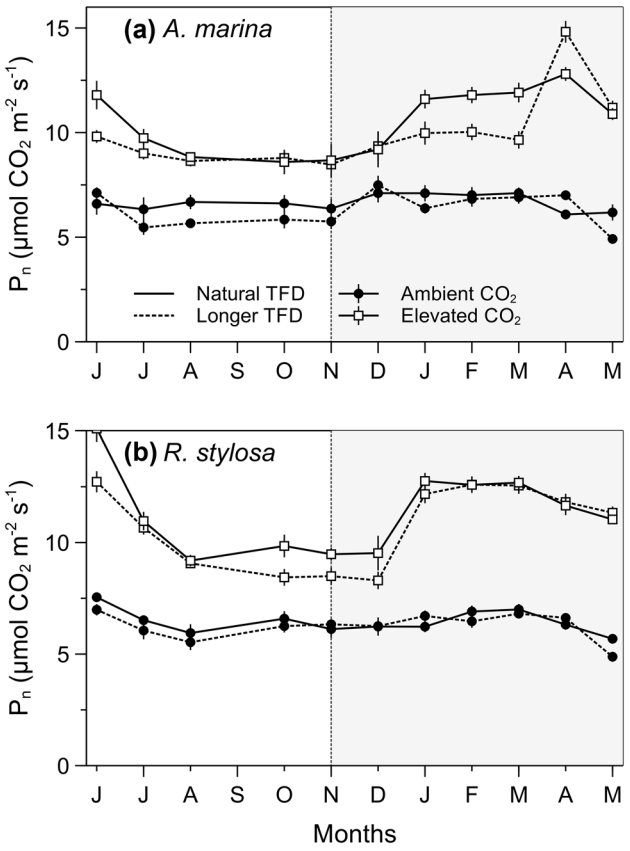


Fig. 2 Annual evolution (±SEM) of leaf net photosynthetic rates (P_n, μmol m^{-2} s^{-1}) for **a** *A. marina*, and **b** *R. stylosa*. Colored markers: ambient CO_2 concentrations, white markers: elevated CO_2 concentrations. Shaded area represents the warm season

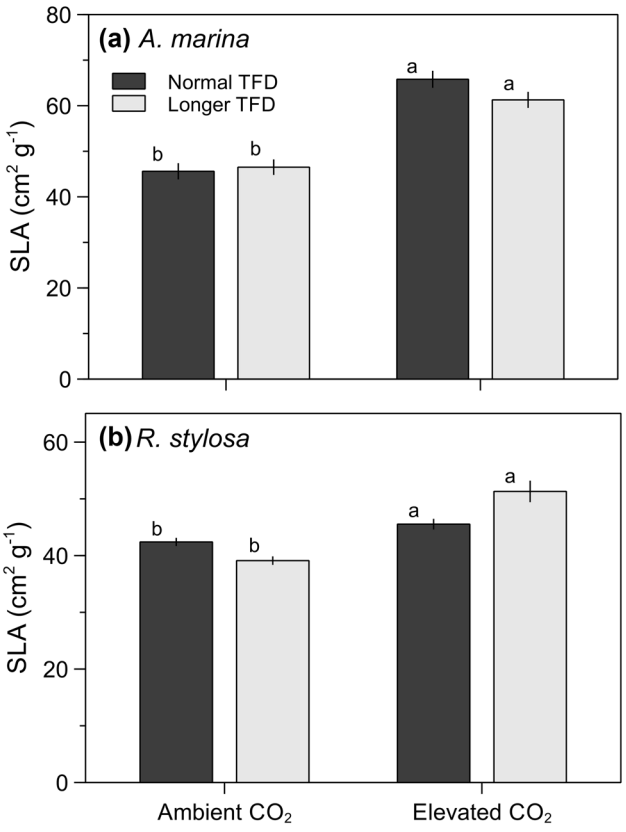


Fig. 3 SLA (cm^2 g^{-1}) of **a** *A. marina* and **b** *R. stylosa* grown in ambient or elevated CO_2, and under normal (dark-gray bars) and longer TFD (gray bars), for 12 months. Values are means ± SEM ($n = 30$). Different letters indicate significant differences ($p < 0.05$) after ANOVA analysis

A. marina and *R. stylosa* showed higher P_n values when growing under elevated than under ambient CO_2 concentrations. When compared to natural TFD, longer TFD slightly reduced P_n under ambient CO_2 concentrations, whereas under elevated CO_2, P_n was higher from 100 to 800 μmol photon m^{-2} s^{-1}, but lower at 1200 μmol photon m^{-2} s^{-1}. Regarding the light saturation points, for *A. marina*, they were, under ambient CO_2 concentrations, 872 and 785 μmol photon m^{-2} s^{-1} for natural and longer TFD, respectively, whereas under elevated CO_2 concentrations, they were 1490 and 1224 μmol photon m^{-2} s^{-1}. For *R. stylosa*, the light saturation points were, under ambient CO_2 concentrations, 751 and 676 μmol photon m^{-2} s^{-1}, and under elevated CO_2 concentrations, 1591 and 1283 μmol photon m^{-2} s^{-1}, for natural and longer TFD, respectively. In addition, dark respiration estimated from the light curves was systematically higher from 5 to 20% than real values measured at night during the same period of the year (Table 3); however, these differences were not significant in both species and in any of the four treatments.

Maximum quantum efficiency of PSII photochemistry (F_v/F_m) during the warm season

For *A. marina*, mean values of F_v/F_m under ambient CO_2 concentrations were 0.79 ± 0.08 and 0.79 ± 0.06 for natural and longer TFD, respectively. Under elevated CO_2 concentrations, F_v/F_m had mean values of 0.78 ± 0.06 and 0.80 ± 0.05, for natural and longer TFD, respectively. For *R. stylosa*, mean values of F_v/F_m were, under ambient CO_2 concentrations, 0.81 ± 0.07 and 0.79 ± 0.07, and under elevated CO_2 concentrations 0.77 ± 0.09 and 0.78 ± 0.06, for natural and longer TFD, respectively. Statistical results are reported in Table 2.

Stomatal density

The results of stomatal density for *A. marina* and *R. stylosa* are presented in Fig. 5. For both species, stomatal density was significantly reduced under elevated CO_2 in comparison to ambient CO_2 concentrations, whereas within each CO_2

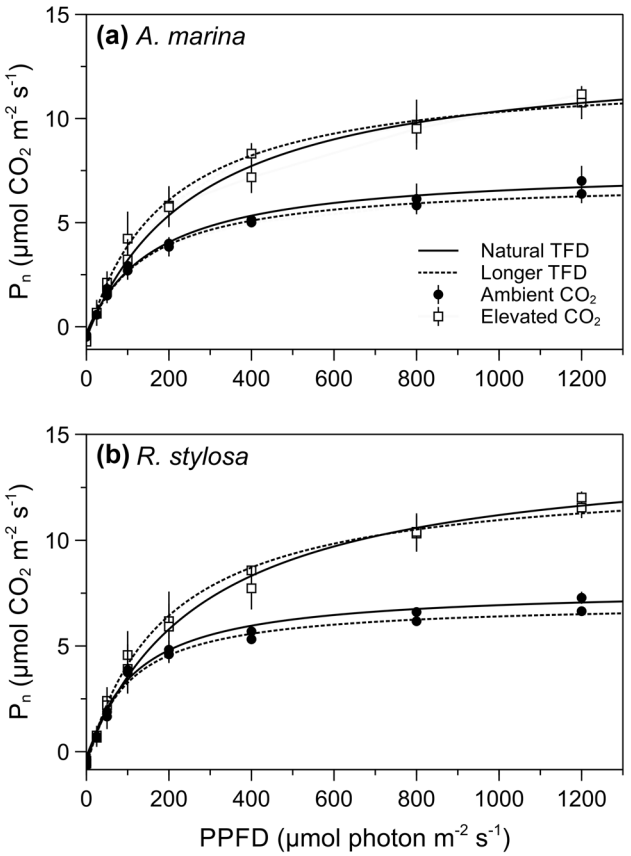


Fig. 4 Pn/PPFD curves for *A. marina* (**a**) and *R. stylosa* (**b**) at the end of the experiment. ($n = 3 \pm$ SEM). Colored markers: ambient CO_2 concentrations, white markers: elevated CO_2 concentrations

Table 3 Comparison between dark respirations values estimated from the light curve responses to the real values measured at night at the same period of the year (June 2017)

	A × N	E × N	A × L	E × L
Avicennia marina				
D_r measured	0.29 ± 0.11	0.41 ± 0.07	0.35 ± 0.14	0.34 ± 0.16
D_r estimated	0.31 ± 0.02	0.47 ± 0.07	0.40 ± 0.09	0.38 ± 0.07
Rhizophora stylosa				
D_r measured	0.20 ± 0.08	0.21 ± 0.03	0.22 ± 0.07	0.17 ± 0.04
D_r estimated	0.23 ± 0.04	0.25 ± 0.06	0.23 ± 0.02	0.19 ± 0.05

A × *N* ambient CO_2 and normal TFD, *E* × *N* elevated CO_2 and normal TFD, *A* × *L* ambient CO_2 and longer TFD, *E* × *L* elevated CO_2 and longer TFD. Values ± SD ($n = 3$)

treatment, no significant differences in stomatal density were observed under natural or longer TFD (Fig. 5a, b; Table 2).

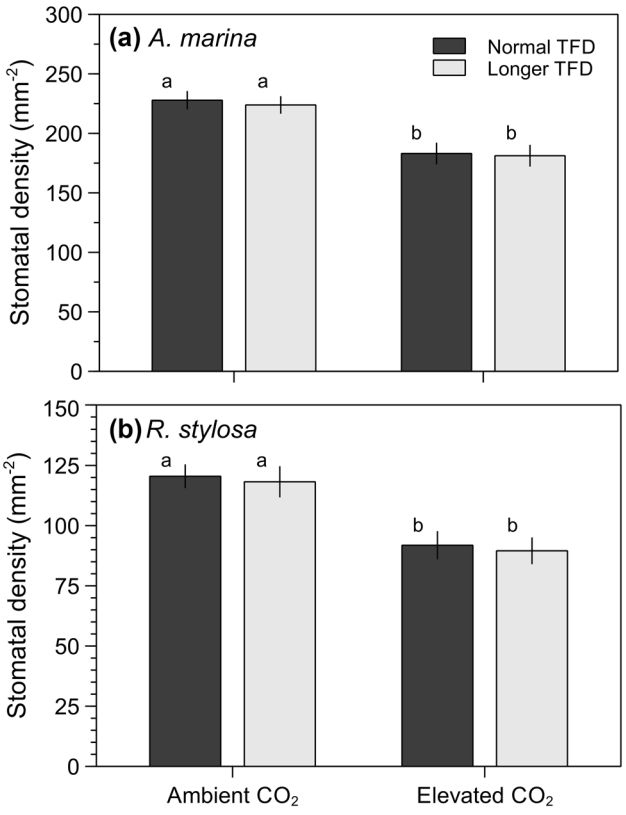


Fig. 5 Stomatal density ($mm^{-2} \pm$ SEM) ($n = 15$) of **a** *A. marina* and **b** *R. stylosa* grown in ambient or elevated CO_2, and under normal (dark-gray bars) and longer TFD (gray bars), for 12 months. Different letters indicate significant differences ($p < 0.05$) after ANOVA analysis

Discussion

Future sea-level rise will affect mangrove photosynthesis

Sea-level rise will result in an increase of the tidal flooding duration for mangroves. In our experiment, applying a longer tidal duration to *Avicennia marina* and *Rhizophora stylosa* seedlings resulted in a decrease of 5% and 3% in photosynthesis, and of 23% and 2% in WUE, for *A. marina* and *R. stylosa*, respectively. However, these reductions were lower than those reported for other stressing factors, such as for example, salinity, as demonstrated by Ball et al. (1997) on *R. stylosa* and *R. apiculata*. Tidal flooding may induce a rapid deficit in oxygen in the soil due to roots and microorganisms respiration (Naidoo et al. 1997). In this study, no oxygen measurements were performed, however, depending on other studies, a decrease of 28% of oxygen could be observed after 6 h of flooding (Skelton and Allaway 1996), or of 100% after 3.5 h, as reported for *A. marina* seedlings (Hovenden et al. 1995). In this later case, the deficit of oxygen led to a complete anoxia of the root system. During flooding events,

mangrove roots may use all their internal oxygen content, and then start to metabolize anaerobically (Krauss et al. 2008). Mangroves are well-adapted to waterlogging condition of their soil, and generally respond by producing lenticels on basal stems or root structures to help offset the effects of low soil oxygen levels (Krauss et al. 2008). However, in our study, *A. marina* and *R. stylosa* were 3 years old at the end of the experiment, and their number of lenticels was limited due to their size and only a few seedlings started to produce pneumatophore or prop roots. Similar results of a decrease in photosynthesis and water-use efficiency with increasing tidal flood duration were previously observed on seedlings but also on mature mangrove trees (Youssef and Saenger 1996; Naidoo et al. 1997; Chen et al. 2005). In their work on *Kandelia candel*, Chen et al. (2005) showed that during anaerobic conditions, the production of abscisic acid (ABA) increased. The latter stimulates stomatal closure, and thus reduces photosynthesis (Kozlowski 1984). No hormone measurements were made in our study, but we suggest that a similar mechanism may be involved in the observed decrease of photosynthesis for *A. marina* and *R. stylosa* when subjected to longer tidal flooding, as observed by Chen et al. (2005). Reduced photosynthesis during longer immersion time may also result from the inhibition of the RuBisCO enzyme activity (Ellison and Farnsworth 1997; Pezeshki et al. 1997). Further study should now examine precisely these hypotheses.

All F_v/F_m values reported in our study for *A. marina* and *R. stylosa*, with either elevated CO_2 or longer tidal flooding, indicated that leaves were photosynthetically actives, with ratios between 0.77 and 0.81, indicative of healthy photosystems and absence of significant stressing factors damaging the photosynthetic functions (Lichtenthaler et al. 2005; Sobrado 2008; Orekhov et al. 2015). In addition, in their study on *Rhizophora stylosa* in Australia, Cheeseman et al. (1997) observed mean values of F_v/F_m of 0.801, which is similar to the values we found in our study. In their study, Cheeseman et al. (1997) observed a decrease in the PSII efficiency at high level of irradiance, and they suggested that downregulation of PSII efficiency, rather than damage, is responsible of this decrease, as indicated by the values of F_v/F_m. Consequently, we suggest that downregulation of PSII is also responsible of the decrease of the photosynthetic efficiency observed in this study for high irradiance levels (Fig. 4). We further suggest that the 5–20% differences between dark respiration rates estimated from the light curves and the one measured at night may be due to temperature variation between day and light, as respiration rates are also temperature depend (Tjoelker et al. 2001; Atkin and Tjoelker 2003; Smith and Dukes 2013).

Elevated atmospheric CO_2 concentrations will increase mangrove net productivity

According to our initial hypothesis, elevated CO_2 significantly stimulated photosynthesis, which was enhanced by more than 37% for *A. marina* and by more than 45% for *R. stylosa*. In our study, the initial increase of photosynthesis was maintained after 1 year of enrichment, and no downregulation was observed, contrary to some previous observations of photosynthetic acclimation after long-term exposure to elevated CO_2 (Farnsworth et al. 1996). In addition, dark respiration was not affected by elevated CO_2 concentrations, either for *A. marina* or for *R. stylosa*, which is different from the results of Farnsworth et al. (1996) who observed a slight decrease of dark respiration with elevated CO_2. Consequently, elevated CO_2 induced a stimulation of photosynthesis but did not influence plant dark respiration, suggesting that the productivity of mangroves seedlings may be further enhanced with future climate change, which is in accordance with previous studies showing increase of the net CO_2 exchange rate (Farnsworth et al. 1996; Ball et al. 1997; Reef et al. 2015).

Surprisingly, SLA increased for both species under elevated CO_2 (Fig. 3), oppositely to the results of other studies (Ball et al. 1997; McKee and Rooth 2008; Reef and Lovelock 2014). This is an important result, as an increase in SLA will lead to a higher potential for carbon acquisition by photosynthesis but also for light interception. Consequently, even if elevated CO_2 had no effect on photosynthesis in low light conditions, the increase of SLA may promote the growth of *A. marina* and *R. stylosa* seedlings in shaded area. Finally, light response of both species to elevated CO_2 was consistent with previous studies (Ziska et al. 1990; Drake and Leadley 1991; Kubiske and Pregitzer 1996; Herrick and Thomas 1999), having higher effect of elevated CO_2 at high irradiance (Fig. 4). Photosynthesis was stimulated by elevated CO_2 from low lights levels in both species, suggesting that not only sun exposed leaves, but also shaded leaves will fix more CO_2 in the future, therefore further increasing mangroves productivity. Seedlings recruitment may be also promoted, as it was demonstrated that seedlings survivorship is strongly affected by light availability (Tamai and Iampa 1988; Smith and Lee 1999; Lopez-Hoffman et al. 2007).

Increase in temperature will raise the beneficial effect of elevated CO_2

We observed a clear difference in the photosynthetic response to elevated CO_2 between the cool season and the warm season, which increased from 32 to 40% and from 38 to 45% for *A. marina* and *R. stylosa*, respectively (Fig. 2). Although photosynthesis of tropical C3 species such as *A. marina* and *R. stylosa* can operate between 15 and 45 °C,

there is a temperature optimum for which it will be maximal (Sage and Kubien 2007). In their review, Gilman et al. (2008) indicated that this optimum lies between 28 and 32 °C for mangroves species, however, it appears to be species-specific, as lower values of 24.5 °C have been reported for *A. germinans* (Reef et al. 2016) and of 26.8 °C for *A. marina* (Leopold et al. 2016). In our study, mean monthly temperatures increased from 22.3 to 26.7 °C during the warm season, which is close to the optimal temperatures reported above, therefore confirming the hypothesis of temperature as a limiting factor for photosynthesis during the cool season under elevated CO_2. With future climate change, the global temperatures are predicted to rise by 0.3 to 4.8 °C, depending on prediction models (Stocker et al. 2013), and our work suggests that the combination of elevated CO_2 with the increase of temperature may further promote the CO_2 fixation by mangrove trees. However, it seems that this beneficial effect may be inhibited if temperatures increase to more than 40 °C (Andrews et al. 1984; Gilman et al. 2008; Reef et al. 2016), which may happen with future climate changes, particularly in the actual arid or semi-arid regions.

Elevated CO_2 will help mangroves trees to resist drought

We observed that growth under elevated atmospheric CO_2 resulted in a significant reduction of stomatal density, with more than 19% and 23% for *A. marina* and *R. stylosa*, respectively. The more likely is that this effect was induced by the decrease of stomatal conductance, as previously reported by Lammertsma et al. (2011), which was already observed in mangrove trees grown under elevated CO_2 (Snedaker and Araújo 1998; Reef et al. 2015). Decrease in stomatal density, and thus in stomatal conductance, probably contributed to the decrease in transpiration rates (Fig. 1). The combination between higher net photosynthetic rates and lower transpiration rates leaded to an increase in water-use efficiency, and our results showed that this parameter was enhanced by more than 45% for *A. marina* and more than 50% for *R. stylosa* under elevated CO_2, consistently with previous observations (Reef et al. 2015). As atmospheric CO_2 concentrations will continue to rise in the future (Collins et al. 2014), it is possible that the stomatal density will continue to decline, thereby preventing water loss by further reduction of transpiration rates. Improving water-use efficiency might be a key for mangroves to resist drought episodes, which will increase in frequency with future climate change (Dai 2013). Due to the semi-arid climate, mangrove trees in New Caledonia are often stunted in growth. They suffer from the elevated salt concentration within the sediment due to the high evaporation of the water and the low inputs by rain or river discharges (Marchand et al. 2011). Consequently, they have a limited productivity (Leopold et al. 2016). Enhancement of water-use efficiency with future climate change will, in return, promote growth and productivity of these trees, and finally will improve their carbon fixation and as so, their role in climate change mitigation. Expanding mangrove forests within arid and semi-arid regions is another major challenge, as it could be the case, for example, on the west coast of South Africa. In this region, mangrove expansion is limited to the tropics, notably due to the aridity of the Sahara Desert in the north, and the Namib Desert in the south (Ward et al. 2016) preventing mangrove seedlings from colonizing the northern and southern subtropical areas. Mangrove plants distribution is affected by many parameters, including temperature, precipitation, pore-water salinity, length of tidal immersion, etc (Duke et al. 1998). The results presented herein suggest that climate changes will enhance mangrove photosynthesis and will allow mangrove juveniles to colonize new areas, which was recently observed with either a poleward migration or a landward migration of mangroves depending on the region (Gilman et al. 2008; Saintilan et al. 2014).

Conclusions

Our results highlight that future climate changes, and particularly elevated CO_2 and increased tidal flooding duration, will strongly affect mangroves physiology. In this study, elevated CO_2 (800 ppm) significantly enhanced photosynthesis by more than 37% and 45% for *A. marina* and *R. stylosa*. However, our results do not support the previous observations of a downregulation of photosynthesis. Additionally, dark respiration was not affected by elevated CO_2, therefore implying a higher carbon gain for the mangrove seedlings studied. Season was also a key driver of the leaf-gas exchanges, with an increase of photosynthesis during the warm period for both species. Consequently, future increase in global temperatures with climate change will further enhance the productivity of the trees, as long as it does not exceed the species-specific optimal temperature for photosynthesis. When increasing tidal flooding duration, photosynthetic rates were slightly reduced but not enough to offset the carbon gain induced by the elevated CO_2 concentrations. Additionally, elevated CO_2 reduced transpiration rates, leading to a significant increase in water-use efficiency, which may favor mangrove expansion, specifically in arid or semi-arid regions. As both species responded similarly to the experiment, we suggest that climate changes may not favor the development of one species over the other, and thus may not affect their relative repartition along the intertidal areas. This study thus provided useful information about the response of mangrove seedlings to future climate change. Further research will now be needed to evaluate the effects of future climate change on the carbon storage capacities of

the whole ecosystem. Indeed, mangroves are recognized for their role in sequestering carbon both in their biomass and in their soils. Therefore, understanding how elevated CO_2 and prolonged water flooding will affect mangrove plant tissues composition, and thus the diagenesis of mangrove-derived organic matter in soils could help to understand the future role of mangrove ecosystems in climate change mitigation.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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