Mangrove root biomass and the uncertainty of belowground carbon estimations

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Abstract

Mangroves sequester large amounts of carbon (C) and they are increasingly recognised for their potential role in climate change mitigation programs. However, there is uncertainty in the C content of many mangrove forests because the amount of C stored in the roots is usually estimated from allometric equations and not from direct field measurements. There are only a handful of allometric equations in mangroves that are used worldwide to estimate root biomass, however, root biomass can vary from the allometric relationship if the environmental conditions are different from those where the equation was developed. In this study, we compiled recent information on how mangrove roots are affected by environmental conditions. Then, we explored the effect of sampling methodology on root biomass estimations. Finally, we compared published values of root biomass from field measurements against our estimations from allometric equations. The goal was to calculate the uncertainty associated with the estimation of root biomass and thus, the belowground C content of mangroves. The results showed that sampling methodology has a significant effect on root biomass estimations. The highest biomass estimations are reported where both live and dead roots are measured and when the roots are sampled by digging trenches. When comparing measured values against estimations from allometric equations, on average the general allometric equation provided root biomass values that were $40 \pm 12\%$ larger than those obtained from field measurements with cores. The result suggests that either: a) sampling with cores largely underestimates root biomass, or b) allometric equations overestimate root biomass when used outside the region where they were developed. The uncertainty in root biomass estimates from allometric equations corresponds to 4 to 15 % of the ecosystem C stock (trees + soil), with higher uncertainties in forests with low tree density and low interstitial salinity. We provide a statistical model that includes salinity, forest density and

root biomass to correct for this systematic bias. The estimated uncertainty is important to consider when quantifying C budgets at large spatial scales and to validate methodological approaches to C stock estimations.

Keywords: allometric equations; blue carbon; carbon stocks; forested wetlands; salinity

1. Introduction

Mangroves are productive tropical forests and have a large capacity for carbon (C) storage (Donato et al., 2011). Estimations of C stocks of mangroves have become increasingly important in recent years, as mangroves are key participants in climate change mitigation projects. Mangroves are one of the most threatened forests; in the last quarter century they have declined by 35 to 86% of their original area (Duke et al., 2007; Hamilton and Casey, 2016). The loss of mangroves causes the release of considerable amounts of CO₂ to the atmosphere (Lovelock et al., 2011). Accurate C stock estimations are needed to quantify mangrove contributions to C mitigation strategies.

Mangrove C stocks are the sum of carbon stored in tree shoots, roots, downed wood, and soil. From these, the most important component is the soil, which accounts for more than 50% of the total C stock (Kauffman and Donato, 2012). The second most important component of mangrove C stocks are the trees, which include aboveground biomass and live roots (Kauffman and Donato, 2012). Aboveground biomass has been extensively studied using measurements of morphological parameters of the tree (e.g. trunk diameter, height) and allometric relationships developed for many mangrove species, regions, and climates around the world (e.g. Komiyama et al., 2005; Soares and Schaeffer-Novelli, 2005). Soil C content has been directly measured within the soil profile following standard methodologies (e.g. Kauffman and Donato, 2012). In contrast, measurements of root biomass are scarce, creating a significant uncertainty in the global C budget (Alongi, 2014). Field measurements of root biomass are labour intensive and difficult, thus root biomass has generally been estimated from allometric equations. Allometric equations estimate the relationship between aboveground morphological parameters and belowground

biomass. Some of the allometric equations that have been developed are species specific (e.g. Tamai et al., 1986 for *Rhizophora* sp) and some are general equations for all mangrove species (e.g. Komiyama et al., 2005). Allometric equations have been developed for a few biogeographic regions (e.g. Florida, Southeast Brazil, Southeast Mexico, Thailand, Micronesia), but they are widely applied to mangrove forests throughout the world (e.g. Yucatan, Mexico; Adame et al., 2013). Estimations using allometric equations are extremely useful to obtain data that would otherwise be unavailable, however, such generalities carry inherent uncertainties (Njana et al., 2015).

In this study, we explore the uncertainty of root biomass estimations, and thus belowground C, due to field sampling constraints and limited availability of allometric equations. First, we review recent research on mangrove root biomass and analyse how environmental factors, such as forest structure and salinity, affect the ability of allometric equations to predict root biomass. Second, we analyse different sampling methodologies to estimate how they might affect root biomass estimations. Finally, considering the limitations of sampling strategies for root biomass, we estimate the uncertainty of belowground C stock estimations for mangroves.

1.1 Biomass allocation in mangrove roots

Mangroves are considered ‘bottom heavy plants’ as they invest much of their biomass into their root system (Komiyama et al., 2008, 2000). Mangroves have two kinds of root systems adapted to the anoxic and saline conditions of mangrove habitats: aerial roots that grow above the soil surface, and belowground roots. Belowground root biomass in mangroves generally contributes up to 60% of the total tree biomass (Khan et al., 2009; Komiyama et al., 1987; Tamooch et al.,

2008). However, in some rare cases, such as in hypersaline flats in Australia, root biomass may exceed aboveground biomass by a factor of four or more (Saintilan, 1997). In temperate and boreal terrestrial forests, root biomass usually accounts for approximately 20% of the plant biomass (Jackson et al., 1996). It is believed that mangroves invest more fixed C to their root system compared to other plants in order to transport oxygen, maximize water uptake, retain nutrients, and increase stability in an anoxic and waterlogged environment (Ball, 1988a; Reef et al., 2010). Thus, root biomass per area in mangrove forests may be higher than the root biomass of terrestrial forests.

1.2 Root biomass distribution

Trends in root distribution are based on measures of root size, root density, and penetration depth. Standards for root diameter classes do not exist, although the following classifications are commonly used and widely recognized: (1) fine, 0-2.0 mm, (2) small, 2-5 mm (3) medium/coarse, >5 to 20 mm, and (4) large roots, >20 mm (Vogt et al., 1998). Other classifications define the limit between small and medium roots as 2 mm, because fine roots (< 2 mm) are structures for water and nutrient uptake, while medium roots (2-4 mm) are transport conduits and support structures (Gleason and Ewel, 2002). Most estimates on root biomass in mangroves only include roots < 20 mm, because estimations of large roots requires laborious excavations of large soil trenches or pits (Komiyama et al., 1987; Njana et al., 2015).

In mangroves, the contribution of roots of different size classes to the total biomass is variable. In Thailand, fine roots (< 2 mm) contributed 44-66% to the total root biomass (Komiyama et al., 1987). Conversely, in mangroves of Florida, Mexico, and Kenya medium

112 roots (>5- 20 mm) accounted for the majority of root biomass (Adame et al., 2014; Castañeda-
113 Moya et al., 2011; Tamooch et al., 2008). Similarly, in 3 year-old restored mangroves in Gazy
114 Bay, Kenya, medium roots (>3 mm) accounted for 65-95% of the total root biomass (Lang'at et
115 al., 2013). The difference in root size class contributions may be due to differential productivity
116 and decomposition rates in fine versus coarse roots (Tamooch et al., 2008), which differ among
117 locations and mangrove species. For example, in Belize, the contribution of fine roots to the total
118 root biomass of *Rhizophora mangle* is higher compared to *Avicennia germinans* (Mckee, 1995).
119 In Kenya, the contribution of medium and fine roots to the total root biomass was lower for
120 *Rhizophora mucronata* (24%), compared to *Sonneratia alba* and *Avicennia marina*, whose
121 medium and fine roots contributed 45% to the total root biomass (Tamooch et al., 2008).

122
123 Mangrove root biomass decreases with soil depth. In mangrove forests in northern
124 Australia, 80% of the root biomass was concentrated in the top meter of soil (Boto and
125 Wellington, 1984). In Florida, shallow (0-45 cm depth) root biomass ($2,584 \pm 249 \text{ g m}^{-2}$) was
126 greater than deeper (45-90 cm depth) root biomass ($1,008 \pm 205 \text{ g m}^{-2}$), and accounted for 57-
127 78% of the total root biomass (Castañeda-Moya et al., 2011). Similarly, in Gazi Bay, Kenya, root
128 biomass decreased with soil depth, with 44 to 67% of the total live root biomass concentrated in
129 the first 20 cm of soil (Tamooch et al., 2008). A similar pattern is found in terrestrial vegetation,
130 where 75% of the root biomass is concentrated in the top 40 cm of soil (Jackson et al., 1996).

131
132 Root biomass varies among species. In Kenya, reforested stands of *A. marina* had a root
133 biomass of 43.7 t ha^{-1} compared to *S. alba* with $53.4\text{-}75.5 \text{ t ha}^{-1}$, both of which were higher than
134 the root biomass of *R. mucronata* with $7.5\text{-}24.9 \text{ t ha}^{-1}$ (Tamooch et al., 2008). In Yucatan, Mexico,

higher root biomass was measured in forests dominated by *A. germinans* compared to those dominated by *R. mangle* and *Laguncularia racemosa* (Adame et al., 2014). In subtropical Australia, the highest root biomass was measured in stands of *Rhizophora stylosa* and *A. marina* compared to those of *Aegiceras corniculatum*, *Excoecaria agallocha* and *Ceriops australis* (Saintilan, 1997). Mixed species forests have higher root yield, especially when *A. marina* is present (Lang'at et al. 2013).

Root biomass increases with forest age. A replanted mangrove forest of *Rhizophora apiculata* at 5 years had 23.1 t ha⁻¹ of roots; at 25 years, root biomass increased to 35.6 t ha⁻¹ (Alongi and Dixon, 2000). Similarly, a 6 year-old plantation of *R. mucronata* had 7.5 t ha⁻¹ of root biomass; at 12 years, the biomass increased to 24.9 ± 11.4 t ha⁻¹, which was lower than values for the natural stands of 35.8 t ha⁻¹ (Tamooch et al., 2008). In Brisbane, Australia, regrowth mangrove forests of *A. marina* achieved similar root biomass to natural stands after 25 years of growth (118 vs. 121 t ha⁻¹; Mackey, 1993).

Root biomass is strongly dependent on conditions of resource gradients such as nutrients, and regulator gradients such as salinity and flooding (Castañeda-Moya et al., 2011). The root biomass variation under these gradients will be explored in the following sections.

1.3 Resources gradients and root biomass

Most mangrove species are highly sensitive to variation in nutrient availability, with nitrogen (N) and phosphorus (P) being the nutrients most likely to limit growth (Reef et al., 2010). Species differences in tolerance to low and high nutrient availability are reflected in the distribution of

mangroves. For instance, where their distributions overlap, *R. mangle* often dominates in low nutrient environments, whereas, *A. germinans* dominates in areas with high nutrient availability (Mckee, 1993; Sherman et al., 1998). Additionally, the location of the forest across the intertidal affects nutrient limitation. For example, on offshore islands in Belize, *R. mangle* growth was N-limited in the low intertidal, P-limited in the high intertidal, and N- and P- limited in the transition zone (Feller et al., 2003).

Nutrient limitation affects root production. The resource-ratio hypothesis predicts that plants optimise a limiting resource in exchange of energy invested in other processes (Tilman, 1985). Mangroves can increase root: shoot (R:S) ratios when they need to maximize the capture of nutrients (Khan et al., 2009; Lovelock et al., 2014; Naidoo, 2009). Based on the resource-ratio hypothesis, under nutrient limitation, root biomass would be high. Supporting this hypothesis, mangroves growing in P-depleted soil in Florida had higher root biomass compared to sites where soil P was higher (Castañeda-Moya et al., 2011). In Micronesia, productivity of roots < 20 mm in diameter did not vary significantly along a P gradient, but the distribution of total standing root biomass and fine root productivity followed patterns of N:P ratios, with larger biomass associated with relatively lower P concentrations (Cormier et al., 2015). However, in Yucatan, Mexico, contrary to the expected pattern, root biomass was highest where soil P was high (Adame et al., 2014). Similarly, high N and P concentrations stimulated root growth in trees of *A. marina* (Hayes et al., 2017)

There are only a few studies on the effects of nutrients on root production, but it seems that nutrients do not act alone and are highly influenced by other factors such as species

composition, competition, decomposition rates, and the hydroperiod (Feller et al., 2003; Simpson et al., 2013). For instance, fine root biomass in Florida was negatively correlated with soil P, but also with inundation frequency (Castañeda-Moya et al., 2011). In Florida, USA, the response of root biomass to N additions was dependent on whether mangrove seedlings were in competition with saltmarsh species for nutrient acquisition (Simpson et al., 2013). Seedlings of *A. germinans* grown in low nutrient conditions and elevated CO₂, had significantly higher root biomass compared to those grown under ambient CO₂ conditions (Reef et al., 2016), even when the ambient CO₂ seedlings were given higher nutrient concentrations. In Yucatan, Mexico, belowground biomass increased with P in a forest dominated by *A. germinans* with low inundation frequency and high salinity (Adame et al., 2014), factors that seem to be associated with high root production and low decomposition rates.

1.4 Regulators gradients and root biomass

In addition to resource gradients, plant biomass is also influenced by various regulator gradients (Huston, 1997). In mangroves, regulators include common stressors such as salinity, hydrogen sulphide, and flooding (McKee and Mendelssohn, 1988; McKee and Mendelssohn, 1987). Mangrove regulators influence growth, reproduction, and allocation of C in mangrove roots (Reef et al., 2016, 2015, 2010).

Although mangroves are adapted to highly saline environments, soil salinity has long been recognized as an important factor limiting mangrove growth and productivity (Clough 1984). Low and moderate salinity stimulate growth of mangrove trees, but a further increase in salinity reduces their growth (Ball, 1988b; Cherian et al., 1999). Salinity also affects R:S ratios

of mangroves, as the case of mangroves growing in a river in subtropical Australia, whose R:S ratios increased with increasing salinity (Saintilan, 1997). A similar result was found in the Dominican Republic, where not only R:S but also fine root biomass increased with salinity (Sherman et al., 2003). Salinity decreased the length and diameter of roots of *A. germinans* seedlings and increased tissue density (Reef et al., 2015). Thus, salinity might reduce the growth and biomass of the aboveground plant, but increase root biomass, alter its structure, and modify decomposition rates.

The frequency of flooding in mangrove forests affects the amount of hydrogen sulphide and soil redox potential, both factors associated with root growth (Mckee, 1993). In glasshouse experiments with seedlings of mangrove species, flooding decreased root biomass of *A. germinans*, but increased root biomass of *R. mangle*; additionally, hydrogen sulphide decreased root biomass of *A. germinans* and increased R:S of *R. mangle* (Mckee, 1993). Overall, these results suggest that the response of belowground production to flooding varies among mangrove species.

2. Sampling techniques

Most methodologies for measuring root biomass in forests, including mangroves, carry uncertainties and biases (Publicover and Vogt, 1993; Singh et al., 1984). Currently, most field studies are done by taking several cores of about 5-10 cm in diameter from the sediment. The relatively narrow cores represent only a small portion of the forest, which is then extrapolated to larger areas. Root biomass is greater close to the base of the trees (Saintilan, 1997; Tamooch et al., 2008), which is the most difficult area to sample due to the obstruction of larger roots.

Sediment cores only allow for roots smaller than 20 mm in diameter to be sampled, further limiting their ability to measure total root biomass accurately. For example, in Thailand, roots >20 mm accounted for $\approx$ 30-70% of total root biomass (Komiyama et al., 1987). Therefore, it is likely that a majority of studies using narrow cores underestimate mangrove root biomass.

Spatial variation is inherent to estimates of root biomass and large associated errors are common (Fairley and Alexander, 1985). Differences in sampling methods such as number of replicates, size of roots sampled, and sampling depth makes comparisons amongst locations difficult (Mokany and Raison, 2006). For instance, the use of different sampling approaches has a large impact on root biomass estimations; our metanalysis shows that root biomass measured with the trench method was significantly higher than root biomass measured with any other approach (Fig. 1; $F_{3,50}=16.8$, $p < 0.001$). Excavating all the roots within a trench or pumping the soil from the roots around a tree provide biomass values that were about three times larger than those obtained with any other method. By excavating trenches, roots of all size classes are sampled, including those with a diameter > 20 mm, which are not included in other methods (Fig. 1, Table 1).

Another difference in methodological approach accountable for a large proportion of variation in root biomass is the inclusion of dead roots (Table 1, Fig. 1). Dead roots account for a significant but highly variable amount of the total root biomass with values ranging from 11 to 95% (Chalermchatwilai et al., 2011; Robertson and Alongi, 2016; Tamooch et al., 2008). The accumulation of dead roots is likely the result of slow rates of decomposition in anoxic mangrove soils (Chalermchatwilai et al., 2011). The proportion of dead to live roots has been

found to vary among species, forest age, and soil depth. Among tree species, the contribution of dead roots to total root biomass was lowest for a mixed forest of *Avicennia* and *Sonneratia* (11%), intermediate for a forest of *Rhizophora* (28%), and highest for a forest of *Xylocarpous* with (66%; Chalermchatwilai et al., 2011). Dead root biomass is highest in replanted stands of mangroves at 6 years compared to mangroves at 12 years and natural stands (Tamoooh et al., 2008). Despite the large contribution of dead roots to total root biomass, most studies in the past either excluded them from their calculations, or pooled them with live roots (Table 1). Separation of dead and live roots with colloidal silica (e.g. Robertson and Alongi, 2016) or through density differences between dead and live tissue (e.g. Castañeda-Moya et al., 2011) are cost-effective methods that should become standard practice. The separation of dead and live roots is important, because dead root biomass values are necessary for estimations of C stocks, while live root biomass values are needed to understand tree biomass partitioning

Finally, the depth at which roots are sampled affects root biomass estimations. As described above, most root biomass (> 80%) is concentrated in the first meter of soil, with > 50% of total root biomass in the first 45 cm (Boto and Wellington, 1984; Castañeda-Moya et al., 2006; Tamoooh et al., 2008). Thus, studies that integrate over depths shallower than 45 cm are likely underestimating total root biomass.

The large discrepancies in root biomass values obtained from different methodological approaches have important implications. Despite the general acceptance that mangroves have high R:S and large root biomass, our data set shows that in general, mangrove root biomass and R:S are similar to those from terrestrial biomes (Table 1, Mokany and Raison, 2006). The

273 exception is scrub mangroves and forests growing at high salinity, which had R:S values >1
274 (e.g. Castañeda-Moya et al., 2011; Saintilan, 1997).
275
276
277 **Table 1.** Root biomass (total or < 20 mm diameter and fine or < 2 mm diameter) and root: shoot
278 (R:S) ratios for mangroves sampled with different methodologies: cores, felled trees and
279 trenches. *Rh* = *Rhizophora*; *Av* = *Avicennia*; *La* = *Laguncularia*; *Ce* = *Ceriops*. Sampling strategy
280 refers to the number of samples, depth that roots were sampled to, size range of the roots
281 sampled, and whether live and dead roots were measured separately (live and dead) or pooled
282 together (live + dead).

Location/site	Sampling strategy	Species/ vegetation type	Total root biomass (ton ha ⁻¹)	Fine root biomass (<2 mm; ton ha ⁻¹)	R:S	Reference
CORES						
Yela, Kosrae Micronesia	Live and dead Root size < 20 mm, 45 cm depth n= 80	Mixed, fringe	9.5	1.5	0.07	Cormier et al., 2015
		Mixed, interior	11.9	1.8	0.05	
		Mixed, riverine	14.3	1.8	0.05	
Sapwala, Pohnpei, Micronesia		Mixed, fringe	13.7	2.9	0.02	
		Mixed, interior	26.4	5.7	0.05	
		Mixed, riverine	4.5	1.7		
Hinchinbrook Island Australia	Live and dead Root size >2mm< 100 cm depth; n = 60	Low intertidal, <i>Rh</i>	4.3	0.8	0.11	Alongi and Robertson 2016
		Mid intertidal <i>Rh</i>	4.4	1.1	0.27	
		High intertidal <i>Ce</i>	3.3	0.9	0.14	
	Live	<i>A. germinans</i> mouth	30.4	3.2	0.31	Adame et al., 2014

Celestun, Yucatan, Mexico	Root size < 20mm, 35 cm depth; n= 24	<i>R. mangle</i> mid lagoon	11.3	1.8	0.18	
		<i>L. racemosa</i> inner lagoon	9.5	1.7	0.16	
Taylor River, US (TS/Ph-6)	Live Root size < 20 mm	<i>R. mangle</i> - scrub	23.2	3.2	1.96	Castañeda-Moya et al., 2011; Castañeda 2010.
(TS/Ph-7)	90 cm depth	<i>R. mangle</i> - scrub	46.7	5.0	4.15	
(TS/Ph-8)	n= 60	<i>Ce</i> - fringe	43.5	6.6	10.69	
Shark River, US (SRS-4)		<i>R. mangle</i> - riverine	31.9	5.8	0.35	
(SRS-5)		<i>R. mangle</i> - riverine	43.8	4.4	0.45	
(SRS-6)		<i>L. racemosa</i> - <i>R. mangle</i> riverine	25.3	3.5	0.19	
Western Australia	Live and dead	<i>R. stylosa</i>	45.6		0.19	Alongi et al., 2000.
	40 cm depth; n=18	<i>A. marina</i>	16.3		0.17	
Trat River, Thailand	Live and dead	<i>Avicennia-Sonneratia</i>	15.9	10.8		Chalermchatwilai et al., 2011
	Root size <20 mm	<i>Rh</i>	42.9	21.9		
	30 cm depth; n =25	<i>Xylocarpus</i>	134.7	91.4		
Gazi Bay, Kenya	Live and dead	<i>R. mucronata</i>	7.5-35.8			Tamooh et al., 2008
	Root size >5 mm to <40 mm	<i>Sonneratia alba</i>	48.4-75.5			
	60 cm depth; n=332	<i>A. marina</i>	39.1-43.7			
Utwe and Okat River Kosrae, Micronesia	Live and dead	<i>Bruguiera</i>	8.0	8.0		Gleason & Ewel 2002
	Root size <4mm;	<i>Rh</i>	7.7	6.0		
	30 cm depth; n=30	<i>Sonneratia</i>	9.7	8.7		
Gazi Bay, Kenya	Live + dead 60 cm depth; n=36	<i>R. mucronata</i>	24.9		0.23	Kairo et al., 2008
Samana Bay,	Live + dead	<i>R. mangle</i> - <i>L. racemosa</i>	66.0	7.9		Sherman et al., 2003

Dominican Republic	Root size < 20 mm 30 cm depth; n=200					
Hawkesbury River, Australia	Live + dead; n=56	<i>A. marina</i>	~50-170		0.28-4.10	Saintilan 1997a
		<i>Aegiceras corniculatum</i>	~30-180		0.40-1.90	
Mary River, Australia	Live estimate n=224	<i>A. marina</i>	~10-60		~0.4-1.3	Saintilan 1997b
		<i>Aegiceras corniculatum</i>	~20-70		~0.4-3.0	
		<i>Exoecaria agallocha</i>	~10-60		~0.2-0.4	
		<i>R. stylosa</i>	~100-110		~1.2-1.6	
		<i>C. australis</i>	~40		~0.2-3.3	
Majana, Cuba		<i>A. germinans</i>	10.8	0.61		Fiala & Hernandez 1993
Brisbane River, Australia	Live +dead 30 cm depth; n=10	<i>A. marina</i>	119		0.58	Mackey 1993
Lane Cove River, Australia	Live +dead 45 cm depth; n=20	<i>A. marina</i>	153.8		1.22	Briggs 1977
Mangawhai, New Zealand	Live + dead 100 cm depth; n=30	<i>A. marina</i>	131.6	76.2	1.73	Tran 2013
FELLED TREES						
Sundarbans, India	n=100 trees	<i>Mixed forest</i>	15.3-39.6		0.23	Ray et al., 2011
Okinawa Is, Japan	n=5 trees	<i>Kandelia obovata</i>	51.1		0.47	Hoque et al., 2011
Shenzhen, China	50 cm depth; n=9 trees	<i>A. corniculatum</i> , <i>Kandelia candel</i> , <i>A. marina</i>	33.1 3.9 1.2		0.40	Tam et al., 1995

Magueyes Is. Puerto Rico	n=10 trees	<i>R. mangle</i>	3.9			Golley et al., 1962
TRENCH						
Sapwalap River, Pohnpei, Micronesia		Mixed inland	269			Mori et al., 1997
		Mixed estuary	348			
		Mixed fringe	359			
Thailand	Live estimated 60 cm depth; Root size <40 mm n= 30 blocks from one tree	<i>C. tagal</i>	87.5		1.11	Komiyama et al. 2000
	Live + dead; 1 m depth Root size <2 to >50 mm n= 310 blocks from two trees	<i>Sonneratia</i>	171.8	103.7		Komiyama et al., 1987
		<i>Bruguiera</i>	242.6	137.5		
		<i>Rhizophora</i>	509.5	236.4		
Okinawa, Japan	Live + dead n≈ 50 blocks from one plot	<i>Kandelia obovata</i>	46.1		0.58	Khan et al., 2009

283 * Values estimated from graph

284

285 3. Aboveground parameters associated with root biomass- A meta-analysis

286 We analysed the published data to identify common parameters that affect root biomass. We

287 selected studies where: a) roots were sampled with cores, thus included roots < 20 mm in

288 diameter b) live roots were separated from dead roots, c) roots were sampled to a depth of at

289 least 35 cm, and d) the structure of the forest (tree density and diameter at breast height, DBH)

was reported in the literature. We extrapolated root biomass to one meter depth, considering that 75% of the root biomass is concentrated in the top 45 cm (Castañeda-Moya et al., 2011). The mean root biomass (< 20 mm diameter) for studies that complied with the requirements (7 studies, Table S1) was $33.6 \pm 3.2 \text{ ton ha}^{-1}$ with a range of 6.1 to 85.4 ton ha^{-1} . We found that highest root biomass was found in dense stands of trees with small DBH (Fig. 2B-C: $R^2 = 0.32$ $p = 0.0003$ $n = 37$ and $R^2 = 0.26$ $p = 0.0015$ $n = 34$, for root biomass versus tree density and DBH, respectively, SPSS Statistics v21, IBN, NY, USA). A similar association has been found in terrestrial forests (Litton *et al.* 2002). At local scale, the association between high tree density and large root biomass in mangroves has also been observed. In Kenya, root biomass was higher in dense stands of replanted mangroves compared to natural stands (Tamooh et al., 2008). Similarly, in mangroves in Thailand and Mexico, highest root biomass was found in forest with high tree density (Adame et al., 2014; Komiyama et al., 1987). Highest root biomass in dense forests may be due to nutrient competition among trees (Lang'at et al., 2013). We can conclude that there is a trend of high root biomass in dense mangrove forests, especially those with densities $> 1,000 \text{ trees ha}^{-1}$ and DBH $< 10 \text{ cm}$ (Fig 2 B,C).

4. Uncertainty in belowground C stock estimations

Roots account for about 1 to 16% of the total C stock (Adame et al., 2015, 2013), however, this estimate is uncertain, as root biomass is usually indirectly estimated with allometric equations. To determine the level of uncertainty of such estimations, we compared published values of root biomass measured in the field with cores against root biomass estimated with allometric equations. We tested two kinds of equations: the general allometric equation developed for all mangrove species (Komiyama et al. 2005) and species-specific allometric equations. The general

equation is based on the relationship between root biomass, DBH and wood density (obtained from Chave et al., 2009; Zanne et al., 2009). The species-specific equations are generally based on the relationship between root biomass and DBH of the tree. We used the equations from Comley and Guinness for *A. marina* (2005), Smith and Whelan (2006) for *R. mangle*, *L. racemosa* and *A. germinans*, Ong et al. (2004) for *R. apiculata*, and Tamai et al. (1986) for *Brugueira spp* and other *Rhizophora spp*. We only included studies where forest structure (DBH, forest tree density) were available from the same location where roots were sampled (number of studies =7; Fig. 3). We conducted a linear regression between root biomass measured in the field with cores against root biomass estimated from allometric equations. Deviations from the 1:1 relationship were expected, as allometric equations include large roots, while cores only account for roots < 20mm in diameter.

Our results show that estimated root biomass by allometric equations and those measured in the field with cores largely deviated from a 1:1 relationship (Fig. 3). Estimations of root biomass from the general allometric equation were on average $43 \pm 12 \text{ ton ha}^{-1}$ higher than root biomass measured in the field with cores ($p < 0.001$); species-specific allometric equations were on average $35 \pm 27 \text{ ton ha}^{-1}$ higher. However, root biomass estimated with the species-specific equation had a closer 1:1 relationship with measured root biomass than root biomass estimated with the general equation (Fig. 3). Discrepancies between field measurements and allometric equations of about ten-fold have been previously noted in other studies (e.g. Khan et al., 2009; Komiyama et al., 1987).

The differences between measured and estimated root biomass were variable among forest type. Differences were highest (450-1500%) in forests with low tree density, low interstitial salinity, and low root biomass (Fig.4 A-C). Differences also varied with mangrove species, with most studies on *Rhizophora* forests overestimating root biomass, while studies on *Sonneratia* forests underestimating root biomass (Fig.5). These results are consistent with our findings from the literature that despite tree size, root biomass is highest in dense forests with high salinity dominated by *Avicennia* sp. Thus, if allometric equations overestimate root biomass, the overestimation is lower in sites which have naturally high root biomass. This relationship can be described with a multiple regression model (R Core Team 2016) with forest tree density and salinity as predictors of the overestimation (%) of root biomass (Table 2).

Table 2: Regression of the overestimation of root biomass (%) as predicted by forest tree density (trees ha⁻¹) and salinity (ppt). The model has an adjusted R²= 0.24: p = 0.013

	Estimate	Std. Error	t value	p-value
Intercept	1776.8	486.4	3.65	0.0013
Ln (density)	-93.6	47.09	-1.99	0.0583
Ln (salinity)	-241.1	130.35	-1.85	0.0767

We can apply this model to the example in Adame et al. (2015), where root biomass of riverine mangroves in Mexico was estimated with the general equation (Komiya et al., 2005). In one location -Las Palmas- the forest was dominated by *A. germinans*, had relatively high tree density of 5,370 trees ha⁻¹, interstitial salinity of 28.9 ppt and estimated root biomass of 268.7 ton ha⁻¹. In another location -Zacapulco-, the forest was dominated by *R. mangle*, forest density was

lower with 1,765 trees ha⁻¹, interstitial salinity was also lower with 7.6 ppt and estimated root biomass was 127.8 ton ha⁻¹. Despite leaving a considerable proportion of variation unexplained ($R^2 = 0.24$), our model (Table 2) produces a predicted overestimation, which can be applied to the initial estimates to produce a revised estimated root biomass (with 95% confidence intervals).

$$\text{Las Palmas: } 1776.8 - 93.6 \times \ln(5370) - 241.1 \times \ln(28.9) = 162\% (\pm 157\%)$$

$$\text{Zacapulco: } 1776.8 - 93.6 \times \ln(1765) - 241.1 \times \ln(7.6) = 588\% (\pm 370\%)$$

Accounting for this systematic error, we can estimate that root biomass is more likely to be $268.7/(1+1.62) = 102.5$ ton ha⁻¹ for Las Palmas (95% CI, 64 – 256 ton ha⁻¹) and $127.8/(1+5.88) = 18.6$ ton ha⁻¹ for Zacapulco (95% CI, 12 – 40 ton ha⁻¹). As a result of this correction, the ecosystem C stock of these forests decreased between 6 to 10%. On average, root biomass estimated with the general allometric equation (Komiya et al., 2005) was $40 \pm 12\%$ higher than root biomass measured in the field with cores. Thus, if we consider roots to account for about 10% of the ecosystem C stock, about 4% of mangrove ecosystem C stocks are overestimated or are uncertain.

Our results highlight the fact mangrove physiognomy is different from terrestrial trees as it strongly affected by unique environmental factors such as salinity (Lovelock *et al.* 2015). Allometric equations whose sole basis is the physical structure of the tree do not fully account for environmental factors which appear to systematically affect root biomass and therefore, may have limited application in many mangrove outside the region where they were developed.

5. Policy implications

Mangroves and other vegetated coastal habitats will be used increasingly in C sequestration and global climate change mitigation strategies (e.g. Duarte et al., 2013; Murdiyarso et al., 2015).

With the expansion of voluntary and regulatory C credit and trade markets worldwide, comprehensive data are imperative for calculating an equitable value for the loss or exchange of critical ecosystems.

Much has been done to identify global standards for quantifying and measuring coastal C. For example, Verified Carbon Standard and the American Carbon Registry create verifiable protocols relevant to policy makers. Standardized information will better inform efforts such as the United Nations Reducing Emissions from Deforestation and Forest Degradation Programme (REDD+), as well as other US and international agencies. These and other private organizations finance projects that support climate change mitigation through coastal C management and emissions reductions actions. In order for these groups to be successful, accurate estimates of C stocks and sequestration rates are necessary for the development of policies that will promote the conservation of C in coastal ecosystems (sensu Alongi, 2011).

Conclusions

We conclude that mangrove root biomass is likely to be higher in dense forest, with trees of small DBH, where salinity is high and tidal flooding is infrequent. We also conclude that sampling approach has an impact on root biomass estimations, with highest root biomass values estimated from trenches where all roots are excavated. Root biomass obtained from allometric equations is on average 40% higher than biomass measured in the field, but in some locations

overestimations > 1000% were found. Our results suggest that either: a) root biomass is underestimated when measured with cores in the field, or b) allometric equations overestimate root biomass when applied to regions different from where they were firstly developed. Importantly, we found that there is a systematic error when estimating root biomass from allometric equations, with higher uncertainty in forest with low interstitial salinity and low tree density. The uncertainty due to limitations of root C estimations accounts on average for 4% of the total C stock, but in some forests it could be 10% of the total C stock.

To reduce errors in root biomass estimations the following guidelines should be considered:

- 1- Sampling of roots should include depths of at least 45 cm deep
- 2- Roots should be divided in at least two size classes: < 2mm and > 2 mm
- 3- Dead and live roots should be separated
- 4- Consider spatial variability in root biomass with distance from the base of the tree
- 5- Use species-specific allometric equations where possible
- 6- In mangrove forests with low interstitial salinity and low tree density, root biomass values derived from allometric equations that were not locally developed are likely to be highly uncertain. The model proposed in Table 2 that includes tree density and salinity can correct this systematic error, but further research could improve the goodness of fit of the prediction model.

Quantifying the uncertainties and errors associated is a key component in estimations of the C stock of mangrove forests and are necessary in formulating policy to ensure that

423 these ecosystems are fairly valued. Following these recommendations should improve C
424 estimations and reduce uncertainties associated to belowground components of mangrove
425 forests.

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Figure legends

Figure 1. Root biomass of mangroves (fine or < 2 mm diameter, and large or > 2 mm diameter) estimated with different methodological approaches: cores that included only live roots, cores that included live and dead roots, felled trees, and excavating trenches. Root biomass measured by excavating trenches was significantly higher than root biomass obtained with any other approach ($F_{3, 50} = 16.8$, $p < 0.001$). Data is from: Adame et al., 2014; Alongi et al., 2000; Briggs, 1977; Castañeda-Moya et al., 2011; Chalermchatwilai et al., 2011; Cole et al., 1999; Cormier et al., 2015; Fiala and Hernandez, 1993; Gleason and Ewel, 2002; Golley et al., 1962; Hoque et al., 2011; Kairo et al., 2008; Komiyama et al., 2000, 1987; Mackey, 1993; Mori et al., 1997; Ray et al., 2011; N Saintilan, 1997; N. Saintilan, 1997; Sherman et al., 2003; Tam et al., 1995; Tamooch et al., 2008; Tran, 2013.

Figure 2. Association between live root biomass (< 20 mm diameter) sampled with cores and extrapolated to 1m depth and A) aboveground biomass; B) diameter at breast height, DBH [log (cm)]; C) tree density [log (trees ha⁻¹)]. The regression lines, if present, are significant ($p < 0.001$; DBH, $n = 37$; tree density $n = 34$). Data is from: Adame et al., 2014, Alongi 2000, Alongi and Robertson 2016, Castañeda-Moya et al., 2011, Cormier et al., 2015, Tamooch et al. 2008. Forest aboveground biomass, DBH and tree density values were obtained from each study or from Castañeda 2010, Devoe and Cole 1988, Ewel et al., 1998, Kairo et al., 2008, and Slim et al., 1996.

Figure 3. Association between field measurements of root biomass (< 20 mm) extrapolated to 1m depth and root biomass estimations using (A,C) species-specific allometric equation derived from aboveground structure and (B,D) a general allometric equation based on diameter at breast

height (DBH) and wood density (Komiyama et al., 2005, developed in Thailand; Zanne et al., 2009). The dashed line represents a positive 1:1 relationship between measured and estimated root biomass. Data is from Adame et al., 2014 (Yucatan, Mexico), Alongi 2000 (Western Australia), Castañeda 2010, Castañeda-Moya et al., 2011 (Florida USA), Cormier et al., 2015 (Micronesia), Kairo et al., 2008, Tamooh et al., 2008 (Gazi Bay, Kenya).

Figure 4. Difference (%) between root biomass (live, < 20 mm) extrapolated to 1m depth measured in the field with cores and root biomass estimated from the general allometric equation (Komiyama et al., 2005) versus A) forest tree density (trees ha⁻¹), B) interstitial salinity (ppt), C) root biomass (ton ha⁻¹). Data is from Adame et al., 2014, Alongi 2000, Castañeda-Moya et al., 2011, Cormier et al., 2015, and Tamooh et al., 2008.

Figure 5. Difference (%) between root biomass (live, < 20 mm) extrapolated to 1m depth measured in the field with cores and root biomass estimated from the general allometric equation (Komiyama et al., 2005) and mangrove species. Data is from Adame et al., 2014, Alongi 2000, Castañeda-Moya et al., 2011, Cormier et al., 2015, and Tamooh et al., 2008.