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 recognized 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 ± 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 4–15% 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.

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 35–86% of their original area (Duke et al., 2007; Hamilton and Casey, 2016). The loss of mangroves causes the release of considerable amounts of CO_2 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; Tamooh 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, 1997a). 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, > 5–20 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 roots (> 5–20 mm) accounted for the majority of root biomass (Adame et al., 2014; Castañeda-Moya et al., 2011; Tamooh et al., 2008). Similarly, in 3 year-old restored mangroves in Gazy Bay, Kenya, medium roots

(> 3 mm) accounted for 65–95% of the total root biomass (Lang'at et al., 2013). The difference in root size class contributions may be due to differential productivity and decomposition rates in fine versus coarse roots (Tamooh et al., 2008), which differ among locations and mangrove species. For example, in Belize, the contribution of fine roots to the total root biomass of *Rhizophora mangle* is higher compared to *Avicennia germinans* (Mckee, 1995). In Kenya, the contribution of medium and fine roots to the total root biomass was lower for *Rhizophora mucronata* (24%), compared to *Sonneratia alba* and *Avicennia marina*, whose medium and fine roots contributed 45% to the total root biomass (Tamooh et al., 2008).

Mangrove root biomass decreases with soil depth. In mangrove forests in northern Australia, 80% of the root biomass was concentrated in the top meter of soil (Boto and Wellington, 1984). In Florida, shallow (0–45 cm depth) root biomass (2584 ± 249 g m^{-2}) was greater than deeper (45–90 cm depth) root biomass (1008 ± 205 g m^{-2}), and accounted for 57–78% of the total root biomass (Castañeda-Moya et al., 2011). Similarly, in Gazi Bay, Kenya, root biomass decreased with soil depth, with 44–67% of the total live root biomass concentrated in the first 20 cm of soil (Tamooh et al., 2008). A similar pattern is found in terrestrial vegetation, where 75% of the root biomass is concentrated in the top 40 cm of soil (Jackson et al., 1996).

Root biomass varies among species. In Kenya, reforested stands of *A. marina* had a root biomass of 43.7 t ha^{-1} compared to *S. alba* with 53.4–75.5 t ha^{-1}, both of which were higher than the root biomass of *R. mucronata* with 7.5–24.9 t ha^{-1} (Tamooh 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, 1997a). 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} (Tamooh 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).