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REVIEW

Global mangrove root production, its controls and roles in the blue carbon budget of mangroves

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Abstract

Mangroves are among the most carbon-dense ecosystems worldwide. Most of the carbon in mangroves is found belowground, and root production might be an important control of carbon accumulation, but has been rarely quantified and understood at the global scale. Here, we determined the global mangrove root production rate and its controls using a systematic review and a recently formalised, spatially explicit mangrove typology framework based on geomorphological settings. We found that global mangrove root production averaged $\sim 770 \pm 202$ g of dry biomass $m^{-2} year^{-1}$ globally, which is much higher than previously reported and close to the root production of the most productive tropical forests. Geomorphological settings exerted marked control over root production together with air temperature and precipitation ($r^2 \approx 30\%$, $p < .001$). Our review shows that individual global changes (e.g. warming, eutrophication, drought) have antagonist effects on root production, but they have rarely been studied in combination. Based on this newly established root production rate, root-derived carbon might account for most of the total carbon buried in mangroves, and 19 Tg C lost in mangroves each year (e.g. as CO_2). Inclusion of root production measurements in understudied geomorphological settings (i.e. deltas), regions (Indonesia, South America and Africa) and soil depth (>40 cm), as well as the creation of a mangrove root trait database will push forward our understanding of the global mangrove carbon cycle for now and the future. Overall, this review presents a comprehensive analysis of root production in mangroves, and highlights the central role of root production in the global mangrove carbon budget.

KEYWORDS

belowground, belowground dynamics, belowground production, blue carbon, climate change, coastal wetlands, mangroves, root production

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1 | INTRODUCTION

Mangroves represent some of the most carbon-dense and productive ecosystems in the world. They provide ecosystem services to >200 million people across 123 countries (Costanza et al., 2014; Hutchison et al., 2014; Spalding, 2010). Mangrove functions and services include carbon burial in mangrove soils and its storage for centuries to millennia (Donato et al., 2011; McLeod et al., 2011). Whether mangroves will continue to act as a carbon store and sink in the future is still uncertain under multiple global changes (Arnaud et al., 2020; Lovelock, 2020; Lovelock et al., 2015; Rogers et al., 2019; Saintilan et al., 2020). An accurate forecast of the carbon dynamics and resistance of mangroves to global changes would require a mechanistic understanding of soil organic matter accumulation, notably root dynamics and production (Arnaud, 2021; Cormier, 2021; Kida & Fujitake, 2020).

Root dynamics are important for mangrove resistance to sea level rise (Krauss et al., 2014). Mangroves might withstand sea level rise either through net vertical accretion of soil or by retreating landward within their available accommodation space (Krauss et al., 2014; Middleton & McKee, 2001; Rogers et al., 2019; Saintilan et al., 2020). Organic material dominated by root inputs (Ezcurra et al., 2016; Middleton & McKee, 2001; Rogers, 2021) (i.e. balance between root production and decomposition) has shown to be an important but underappreciated control of soil surface elevation (Arnaud et al., 2020; Cahoon et al., 2003; Ezcurra et al., 2016; Kirwan et al., 2013; Krauss et al., 2014; McKee, 2011; McKee et al., 2007; Saintilan et al., 2020). Carbonate mangrove soils (i.e. build on karstic environments and Holocene reef tops) include a large portion of dead root materials; therefore, an alteration of root production and decomposition will disproportionately modify their soil surface elevations and resilience to sea level rise (McKee et al., 2021). In mangrove geomorphological settings with more mineral soils (e.g. terrigenous delta, estuaries), the elevation change is dominated by sediment inputs, but a change in soil surface elevation might occur if root production and decay are altered (Lang'at et al., 2014; Rogers, 2021), notably under global changes.

Root processes are also a key component of carbon flow and dynamics in mangroves. The production of roots might represent a third of the net primary production in mangroves (Alongi, 2020; Bouillon et al., 2008). Compared to leaves, roots are not washed away by tides and are likely to be chemically and physically protected from degradation (e.g. via compounds inhibiting microbial decomposition and organo-mineral association—the binding of organic matter with minerals) (Kida & Fujitake, 2020; Middleton & McKee, 2001). Therefore, roots are believed by some to form the main autochthonous input for mangrove carbon burial (Bouillon et al., 2003; Kida & Fujitake, 2020; Kristensen et al., 2008). Mangrove roots may also accelerate the mineralisation of SOM through the release of (1) oxygen (Pi et al., 2009), which changes the redox condition of the soil (Inoue et al., 2011; Kristensen et al., 2008), and (2) exudates that may remobilise old protected carbon as observed in forests (Keiluweit et al., 2015; Phillips et al., 2011). Upscaling of those root processes

with their subsequent effects on carbon dynamics is currently limited due to the lack of an updated estimate of global root production, as well as a lack of understanding of the controls and response of root production to global changes (Arnaud et al., 2020; Coldren et al., 2019).

Compared to the aboveground part of mangroves, root production has been little studied (Alongi, 2020). The controls of root production have never been reviewed at a global scale, and the root contribution to carbon burial and losses has been rarely estimated (Cormier, 2021; Ouyang et al., 2017). There is an emerging body of literature on root production and its controls at the site level (Cormier, 2021). Assessing this emerging literature represents an opportunity to critically assess the role of mangrove root processes and forecast the potential impacts of global changes upon them. Such effort is constrained by the absence of a comprehensive and up-to-date dataset based on a systematic review of recent mangrove root production measurements. Systematic reviews are based on a clearly formulated question and use systematic and explicit method to identify, select, critically appraise and analyse relevant research (Wright et al., 2007, see also Pullin & Stewart, 2006) in contrast to general reviews that aims at presenting the state of scientific knowledge not exhaustively (Pullin & Stewart, 2006). Recent estimates of mangrove root production (Alongi, 2020; Twilley et al., 2017) have contributed to increasing our general understanding of root production, but did not follow the methodology of a systematic review (Pullin & Stewart, 2006). The closest to a systematic review to date is the review of Bouillon et al. (2008), but it included only the five studies available at the time ($n = 16$ data points) (Bouillon et al., 2008).

Mangrove spatial heterogeneity (e.g. in terms of productivity, soil carbon content and burial) is influenced by geomorphological settings (Breithaupt & Steinmuller, 2022; Rovai et al., 2016, 2018; Twilley et al., 2018). Geomorphological settings of mangroves have been defined as deltas, estuaries, lagoons and open coasts (Table 1) depending on sediment type (terrestrial vs. carbonated) and physical forces (e.g. river, tides, wave) that determine mangrove environmental factors, such as the hydrology (e.g. inundation duration and frequency), the nutrient soil loads and limitations (e.g. nitrogen-to-phosphorus ratio), as well as the soil biogeochemical properties (e.g. salinity, redox) (Rovai et al., 2018; Twilley et al., 2018; Woodroffe et al., 2016). The geomorphological settings therefore control key environmental factors (e.g. soil nutrients, salinity, inundation) that have been shown to regulate mangrove net primary production, allocation of carbon between the aboveground and the roots of mangroves, as well as the mangrove root production in local-scale studies (Adame et al., 2014; Ball, 1988; Ball & Pidsley, 1995; Burchett et al., 1989; Castañeda-Moya et al., 2013; Hayes et al., 2017; McKee et al., 2007; Naidoo, 1987, 1990; Nguyen et al., 2015; Ola et al., 2018; Twilley et al., 2018). Despite this acknowledged spatial variability (Breithaupt & Steinmuller, 2022; Rovai et al., 2018; Twilley et al., 2018), recent global mangrove root production estimates have upscaled an average or median plot-scale root production value (Alongi, 2014, 2020; Twilley et al., 2018). To move beyond the generalised extrapolation of data, a mangrove typological framework based on mangrove geomorphological settings

TABLE 1 Definition of mangrove geomorphological settings from Worthington et al. (2020) used in this study.

Geomorphological settings	Sedimentary settings	Definition
Delta	Terrigenous	Shoreline protuberance typified by a wide fan-shaped alluvial plain derived from large volumes of river transported sediment
Estuarine	Terrigenous	Funnel-shaped main channel with bidirectional tidal flows, characterised by large catchment area and high precipitation input
Lagoon	Terrigenous	Shallow coastal waterbody, intermittently separated from ocean inputs. Usually formed parallel to the shore
	Carbonate	See above
Open coast	Terrigenous	Sheltered embayments such as drowned bedrock valleys
	Carbonate	Sheltered environments on oceanic islands behind coral reefs and carbonate banks

is recommended (Breithaupt & Steinmuller, 2022; Rovai et al., 2018; Twilley et al., 2018; Worthington et al., 2020). Disregarding geomorphological settings have disproportionally limited the upscaling of mangrove structural and functional patterns (Twilley et al., 2018). For instance, geomorphological settings have explained most of the mangrove soil organic carbon (SOC) variability (Rovai et al., 2018), and not including it for SOC upscaling underestimated SOC by up to 50% in carbonate mangroves and overestimated up to 86% in deltaic mangroves (Rovai et al., 2018).

Here, we use an alternative approach based on geomorphological settings to critically assess the role of mangrove root production that has largely been overlooked in the literature compared to other aspects of mangrove research (Figure S1). Through the lens of geomorphological settings (Twilley et al., 2018; Worthington et al., 2020), we quantify the global root production (<20 mm diameter) using a systematic review of root production. We identify environmental controls of root production through a qualitative and quantitative review of the literature. We build on this synthesis to hypothesise the potential effect of global changes on global mangrove root production, and the role of root dynamics in the global mangrove carbon budget. We conclude by outlining a vision of future research directions and actions to increase our understanding of root processes, and ultimately our understanding of the full mangrove carbon cycle now and into the future.

2 | BUILDING THE ROOT PRODUCTION DATABASE

We collected published studies from the Web of Science and Scopus bibliographic databases using search terms, such as 'mangrove' and 'root producti*' (see Supplementary Material 1.1 and Table S1 for exhaustive description). The search string resulted in 145 articles from Scopus and 131 from Web of Science (as of 23 March 2022). For inclusion in the systematic review, the root production measurement had to be conducted (1) in situ with direct measurement of mangrove belowground root production (e.g. not through allometric equations) that could be converted into mass, and at a depth >15 cm; (2) in mangroves having trees being at least 4 years old; (3) in mangroves that did not have

experimental treatments or extreme events (e.g. hurricanes) having led to high tree losses. In total, we had 90 valid root production measurements extracted from 24 articles. We also collected a comprehensive list of 18 factors associated with the root production measurements including methodological, geographical, meteorological, ecological and edaphic factors (Table S2) that have been shown to control mangrove root production, or that were likely to influence it (Adame et al., 2014; Castañeda-Moya et al., 2011; Coldren et al., 2019; Cormier et al., 2015; Eugenia & Sánchez, 2005; Gleason & Ewel, 2002; Kihara et al., 2022; Lang'at et al., 2013; McKee & Faulkner, 2000; Muhammad-Nor et al., 2019; Rivera-Monroy et al., 2017). We retrieved the geographical coordinates of each root production measurement using Google Maps when they were not reported in the study. All geographical coordinates provided in articles were confirmed using Google Maps (www.google.fr/maps). We used these geographical coordinates to extract for each root production measurement their bioregions from the map of Spalding et al. (2007), their meteorological variables from the WorldClim high spatial resolution climatic map (30s) (Fick & Hijmans, 2017) and their tidal amplitude data from the map of Rovai et al. (2018). We defined the geomorphological settings for each literature-derived root production rate using the map of Worthington et al. (2020). The geomorphological classification of Worthington et al. (2020) was made by combining remote sensing data, machine learning and reviews of >500 geomorphological settings by mangrove experts. The reported accuracy was ~90% for geomorphological settings at the global scale. Despite the embedded uncertainties in geomorphological maps of regional ecosystems, which is the case with the Worthington et al. (2020) maps, this novel, global-scale classification provides a very first opportunity to advance the understanding of mangrove ecosystem dynamics, notably root production. Yet, future refinements of the map of Worthington et al. (2020) with more ground data should be a possibility for future research. We also confirmed each geomorphological setting given in the map of Worthington et al. (2020) using satellite images from Google Maps (www.google.fr/maps) and the definition of geomorphological settings in Table 1. When the geomorphological setting was not available or incorrect (based on visual observation of the authors) in the map of Worthington et al. (2020), we re-classified the geomorphological setting strictly based on the definition given in Worthington et al. (2020) (see

Table 1. To limit any subjectivity, we proofed the geomorphological settings with the literature (Table S3) when available.

We manually extracted all the other factors from the studies themselves or associated PhD theses and articles. We used Plotdigitizer (<https://apps.automeris.io/wpd>) to extract data from the figures. A quality check was done for each environmental data and root production measurement (e.g. Table S3). The root production was measured with ingrowth core (83%) and sequential coring (17%) at a depth often limited to 45 cm (90%) (Figure 1). When coring or using ingrowth bags, large roots (>20mm) are not well sampled (Adame et al., 2017). Therefore, our analysis does not include roots >20mm diameter. The reported root production across studies is accessible in Arnaud et al. (2023), which is the database of this article published in the Zenodo repository.

3 | MANGROVE ROOT PRODUCTION AT A GLOBAL SCALE

The mangrove root production measurements spanned all continents having mangroves and were found across all geomorphological settings. Geomorphological settings have allowed a better understanding and upscaling of mangrove structural and functional patterns than latitude or bioregions alone (Rovai et al., 2016, 2018; Twilley

et al., 2018). Geomorphological settings determine mangrove environmental factors, such as the hydrology (e.g. inundation duration and frequency), the nutrient load and salinity of the mangrove soils (Rovai et al., 2018; Twilley et al., 2018; Woodroffe et al., 2016) that are regulating root production (Adame et al., 2014; Ball, 1988; Ball & Pidsley, 1995; Burchett et al., 1989; Castañeda-Moya et al., 2013; Hayes et al., 2017; McKee et al., 2007; Naidoo, 1987, 1990; Nguyen et al., 2015; Ola et al., 2018; Twilley et al., 2018). Therefore, we upscaled the local mangrove root production measurements using the framework of the geomorphological setting proposed by Twilley et al. (2018), in addition to the root production per depth and the global mangrove area of 137,600 km² (Bunting et al., 2018). The full methodology for the computation of root production and possible limitation of that methodology is described in detail in Supplementary Material 1.2, and the data of root production reported in each study are provided in Arnaud et al. (2023).

We found that the mangrove root production averaged $\sim 770 \pm 202$ g of dry biomass m⁻² year⁻¹ or 41 ± 11 TgC year⁻¹ (n=90) globally (Table 2, see Supplementary Material 1.2 for computational method and uncertainties). The mean root production across geomorphological settings was the highest in deltas (808 ± 311 g of dry biomass m⁻² year⁻¹, n=2), followed by estuaries (640 ± 131 g of dry biomass m⁻² year⁻¹, n=21), lagoons (357 ± 27 g of dry biomass m⁻² year⁻¹, n=49) and open coasts (250 ± 49 g of dry biomass

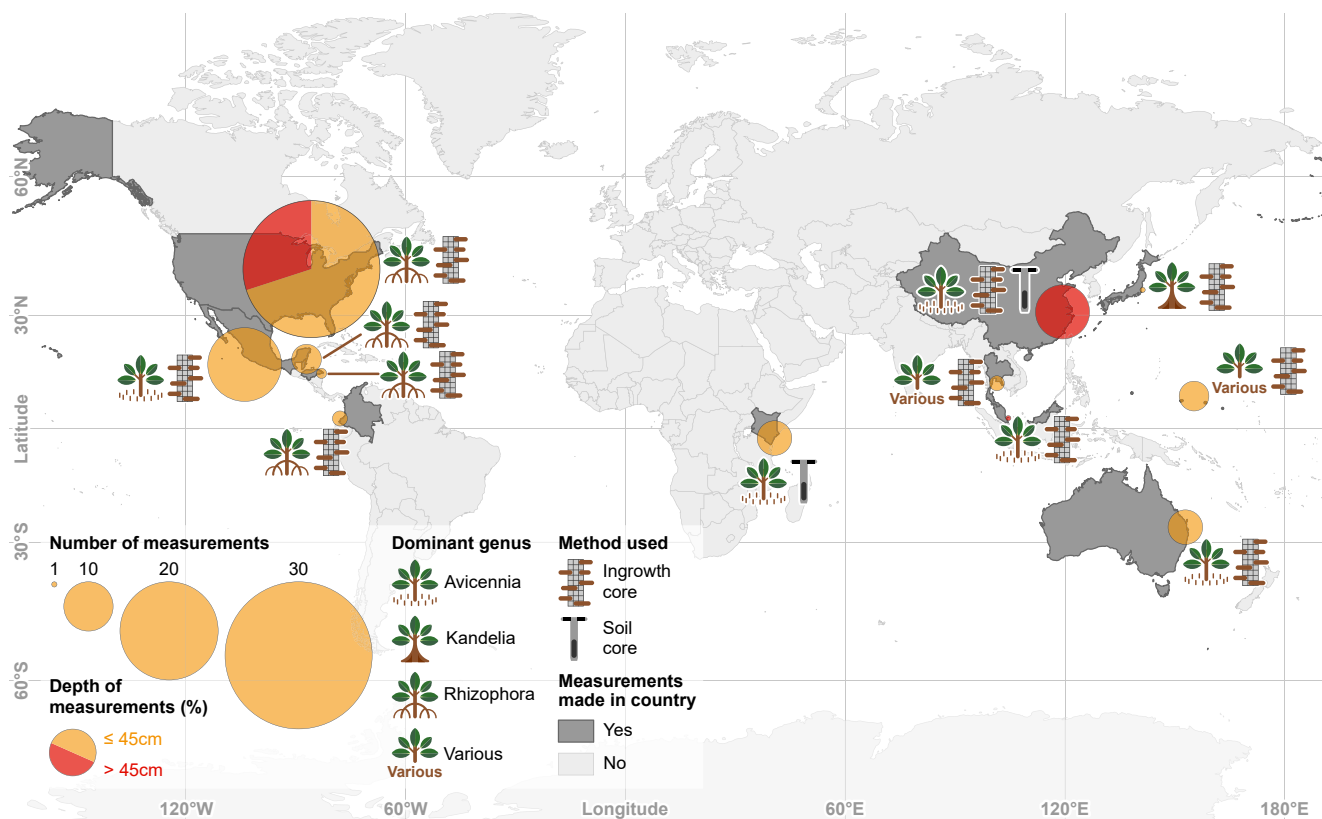


FIGURE 1 Mangrove root production measurements across the world. The countries in dark grey show the geographical distribution of root production measurements across the globe. The circles highlight the number of measurements and the % of measurements above and below 45 cm depth. The methods and the dominant genus of the root production are also shown per country. Map lines do not necessarily depict accepted national boundaries.

$\text{m}^{-2}\text{year}^{-1}$, $n=18$) (Figure 2, see Section 1 for method and uncertainties). The variation of root production was the highest in estuaries. The variation seems not to be related to the spatial distribution (latitudinal or ecoregions) of the measurements or the method used, and requires further investigations. The root production across depths was very heterogeneous being almost two times more important in the top soil (504 ± 174 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, depth=0–37 cm, $n=90$) than in the deep soil (266 ± 28 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, depth=37–73 cm, $n=15$) (Table 2, see Supplementary Material 1.2 for computational method and uncertainties). The estimation of mangrove root production in deep soils is based on a very limited amount of data available ($n=15$) with measurements having various depths, therefore it holds large uncertainties (see Supplementary Material 1.2 for computational method and uncertainties). Yet, omitting root production at depth (37–73 cm) would have resulted in ignoring a third of the total estimated mangrove root production.

This study presents an important step forward to quantify root production in mangroves. Yet, our root production estimate is still uncertain due to measurement gaps in very productive mangrove regions (e.g. in Indonesia) (Figure 1) and at depths below 45 cm, as well as two different methods of measurement used (Figure 1: ingrowth core and sequential coring) (see Section 6). Our root production estimate is two and a half times higher than the previous estimate in Twilley et al., 2017, and one and a half times higher than the one in Alongi (2020) (extracted from Table 2), but ~25% lower than the one

in Bouillon et al. (2008) after all value being normalised for mangrove area. Those differences are mostly due to the inclusion of new observations having higher root production measurements (e.g. in the Central Indo-Pacific) and upscaling methodology. Twilley et al. (2017) estimate was based on three and a half times fewer observations with only limited measurements from the Central Indo-Pacific, which is the most productive bioregion in our dataset (Figure 3). In addition, Twilley et al. (2017) upscaled local root production measurements by doing a mean, not accounting for the impacts of geomorphological settings on mangrove growth and soil properties and hence root production, and therefore likely reducing global estimate of root production (Twilley et al., 2018). Bouillon et al. (2008) estimate is based on very few data points ($n=16$), and was upscaled using a root: aboveground litter production ratio. Yet, biomass allocation between aboveground and belowground responds to environmental stress (e.g. hydroperiod, soil nutrients) and is therefore not constant across mangroves (Adame et al., 2014; Castañeda-Moya et al., 2011, 2013). For instance, stunted mangroves in arid areas might allocate a greater fraction of NPP belowground than other mangroves (Adame et al., 2014; Ochoa-Gómez et al., 2019). It is not possible to explain the differences in root production with Alongi (2020), because the methodology was not fully detailed to compute global root production. Compared to tropical forests, our estimation of mangrove root production (~ 770 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$) is in the higher middle range of tropical forest root production measurements (i.e. 200–810 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$)

TABLE 2 Average (g of dry biomass $\text{m}^{-2}\text{year}^{-1}$) of root production in mangroves, as well as its error range and proportion (%) across soil depths.

Root production	0–37 cm	37–73 cm	0–73 cm
In biomass (g of dry biomass $\text{m}^{-2}\text{year}^{-1}$)	504 ± 174	266 ± 28	770 ± 202
In per cent (% of the total)	65	35	100

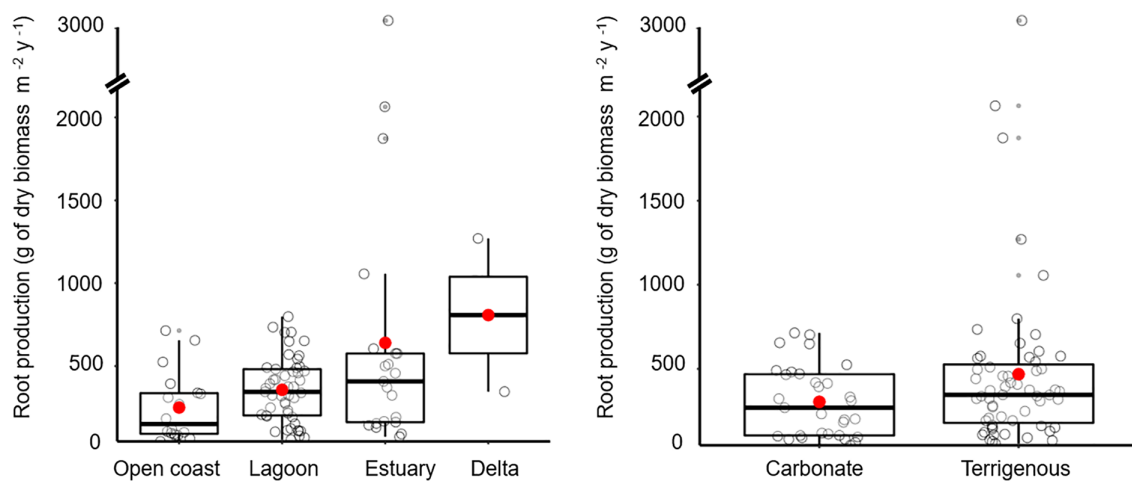


FIGURE 2 Root production across geomorphological and sedimentary settings in g of dry biomass $\text{m}^{-2}\text{year}^{-1}$. Geomorphological settings are defined by Worthington et al. (2020). Carbonate settings are karstic environments and Holocene reef tops. Terrigenous settings are sediment-rich depositional environments as defined in Worthington et al. (2020). Red-filled dots show the sample mean. Bold, horizontal lines show sample medians. The lower and upper hinges correspond to the first and third quartiles of the sample. The upper and lower whisker extends from the hinges to the largest and smallest values, respectively, which is no further from the hinges than 1.5 times the sample interquartile range. Open circles indicate individual measurements, with vertical jitter to reduce overwriting.

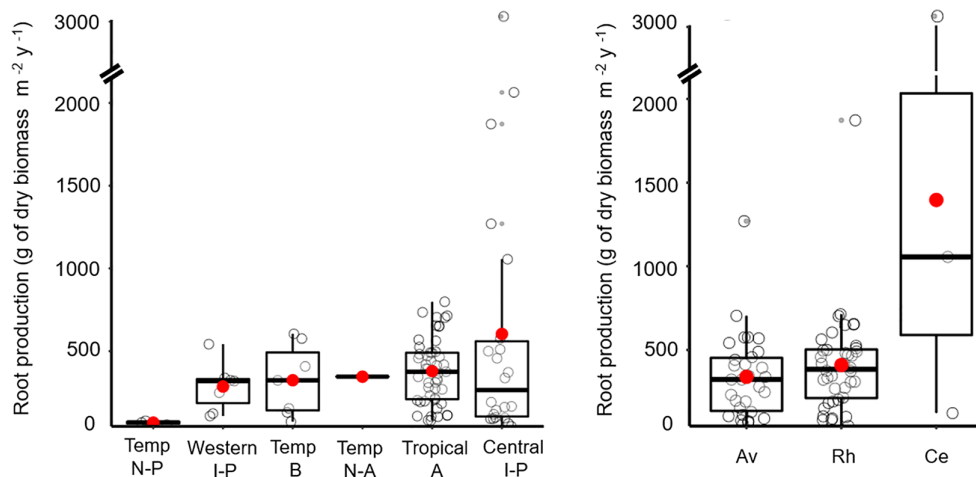


FIGURE 3 Root production across bioregions and genus in g of dry biomass $\text{m}^{-2} \text{year}^{-1}$. N=North, P=Pacific, I=Indo, B=Australasia, A=Atlantic, Temp=Temperate, Av=*Avicennia*, Rh=*Rhizophora*, Ce=*Ceriops*. Red-filled dots show the sample mean. Bold, horizontal lines show sample medians. The lower and upper hinges correspond to the first and third quartiles of the sample. The upper and lower whisker extends from the hinges to the largest and smallest values, respectively, which is no further from the hinges than 1.5 times the sample interquartile range. Open circles indicate individual measurements, with vertical jitter to reduce overwriting.

(Aragão et al., 2009; Cordeiro et al., 2020; Malhi et al., 2011). This suggests that our estimate might be still conservative because mangroves have been shown to allocate disproportionately more carbon to roots than other forests (Twilley et al., 2017).

4 | ENVIRONMENTAL CONTROLS ON MANGROVE ROOT PRODUCTION

We investigated potential macroecological controls of root production that have previously been shown to regulate structural and functional patterns in mangroves (de Albuquerque Ribeiro et al., 2019; Rivera-Monroy et al., 2017; Rovai et al., 2016, 2018), including geomorphological settings, air temperature, precipitation and tidal range. We used linear models, the Akaike information criterion (AIC) and ANOVA to evaluate which set of environmental variables best described and have a significant effect on the variability of the global root production (Supplementary Material 1.3, 2 and Table S4). In addition, we separately reviewed and tested individual factors suspected to control root production using Kruskal–Wallis or Spearman's tests (nonparametric equivalents of the one-way ANOVA and Pearson tests respectively) (Supplementary materials 1.3, 2 and Table S5). These individual factors could not be included in the global model, because it would have required that they were paired with each observation, which was not the case (Arnaud et al., 2023). The full methodology and associated R script are given with in Supplementary materials 1.3 and 2 respectively.

4.1 | Global factors explaining the root production

The root production was best explained with a linear model including the geomorphological settings crossed with the maximum air

temperature of the warmest month and the minimum precipitation of the driest month (Table S4). This combination explained ~30% of the variability of root production from our dataset ($r^2 = .28$; $p < .001$, $n = 90$). The geomorphological settings crossed with the maximum air temperature explained most of the root production variability (19%; $p < .001$), followed by the precipitation of the driest month (4%; $p < .05$) and the geomorphological settings alone but with no significant effect (5%; $p = .2$). No individual study has reported the effect of geomorphological settings crossed with temperature on root production. Yet, similarly to our findings geomorphological settings have been reported to control mangrove SOC (Rovai et al., 2018; Twilley et al., 2018), aboveground net primary production and biomass (de Albuquerque Ribeiro et al., 2019; Rovai et al., 2016). Precipitation has also been shown to control aboveground biomass and production (de Albuquerque Ribeiro et al., 2019; Rovai et al., 2016), but was not the main factor explaining SOC in mangroves (Rovai et al., 2018). Combined with geomorphological settings, the air temperature was an important predictor of mangrove root production, as has been observed across terrestrial ecosystems for temperature, if soil moisture and nutrient availability are not limiting tree growth (Pregitzer et al., 2000). The increase in root production with temperature results from an overall increase in net primary production as observed by Coldren et al., 2019. Therefore, it is also likely that root production decreases when aboveground primary production decreases after reaching the thermal photosynthetic optimum of mangroves (i.e. between 25 and 32°C: Alongi, 2009).

Previous local-scale studies have shown that precipitation was related to mangrove root production as in our findings (Hayes et al., 2019; Reef & Lovelock, 2015), but not all (Arnaud et al., 2021). Two mechanisms explain the increase in mangrove root production with precipitation at the local scale. Precipitation increases the freshwater availability in soil, and mangrove roots have been shown to preferentially uptake freshwater rather than saline water to support

growth for physiological and osmotic pressure reasons (Hayes et al., 2019). Therefore, the input of freshwater might increase over all mangrove tree growth, including roots (Ball et al., 1988; Reef & Lovelock, 2015; Simard et al., 2019). The root: shoot ratio (i.e. the root production vs. the aboveground production) is, however, unlikely to decrease with higher precipitation, because low precipitation might rather lead to more allocation of carbon belowground than aboveground (Adame et al., 2017). The tidal amplitude did not improve the model to explain the variability of mangrove root production in our dataset. The resolution of the tidal amplitude data might be spatially too coarse, or might not reflect well enough the inundation conditions of mangroves, because several studies suggest that mangrove root production and tidal inundation might be closely related (Adame et al., 2014; Ezcurra et al., 2016; Rogers et al., 2019; Saintilan et al., 2020). Therefore, it will be critical to report the frequency and duration of daily inundation for future mangrove root production studies.

4.2 | Bioregions, sedimentary settings, ecological and soil factors

Mangroves from the Central Indo-Pacific bioregion had the highest root production (604 ± 167 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, $n=22$, Figure 3) as has been reported for the aboveground productivity and soil carbon stock (Atwood et al., 2017; Sanderman et al., 2018; Simard et al., 2019). Yet, the difference of root production across bioregions was statistically weak ($p=.09$, $H_{(3)}=9.3$, $n=90$, Table S5) likely because hot-spots of mangrove net primary production have been little studied for root production (e.g. in Indonesia). Mangroves can also be classified following their sedimentary settings (Worthington et al., 2020). Mangroves in terrigenous settings had a higher root production (469 ± 66 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, $n=59$, Figure 2) than in carbonated settings (304 ± 38 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, $n=31$, Figure 2) as reported for the aboveground net primary productivity in the neo-tropics (de Albuquerque Ribeiro et al., 2019). In contrast to the aboveground productivity, the difference in root production between both sedimentary settings was not statistically significant ($p=.12$, $H_{(5)}=8.7$, $n=90$, Table S5) (de Albuquerque Ribeiro et al., 2019). The difference in productivity might be less striking for root production than aboveground production, because the root production responds to overall tree growth, but also to carbon allocation that might be higher towards roots in carbonate settings in response to their limited soil phosphorous content (Twilley et al., 2018). Tree density is often reported in local-scale studies as a potential factor influencing root production in mangroves (Adame et al., 2014; Arnaud et al., 2021), but we did not find a significant relationship between tree density and basal area with root production (tree density: $p=.45$, $r^2=.12$, $n=17$; basal area: $p=.80$, $r^2=.07$, $n=15$; Table S5). Many studies have reported tree density along with root production (almost 40%), but the threshold of diameter at breast height (DBH) for the inclusion of trees in census was very heterogeneous (from all

DBH to $\text{DBH} > 10$ cm) limiting comparisons to 15 measurements. In contrast, the dominant genus of mangrove sites was often reported ($n=87$). The root production was the highest in mangroves dominated by *Ceriops* (1397 ± 850 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, $n=3$, Figure 3). The root production of mangroves dominated by *Rhizophora* and *Avicennia* was more than three times less important than for *Ceriops* (*Rhizophora*: 410 ± 48 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, $n=40$; *Avicennia*: 339 ± 46 g of dry biomass $\text{m}^{-2}\text{year}^{-1}$, $n=30$, Figure 3, Table S5). Yet, only a few measurements have been conducted in mangroves dominated by *Ceriops*.

Nutrients, salinity and bulk density have all been shown to exert local control over mangrove root production or primary production in mesocosm and field studies (Adame et al., 2014; Castañeda-Moya et al., 2013; Hayes et al., 2017; Naidoo, 1987, 1990; Ola et al., 2018). There was a positive significant relationship between total soil nitrogen and root production ($p < .01$, $r^2=.73$, $n=15$, Table S5), but not with total soil phosphorus ($p=.33$, $r^2=.26$, $n=12$, Table S5), which is consistent with mangrove field studies that have reported an increase, a decrease or no change of root production (absolute and relative) with an increase in soil nutrients. An increase in soil nutrients is generally expected to decrease the root: shoot ratio in forests (Nadelhoffer, 2000), meaning that the absolute root production can increase with an increase in nutrients, but proportionally less than the aboveground production (Sullivan et al., 2007). This relative decrease in root production in response to an increase in nutrients does not occur systematically in mangroves (Castañeda-Moya et al., 2011; Hayes et al., 2017). The relative root production response to nutrient availability is likely regulated by other environmental factors (e.g. inundation frequency, salinity, anoxia). For instance, the increase in root growth caused by nutrient enrichment appears only in frequently inundated mangrove soils with high salinity (Adame et al., 2014; Hayes et al., 2017; McKee et al., 2007). Mangrove roots might take advantage of an increase in nutrients to increase their growth to access more freshwater and alleviate environmental stress (Adame et al., 2014; Hayes et al., 2017). We did not find any pattern between bulk density and root production ($p=.61$, $r^2=.07$, $n=44$, Table S5), despite local-scale manipulative studies showing that bulk density controlled the root production of *Avicennia marina* and *Rhizophora stylosa* (higher root production with artificially increased bulk density), but not of *Ceriops australis* (Ola et al., 2018). Globally, there was no effect of pore water salinity on root production across mangrove studies ($p=.46$, $r^2=.10$, $n=53$, Table S5). The response of mangrove root growth to salinity is species dependent, non-linear and not monotonic (Ball, 1988; Ball & Pidsley, 1995; Burchett et al., 1989; Downton, 1982; Naidoo, 1987, 1990; Nguyen et al., 2015). More data and consistent methodology of salinity measurements may be necessary to fully examine the effect of salinity. Many other soil factors are likely to influence mangrove root production, such as soil anoxic-oxic conditions, base cations or the age of the mangrove forest (Arnaud et al., 2021;

Cusack et al., 2018), but they have been rarely reported alongside with root production studies.

5 | LIKELY TRENDS IN MANGROVE ROOT PRODUCTION UNDER FUTURE CLIMATE CONDITIONS

Mangrove root production is likely to be affected by global changes that include warming, changes in precipitation regimes, sea level rise, atmospheric CO₂ rise and coastal nutrient enrichment. Unfortunately, there are limited data available on the mangrove root production responses to global changes. Thus, below we provide perspectives and focus on critical questions that should be addressed about root responses to global changes, guided by our data, previous studies and information from other ecosystems. An increase in mangrove root accumulation with warming has been shown in an outdoor mesocosm (Coldren et al., 2019). We also found a statistically significant effect of air temperature crossed with geomorphological settings on root production, which likely indicates that mangrove root production will be sensitive to temperature variations and extremes in the future. An increase in mean annual air temperature might increase the root: shoot ratio and a rise in root production by increasing the mangrove photosynthetic rate as observed in a mangrove (Coldren et al., 2019) and forests (Norby & Jackson, 2000). Mangroves might grow until a maximum air temperature threshold for photosynthesis (and respiration) as in forests (Norby & Jackson, 2000) assuming that nutrient supply and water are not limited. If resources are limited, the root: shoot ratio might increase under higher temperatures, because mangrove trees might allocate more carbon to roots to explore the soil for nutrients and water uptake. In contrast, if resources are not limited, the increase in temperature might not increase the root: shoot ratio. This hypothesis is important to be tested in mangroves, especially for mangroves close to mega-cities that are prone to eutrophication (Mao et al., 2021).

A lack or a reduction of precipitation may reduce the growth of mangrove trees (Alongi, 2009; Simard et al., 2019) and thus might lead to a reduction of mangrove root production at least temporarily as observed in other ecosystems (Slette et al., 2022). Our data supported this hypothesis with a significant positive effect of precipitation on mangrove root production. For instance, the root production was relatively low (56–79 g of dry biomass m⁻² year⁻¹) in very arid mangroves of Mexico (i.e. the site with the lowest precipitation in our dataset: Ochoa-Gómez et al., 2019), while the root production was four times higher in very wet mangroves (Kihara et al., 2022). Low precipitation might also increase the amount of carbon allocated to mangrove roots to maintain water uptake as observed in terrestrial forests (Brunner et al., 2015). There were no aboveground production data collected, but the ratio of aboveground stock: root production was up to two times higher in arid mangroves (Ochoa-Gómez et al., 2019) than in the wettest mangroves (Kihara et al., 2022; Muhammad-Nor et al., 2019)

suggesting that mangrove trees under low precipitation allocate relatively more carbon to root production as observed in terrestrial forests (Brunner et al., 2015).

The effect of sea level rise on mangrove root production is likely not linear and species dependent (Krauss et al., 2014). This might explain why we did not find any pattern of root production and tidal amplitude (a proxy for inundation: Rovai et al., 2018). Palaeorecords have shown that mangrove peat accretion mostly composed of roots at some sites (Ezcurra et al., 2016; Middleton & McKee, 2001) was stimulated by sea level rise up to 6.1 millimetres per year (Saintilan et al., 2020). Other studies have shown that an increase in inundation duration does not ultimately lead to a reduction in mangrove root decay (Arnaud et al., 2020). Therefore, it is likely that the accumulation of roots with sea level rise results from an increase in root production (Kirwan & Magonigal, 2013) or a change of root traits (e.g. root turnover, root carbon-to-nitrogen ratio, specific root length, root tissue density). There is a strong need for manipulative studies that modify the inundation duration in mature mangroves to better understand and forecast the response of root production to sea level rise. Reporting the duration or frequency of inundation with mangrove root production will help, because as shown above tidal amplitude data only exist in coarse spatial resolution.

The effect of CO₂ enrichment has been tested only in experiments with mangrove seedlings, which showed that CO₂ fertilisation does increase mangrove root production, but decreased root: shoot ratio (except under low nutrient concentration) (Jacotot et al., 2019; Reef et al., 2016). Similarly, free CO₂ air enrichment has also increased root production in terrestrial mature forests and salt marshes in outdoor experiments (Iversen, 2010; Norby et al., 2004; Norby & Jackson, 2000; Noyce et al., 2019). Finally, coastal nutrient enrichment alone sometimes results in a decrease in mangrove root production with an increase in carbon allocated to aboveground organs (Hayes et al., 2017; McKee, 1996; Naidoo, 1987). However, this was shown to be dependent on local conditions. In our dataset, we found that root production was more important in sites with higher nitrogen, likely reflecting an increase in overall plant growth. Ongoing global environmental changes include the interactive effects of multiple drivers that might enhance or offset the effect of individual factors (Jacotot et al., 2019; Reef et al., 2016; Twilley et al., 2017). Yet, too few studies have investigated multiple factors simultaneously preventing accurate forecasting of mangrove root production under future environmental conditions.

6 | IMPORTANCE OF MANGROVE ROOT PRODUCTION AND DYNAMICS FOR CARBON BURIAL AND LOSSES IN MANGROVES

The carbon burial rate can be estimated using the global root decay rate and the root litter production per year (i.e. root necromass production), which equals the mangrove root production multiplied by the root mortality rate (Figure 4). Yet, the root mortality rate has

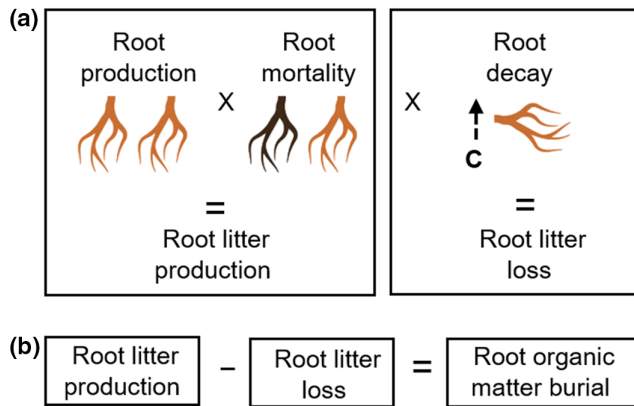


FIGURE 4 Root organic matter burial computation in mangroves. Annual root litter production is the root production multiplied by the root mortality rate (a). Annual root litter loss is the annual root litter production multiplied by the root decay rate (b). The root organic matter burial is annual root litter production subtracted from the annual loss of root litter (c).

been rarely studied in mangroves. A common approach to overcome the lack of root mortality data is to assume that the root system is in equilibrium and that root production equals root mortality (limitations are given below). If we assume that mangrove root production and mortality are in equilibrium, the global dead root production per year equals $\sim 770 \pm 202 \text{ g of dry biomass m}^{-2} \text{ year}^{-1}$ in mangroves ($41 \pm 11 \text{ Tg C year}^{-1}$ for the whole mangrove area; Full methodology is given in Supplementary Material 1.4). Ouyang et al. (2017) estimated that the global root decomposition rate was $0.135\% \text{ day}^{-1}$ ($\sim 49\% \text{ year}^{-1}$) in mangroves based on a systematic literature review and gave a range of litter decomposition per genus (Ouyang et al., 2017). We applied the decomposition rate of the dominant mangrove tree genus of each geomorphological setting to estimate that around $\sim 352 \pm 94 \text{ g of dry biomass m}^{-2} \text{ year}^{-1}$ of the global dead root production ($21 \pm 2 \text{ Tg C year}^{-1}$) can be assumed to be lost through decomposition, either as CO_2 and CH_4 emissions or through lateral loss of DOC and DIC after being consumed by microbes (Full detailed methodology is given in Supplementary Material 1.4). The remaining $\sim 417 \pm 108 \text{ g of dry biomass m}^{-2} \text{ year}^{-1}$ or $23 \pm 5 \text{ Tg C year}^{-1}$ of root-derived carbon is likely buried in mangrove soils, which corresponds to $>90\%$ of carbon buried in mangroves based on the $24 \text{ Tg C year}^{-1}$ burial rate of Breithaupt and Steinmuller (2022) (Figure 5). Our root carbon burial rate is around four times higher than the only one previous estimate (i.e. $\sim 50 \text{ g C m}^{-2} \text{ year}^{-1}$ equivalent to $100 \text{ g dry biomass m}^{-2} \text{ year}^{-1}$ in mangroves; Ouyang et al., 2017). However, in that study, the annual necromass production of mangroves was estimated by multiplying root production ($\text{g of dry biomass m}^{-2} \text{ year}^{-1}$) by root turnover rate (defined as root production divided by biomass) rather than by root mortality (Ouyang et al., 2017: table 3, see Supplementary Material 1.4). Our estimate can still be improved by the inclusion of more field data on mangrove root dynamics, especially for root mortality and by root orders as well as root production at a depth greater than 45 cm. We also considered that our calculation assumes root mortality equals root production for all mangrove roots irrespective

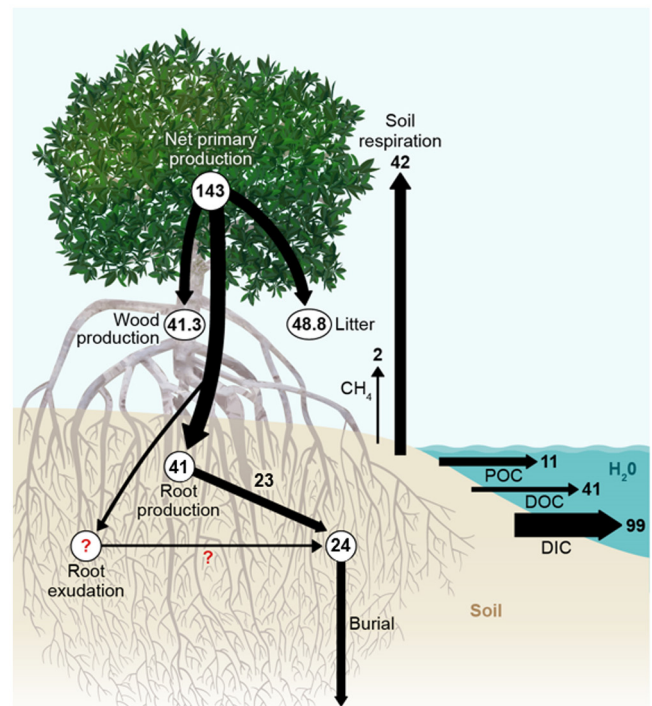


FIGURE 5 The importance of roots for the budget of the major carbon fluxes in the world's mangroves. All values are in Tg C year^{-1} for a mangrove area of $\sim 137,600 \text{ km}^2$. Red question marks are components that have not been quantified. Abbreviations: DIC, dissolved inorganic carbon loss; DOC, dissolved organic carbon loss; POC, particulate organic carbon loss from soil; CH_4 loss from soil and water. Data on root carbon production and root carbon burial are from our estimates; carbon burial is from Breithaupt and Steinmuller (2022); wood production, litter, soil respiration, CH_4 , DIC, DOC and POC are from Alongi (2020: tables 2, 3 & 5); net primary production is the total of wood, litter and root production.

of root orders and functional types, but for instance, fine absorptive roots will likely have a higher rate of mortality than fine transportive roots and coarse roots (Sun et al., 2016). There is no measurement for mangroves, but transportive fine roots die every 5–10 year, while fine absorptive roots die likely every 0.5–2.0 year depending on species and ecosystems (Clark et al., 2001; McCormack et al., 2015). Nevertheless, our estimate strongly strengthens the previous estimate of carbon burial from root-derived carbon (Ouyang et al., 2017) with the inclusion of more data and by using a robust methodology based on geomorphological settings.

Live roots also contribute to mangrove carbon burial and losses through root respiration (i.e. CO_2 emission through autotrophic respiration) and rhizodepositions (i.e. release of labile carbon by roots). Autotrophic root respiration has rarely been quantified for mangrove trees and is highly variable (Lovelock, 2008; Lovelock et al., 2006; Ouyang et al., 2018). In Caribbean mangroves, root respiration accounted for a large portion of the CO_2 efflux from the soil in fringe mangroves, and less than 20% of the CO_2 efflux from scrub mangroves (Lovelock, 2008; Lovelock et al., 2006). Similarly, little is known about mangrove rhizodepositions (Kristensen et al., 2008) and their role in building and stabilising soil carbon stocks (Kida &

Fujitake, 2020). Rhizodepositions include the transfer of carbon from roots into the rhizosphere and the soil through root exudations (including mucilage), root cell sloughing and root-associated symbionts living in the soil (e.g. mycorrhizas) (Jones et al., 2009). No in-situ quantifications of root exudations for mangrove trees exist, but root exudations have been shown to represent between 1% and 20% of the net primary production (NPP) in other temperate and tropical forests (Aoki et al., 2012; Jones et al., 2004; Phillips et al., 2008; Yin et al., 2014). The higher end of root exudation values was reported for tropical forest soils (Aoki et al., 2012) that are nutrient-deficient like mangroves (Reef et al., 2010). If mangrove root exudation would be in the same range as in other forests, mangrove root exudation might be between 1.5 and 28 TgC year⁻¹. While this range is highly speculative and should not be taken as an accurate value, this range shows that root exudates might be important to understand the carbon dynamics in mangroves, notably mangrove carbon losses (CO₂, CH₄ or dissolved carbon exported to open water) (Abril & Borges, 2019; Spivak et al., 2019) and likely the production of stable carbon by microbes metabolising the exudates (Panchal et al., 2022).

7 | UNCERTAINTIES IN THE GLOBAL ESTIMATE OF MANGROVE ROOT PRODUCTION

The estimation of global root production in mangroves could be improved by expanding the geographical distribution and the depth of measurements. Entire continents have been under-represented in previous research efforts, including mangrove ecosystems in South America and Africa, while others are currently better represented, notably North and Central America. Many of the countries holding the most carbon-rich mangroves have no root production measurements. For instance, no root production data are represented in the literature for mangroves in Indonesia, Brazil, Papua-New Guinea and Nigeria, despite those countries together holding over 30% of the world's mangrove area and soil carbon stock (Jardine & Siikamäki, 2014; Sanderman et al., 2018). Some geomorphological settings have also been understudied, like the Delta ($n=2$), while they are likely the most productive in terms of net primary production and root production (Figure 2).

In addition, most root production studies have limited their investigation to the top 0 to 45 cm depths (90% of the compiled data), but root production has been shown to occur well below this soil layer (Arnaud et al., 2021; Castañeda-Moya et al., 2013; Cormier, 2021; Xiong et al., 2013). Shallow measurements are often justified by the assumption that root production is negligible at depth. This assumption requires justification and nuance, because root production below 45 cm depth accounted for up to 45% of the total root production in some mangroves in the United States (Castañeda-Moya et al., 2011) and up to 40% in some mangroves in China (Xiong et al., 2013), Vietnam (Arnaud et al., 2021) and Malaysia (Muhammad-Nor et al., 2019). The controls of mangrove root distribution at depth are not clear (Arnaud et al., 2021), but are disproportionately important for carbon burial. This

is because root decay is likely to be slower at depth due to reduced microbial biomass, stabilisation of SOM by minerals and reduced supply of root oxygen and exudates (i.e. labile carbon released by roots) (Rasse et al., 2005; Spivak et al., 2019).

Finally, methods to measure root production can lead to strong differences in root production measurements (Hendricks et al., 2006; Kihara et al., 2022) and could be improved. Sequential coring might reflect spatial and temporal variability of root biomass rather than root production (Hendricks et al., 2006; Singh et al., 1984). Ingrowth cores have several limitations, such as between sampling intervals the roots might die and be unaccounted for production, roots can be lost during core washing (up to 30%) (Cahoon et al., 2003; Sierra et al., 2003) or prune after being damaged during the ingrowth core installation. Those limitations should be acknowledged, but can also be overcome in several ways (Li et al., 2013). Minirhizotrons have proved to be suitable in other ecosystems and recently in mangroves (Arnaud, 2021; Arnaud et al., 2021), but this method needs further developments to convert their result into biomass increment (Arnaud et al., 2021).

8 | MOVING FORWARD: A ROADMAP TOWARDS CLOSING EXISTING KNOWLEDGE GAPS ON MANGROVE ROOT PRODUCTION

(1) We advocate for the creation of a scientific network on mangrove root traits, including root production. This MangRoot Network could facilitate collaboration between scientists, increase capacity building for the measurement of root production (e.g. through workshops) and facilitate the creation and the maintaining of a root trait database for mangroves (such as FRED: Iversen et al., 2017 or TropiRoot: <https://tropiroottrait.github.io/TropiRootTrait/>). Such a database, could aim to assess the growing body of literature on mangrove root production and more broadly on root traits (e.g. mortality, exudations) to understand how mangrove root traits vary over time, space and in response to global changes. The network could also trigger large and coordinated in-situ root trait measurements paired with surface elevation tables (i.e. measuring soil accretion rate) to provide a mechanistic understanding of the role of root production in soil accretion across mangroves.

(2) A significant increase in global efforts to observe mangrove root production is required, prioritising currently under-represented geomorphic settings (i.e. delta) and geographic areas, such as Indonesia, South America or Africa. Specific focus is required on carbon-rich mangroves, but also towards quantifying root production in deeper soil layers (~1 m deep) than current practice. Root production studies will also be more valuable to increase our mechanistic understanding if they include multiple treatment effects (e.g. sea level rise crossed with warming) and report several environmental factors (i.e. inundation frequency and duration).

(3) Improved forecasting of mangrove root production is critical. More in-situ research needs to be carried out on the belowground carbon dynamics of mangroves under global change scenarios.

Ecosystem-plot experiments using Free Air CO₂ Enrichment (FACE) crossed with warming have indicated unexpected belowground carbon dynamics, notably in salt marshes (Noyce et al., 2019). The next step is to develop a multifactorial experiment involving manipulated sea levels, warming and FACE that will not only cover root production, but the overall mangrove ecosystem response to global changes (Arnaud, 2020).

9 | CONCLUSIONS

- Global mangrove root production is $\sim 770 \pm 202$ g of dry biomass m⁻² year⁻¹ or 41 ± 11 TgC year⁻¹ over the entire area. The main controls of root production are the geomorphological settings of mangroves in combination with air temperature and precipitation (i.e. $\sim 30\%$ of variance explained; $p < .001$).
- Burial of root-derived carbon is 23 ± 5 TgC year⁻¹ representing $>90\%$ of the total carbon buried in world mangroves. Vertical and lateral losses of carbon derived from mangrove roots were 19 ± 5 TgC year⁻¹ revealing the importance of studying roots to better understand global mangrove losses (e.g. DIC, DOC, CO₂).
- Warming, changes in precipitation and eutrophication are likely to alter mangrove root production. Yet, there are significant knowledge gaps to predict the interactive effects of multiple environmental changes. Creation and enrichment of a mangrove root trait database with root production from understudied regions coupled with large manipulative experiments are promising approaches to further foster our understanding of mangrove carbon dynamics under global changes.

AUTHOR CONTRIBUTIONS

Marie Arnaud led the writing of the manuscript and performed the literature review. Marie Arnaud, Sami Ullah, Stefan Krause, Dang Thuong Huyen, Richard J. Norby designed the study, with critical inputs of Nezha Acil, Nicholas Kettridge and Vincent Gauci. Marie Arnaud analysed the data with the support of Sami Ullah, Stefan Krause and Richard J. Norby. Sami Ullah, Stefan Krause, Richard J. Norby, Dang Thuong Huyen, Nezha Acil, Nicholas Kettridge and Vincent Gauci contributed to the manuscript writing and revisions.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.7766370>.

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SUPPORTING INFORMATION

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