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Exceptionally high mangrove root production rates in the Kelantan Delta, Malaysia; an experimental and comparative study.

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Highlights

- A Malaysian mangrove forest shows exceptionally high annual root production of 12.7 t ha^{-1} yr^{-1}.
- Root productivity showed a strong seasonal trend, peaking during the monsoon season.
- Root turn-over was exceptionally rapid (especially that of fine roots at 0.81 yr^{-1}).
- The root:shoot productivity ratio (at 2.65), was comparatively high.
- Fine root biomass was the major contributor to belowground biomass and biomass production.

Abstract

Mangroves often allocate a relatively large proportion of their total biomass production to their roots, and the belowground biomass of these forests contributes towards globally significant carbon sinks. However, little information is available on root production in mangroves due to the difficulties in carrying out measurements of belowground processes, particularly if there is regular flooding. In this study, we examined fine and coarse root production in the east coast of the Malaysian Peninsula. Ingrowth cores were used over the course of 17 months. In September 2014, twenty cores were randomly placed in each of five plots. Three cores were collected from each plot (fifteen cores in total), once every three months. Each core was divided into five 10 cm layers and root dry mass was recorded. Standing root biomass was also measured at the time of final collection using an additional 15 cores. There was a seasonal pattern in root production, which peaked in March and December 2015, after and during the monsoon season. Root biomass in the cores peaked at 33.23 ± 6.3 t ha^{-1} and 21.46 ± 7.3 t ha^{-1} in March and December respectively. Standing root biomass in February 2016 in the forest was 20.81 ± 2.8 t ha^{-1}. After 17 months, the final root biomass in the cores was 14% less than the standing root biomass. These data suggest surprisingly rapid growth rates and turnover for mangrove roots. Total root biomass significantly increased with root depth and 78% of the roots, in all soil layers, consisted of fine roots (< 3 mm diameter). Soil carbon, nitrogen and phosphorous concentrations were investigated in relation to belowground production, as were soil temperature, salinity and dissolved oxygen. A data review of global studies reporting similar work was carried out. The results are discussed with consideration to the significance of monsoon rainfall for mangrove ecology.

Keywords: Root stock, root production, allocation aboveground, allocation belowground, monsoon season, rapid root turnover.

Introduction

Mangrove forests are very productive ecosystems (Tomlinson 1986; Alongi 2012). Carbon is fixed by the mangrove trees themselves and by associated algal communities on the aboveground roots and forest floor (Alongi 2014). This autochthonous production contributes to the large organic carbon reservoirs typically found in mangroves. In addition, allochthonous inputs from adjacent freshwater and oceanic systems are trapped and stored (Jannerjahn and Ittekkot 2002), with retention of this organic matter and associated nutrients promoting the high primary productivity (Kumara et al. 2010). This combination of high productivity, interception of allochthonous carbon and deep, anoxic soils means mangroves can store exceptionally large amounts of carbon, particularly in belowground deposits, and are one of the most carbon-dense ecosystems on Earth (Donato et al. 2011; Gress et al. 2016).

Studies of mangrove productivity have focused mainly on aboveground biomass using litter fall and stem diameter measurements (Gong and Ong 1990; Robertson and Alongi 1995; Sukarjo et al. 2013; Mitra et al. 2011). The litter fall data help to quantify total productivity and illustrate the sources of organic matter available for secondary consumption (e.g. by crabs), burial or export to the sea. Studies of stem diameter, typically using allometric equations (e.g. Komiyama et al. 2005), provide information concerning biomass accumulation in the tree trunk. However, recent years have seen a growing interest in belowground biomass and productivity, given the roles of mangroves as carbon sinks and coastal buffers. Most studies show mangrove ecosystems are efficient carbon sinks, with the largest carbon stock (more than 90%) consisting of organic carbon in the soil (Donato et al. 2011; Adame et al. 2015; Sanders et al. 2017). This finding is consistent across mangrove forest settings such as estuarine and oceanic mangroves of the Indo Pacific (Donato et al. 2011), different mangrove zonations (Kauffman et al. 2011), and natural or restored mangrove forests (Nam et al. 2016; Sahu et al. 2016). Mangroves have specialized root systems, including aerial roots, which allow respiration during submergence (Alongi, 2009). These complex aboveground features can reduce water current velocity and encourage deposition of particles (Krauss et al. 2003; Kumara et al. 2010). This process of accretion, and the expansion of roots belowground, can lead to vertical elevation of the soil surface. For example, in Caribbean mangroves, refractory roots and other organic materials (e.g. benthic mat algae, leaf litter, and woody debris) are substantially responsible for soil formation (McKee et al. 2007). Surface elevation driven by root growth and accretion can help ensure mangroves keep pace with rising sea levels and help buffer coastlines against the effects of sea level rise (McKee 2011). However, elevation can be inhibited or reversed by natural disturbances such as hurricanes and storms which can cause soil elevation loss (Cahoon et al. 2003; Barr et al. 2012; Cahoon 2006). Similarly, human disturbances may contribute to rapid surface elevation loss (Lang'at et al. 2014; Lovelock et al. 2015).

Understanding what controls mangrove root productivity, turnover and architecture is therefore important in understanding the ecological functions of forests. Several studies have explored the influences of environmental factors such as nutrients on biomass allocation patterns in mangrove forests (e.g., Alongi, 2009). In depleted nutrient settings, mangroves may allocate 40-60% of their production to belowground biomass (Komiyama et al. 1987). This is a strategy for plants to manage their resources efficiently under nutrient stress (Castaneda-Moya et al. 2011). In Floridian mangroves, soil phosphorus is always limiting, which results in stunted forests. Riverine mangroves, growing in more productive sites, tend to allocate proportionately more biomass to aboveground whilst nutrient limited scrub communities show greatest biomass allocation belowground (Castaneda-Moya et al. 2013). Mangroves in Micronesia also show greater proportional root biomass associated with relatively low soil phosphorus (Cormier et al. 2000). Nutrient limitation can interact with other stresses however; for example in a karst lagoon in Mexico with high salinity, greater root biomass and production was found with higher soil phosphorus (Adame et al. 2014). Under long tidal submergence and limited nutrients, high root biomass but lower root production and root turnover were recorded (Castaneda-Moya et al. 2011), perhaps because tidal submergence limits root production.

Many other factors, in addition to nutrients, may influence root production, including tidal range, rainfall, salinity and soil temperature (Komiyama et al. 1987; Saintilan 1997; Paungparn et al. 2016). Seasonality in mangrove root production has been observed, with the highest productivity recorded during the wet and early cool dry season (Paungparn *et al.* 2016). This suggests that root productivity is associated with increased rainfall and thus reduced salinity of porewater. Terrestrial forests show similar patterns, as seasonal root production in rubber trees correlates directly with rainfall (Maeght 2015).

Biomass allocation varies between mangrove species and tree stands. Fast growing species such as *Avicennia marina* allocate proportionally more biomass belowground under optimum environmental conditions, while *Rhizophora mucronata* invests more aboveground (Lang'at 2013). In Gazi Bay, Kenya, the highest belowground biomass was recorded in replanted mangrove forests rather than natural stands. *Sonneratia alba* showed the highest root biomass in comparison to *Avicennia marina* and *Rhizophora mucronata*, perhaps due to its exposed position at the seaward fringe, where investment in roots is needed to anchor the trees against wave impacts (Tamooh *et al.* 2008). There may also be complementarity between different root architectures; an experimental study at the same site demonstrated that mixed mangrove stands show greater proportional belowground productivity than monospecific ones (Lang'at *et al.* 2012).

Despite the newly discovered importance of belowground carbon storage in mangroves, and hence the belowground processes that control it, we still know relatively little about belowground productivity in mangrove forests and how it relates to aboveground productivity. The current study examines belowground productivity in a Malaysian forest and explores the influence of a range of environmental variables on root production. It also investigates the relationship between above and belowground growth rates.

Materials and Methods

Study site

This study was conducted on the Kelantan Delta ($6^0$12' 46.8" N 102^0 10'43.0" E), in the state of Kelantan, on the east coast of the Malaysian Peninsula (Fig. 1). This area consists of 17 small islands (Satyanarayana et al. 2010) with an estimated total deltaic area of 1200 ha (Shamsudin and Nasir 2005). This area experiences the monsoon from November to March, which causes strong currents and brings flooding to adjacent settlements.

The annual rainfall in 2013, 2014 and 2015 was 2235 mm, 2999 mm and 2065 mm, respectively (Malaysian Meteorological Department, 2016); with the highest and lowest spring tides being 1.7 m and 1.4 m above chart datum (Malaysian Hydrographic National Centre, 2018).

The Kelantan delta consists of distributaries channel fed by the Kelantan river flowing to the South China Sea. It receives run-off due to seasonal rainfall and offshore currents, which contribute to the coastal morphology and hydrographical condition (Mohd-Suffian et al. 2004). The forest is composed of five dominant species: *Avicennia alba*, *Bruguiera gymnorrhiza*, *Nypa fruticans*, *Rhizophora mucronata* and *Sonneratia caseolaris* (Satyanarayana et al. 2010). Based on species composition and stand structure, two main vegetation groups are recognised in the delta. The first one, dominated by *S. caseolaris* and *N. fruticans*, is distributed throughout the forest, occupies low-lying to elevated ground and has low to medium salinity. The second group, largely dominated by *A. alba*, is present close to the bay-mangrove boundary, occurs at low to medium elevations and is characterised by relatively high salinity levels (Satyanarayana et al. 2010).

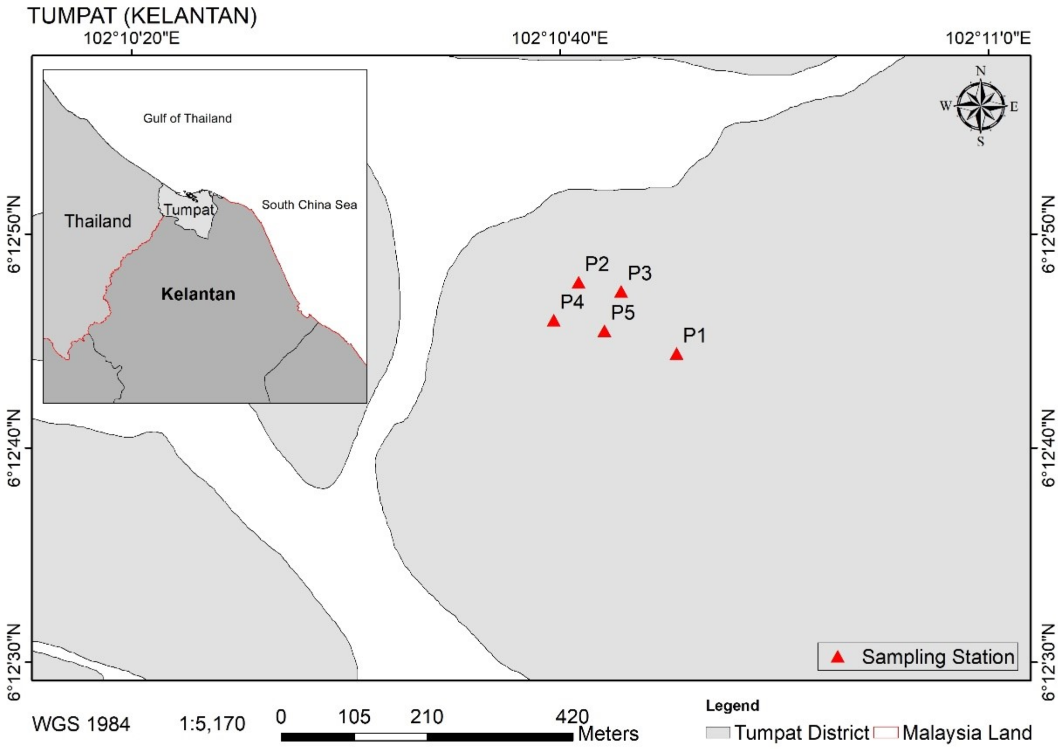

Figure 1. The location of the study site in the Kelantan Delta on the Malaysian Peninsula. The locations of the five *Avicennia alba* study plots are shown by red triangles.

Sampling plots

The experiment was set up in a natural stand of *Avicennia alba*, representative of the corresponding vegetation group in the Kelantan Delta, in September 2014. Five plots of 10 m x 10 m (0.05 ha in total) were established in the mangrove forest (Fig. 1). The plots were chosen randomly to be representative of the area of *A. alba* in the stand. All plots were inundated daily at high tide.

Above ground monitoring

In September 2014 all the *A. alba* trees in each plot were tagged and height and diameter at breast height (DBH) recorded. The point at which DBH was measured was marked to permit accurate repeat measurements at the end of the study in February 2016. Aboveground biomass was estimated using DBH in the allometric equation developed by Komiyama et al. (2005) for mangrove forests of Southeast Asia:

Aboveground biomass (kg ha^{-1}) = 0.251 x ρ x $DBH^{2.46}$

Where ρ (wood density) = 0.560 kg m^{-3}

Aboveground biomass was estimated at the beginning and end of the study (a period of 17 months) and scaled to produce an annual productivity value.

Ingrowth core installation

A total of 100 ingrowth cores (50 cm depth x 15 cm diameter) were placed between 1 and 2 m from major tree trunks, within the five plots, with twenty cores per plot. They were made of plastic mesh (sub-mesh size 1 cm x 1 cm) and inserted vertically to 50 cm depth. To install the cores, a 50 cm deep hole was dug and all the soil removed. All roots found within the soil were removed and chopped into small pieces and then returned to the soil within the core, which was then placed within the hole. This procedure was carried out to ensure representative nutrient conditions in the ingrowth cores, since simply removing roots would remove an important source of nutrients (McKee 2001), while leaving them uncut would have made distinguishing new root growth difficult.

Ingrowth core collection

Three ingrowth cores per plot were collected every three months throughout the study period, i.e. 15 cores in total were collected in December 2014, March 2015, June 2015, September 2015, December 2015 and February 2016. The cores were brought to the laboratory and divided into five layers; 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and 40-50 cm. The roots were washed from each layer using mesh sieves to remove the attached soil particles and debris. They were then rinsed several times until they were free from other materials. Finally they were soaked in water and the living roots separated from the dead roots by hand. The live roots were sorted into two size categories; fine roots (< 3 mm diameter) and coarse roots (> 3 mm diameter). Very few dead roots were found, therefore these are not included in the analyses. All roots were oven dried for approximately 24 hours at 80^{0}C until constant weight.

In February 2016 the root standing stock was assessed by collecting three additional cores from each of the five plots (15 cores in total). Cores were 40 cm deep and 4 cm in diameter and were collected between 5 to 10 m from major tree trunks.

Environmental parameters

In February 2016 a range of environmental parameters were measured in order to examine the association between belowground production and environmental conditions.

i) Soil nutrient analysis

One soil core (15 cm diameter x 50 cm height) was collected from each of the five plots. Each core was separated into five layers (0-10 cm), (10-20 cm), (20-30 cm), (30-40 cm) and (40-50 cm), and each section was analysed separately. The soil was oven dried to constant mass at 80^{0}C for 72 hours and brought back to Edinburgh University, United Kingdom. Soil was analysed for total phosphorus, total carbon, total nitrogen and the C:N ratio was calculated. 10 mg of soil from each layer was weighed for the C and N analysis and the samples measured using an elemental analyser (NC 2500, CE instruments Ltd United Kingdom). Pseudo-total P was determined using an Aqua Regia digestion. 20 g of finely ground soil was dried overnight at 105°C. From this, a 5 g subsample was taken and ashed at 430°C overnight. Then 0.5 g of ashed soil was dissolved in a 5:1 (v/v) mixture of HCl and HNO_3 (respectively) whilst heated to 100°C in a water bath. The sample was evaporated to dryness then re-dissolved with 1ml of 1:1 HCl and filtered through a Whatman 4 filter paper into a 50 ml volumetric flask, then made up to 50 ml with deionised water. The concentration of P was then measured using an Auto Analyzer Applications III (Bran & Luebbe, Germany) using the molybdenate blue procedure outlined in Stewart (1974).

ii) Soil physico-chemical analysis

Pore-water samples were collected at four random locations within each plot during low tide for the determination of salinity, dissolved oxygen and soil temperature. Salinity was examined using a refractometer (Kern optics ORA 1SA, United Kingdom) whilst dissolved oxygen and soil temperature were recorded using a portable multiprobe Pro2030 (YSI Inc., Ohio USA). The multiprobe was inserted to a depth of 30 cm and allowed to settle for two to three minutes prior to measurements.

In order to describe the relationship between above and belowground productivity, several parameters were calculated as follows:

i) Aboveground standing stock and production

Stem DBH data was incorporated into the allometric equation described above, following Komiyama et al. (2005), to derive initial (September 2014) aboveground biomass (dry weight) in t ha^{-1} and final aboveground biomass in t ha^{-1} (February 2016). The difference in biomass between these dates was used to calculate annual aboveground production (t $ha^{-1}year^{-1}$).

ii) Belowground standing stock and production

Roots were weighed and the units converted to gm^{-2} to allow comparison with other studies. The surface area of cores used to calculate root production, was 176.74 cm^2 whereas the surface area of the cores used to calculate standing stock was 12.56 cm^2. These values were scaled and converted to t ha^{-1} for standing stock and t ha^{-1} $year^{-1}$ for root production.

Annual root production was calculated by taking the mean of each of the 6 three-month root biomass totals and converting them to annual production in t ha^{-1} $year^{-1}$.

iii) Root:shoot ratio of aboveground and belowground standing stock and production

Root:shoot ratios were calculated in order to determine allocation to above and belowground components for both standing stock and production.

iv) Root turnover

Root turnover was calculated following Gill and Jackson (2000), by dividing annual root production by root standing stock.

$$\text{Root Turnover } (yr^{-1}) = \frac{\text{Annual belowground production } (t\ ha^{-1}\ yr^{-1})}{\text{Maximum belowground standing stock } (t\ ha^{-1})}$$

Studies from around the world reporting similar research to that described here were analysed and are summarised in Tables 4, 5, 6 and Figure 5.

Statistical analysis

Differences of fine, coarse and total root biomass and soil depth among the months of collection were performed using one-way ANOVAs. Differences in aboveground biomass between months were determined by one-way ANOVA. Log or square root transformations were applied to meet ANOVA requirements for non-normal data. *Post hoc* Tukey tests were performed to find significant differences between month of collection and soil depth. Pearson correlations were performed to find relationships between root and aboveground biomass among environmental variables, including soil nutrients (carbon, nitrogen, C:N ratio and total phosphorus), soil temperature, salinity and dissolved oxygen. Statistical analysis was performed using Minitab 17 software.

Results

Forest structure

Forest characteristics are shown in Table 1. There were no significant differences in any parameters between the plots, therefore data have been combined.

Table 1. *Avicennia alba* forest structure in the Kelantan Delta. Mean ± SE.

Forest characteristics	September 2014	February 2016
Tree density (stems ha^{-1})	1200 ± 0.52	1200 ± 0.52
Average DBH (cm)	17.58 ± 1.04	17.82 ± 1.04
Height (m)	14.13 ± 0.62	-
Basal area (m^2 ha^{-1})	210.96	213.84

Environmental parameters

Physico-chemical parameters of the mangrove forest did not vary across the plots ($p > 0.05$) and data have therefore been combined (Table 2).

The total amount of phosphorus, carbon, nitrogen and the C:N ratio did not vary significantly with soil depth. However although there were no statistically significant differences, there was a tendency for the nitrogen and carbon content to increase with depth. Phosphorus content and the C:N ratio remained consistent with depth. There were no statistically significant correlations between above and below ground production and soil nutrients and physio-chemical parameters.

Table 2. Environmental variables. Data recorded in February 2016 (n = 5).

Environmental data	Mean ± SE
Pore-water salinity (ppt)	12.08 ± 0.88
Pore-water dissolved oxygen (mg/l)	4.45 ± 0.96
Pore-water soil temperature (^{0}C)	27.94 ± 0.08
Total soil phosphorus (% of mass)	0.12 ± 0.01

Soil carbon (% of mass)	2.45 ± 0.18
Soil nitrogen (% of mass)	0.04 ± 0.01
Soil C:N (% of mass)	81.57 ± 9.53

Belowground standing biomass and production

In February 2016, the mean root standing stock across all five plots was 20.81 t ha^{-1} (Table 3). The root biomass was 1225 gm^{-2} ± 123.8 and 856 gm^{-2} ± 153.46 for fine and coarse roots respectively. 59 % of the total root biomass was therefore fine roots.

Total root production was significantly different across the months of collection ($p < 0.001$), ranging from 665 ± 96.4 gm^{-2} to 3322 gm^{-2} ± 626.82 (Figure 2). The highest root production was in March 2015, 180 days after the experimental setup. In terms of root category, fine and coarse root production also varied significantly between the months of collection ($p < 0.001$). The highest fine root production was in March 2015, and lowest in December 2014. Maximum coarse root growth was recorded in December 2015, 15 months after cores were set up and ranged from 598 ± 85.75 gm^{-2} to 2785 ± 468.9 gm^{-2}. In general, fine roots were the main contributor (78% on average) of total root production.

A steep decline in root production was seen in June and September 2015. These are the driest months with minimal rainfall. In fact, there was no record for coarse root production in September 2015. Root production increased again in December 2015 but decreased slightly in February 2016. The average root productivity is 12.7 t $ha^{-1}year^{-1}$.

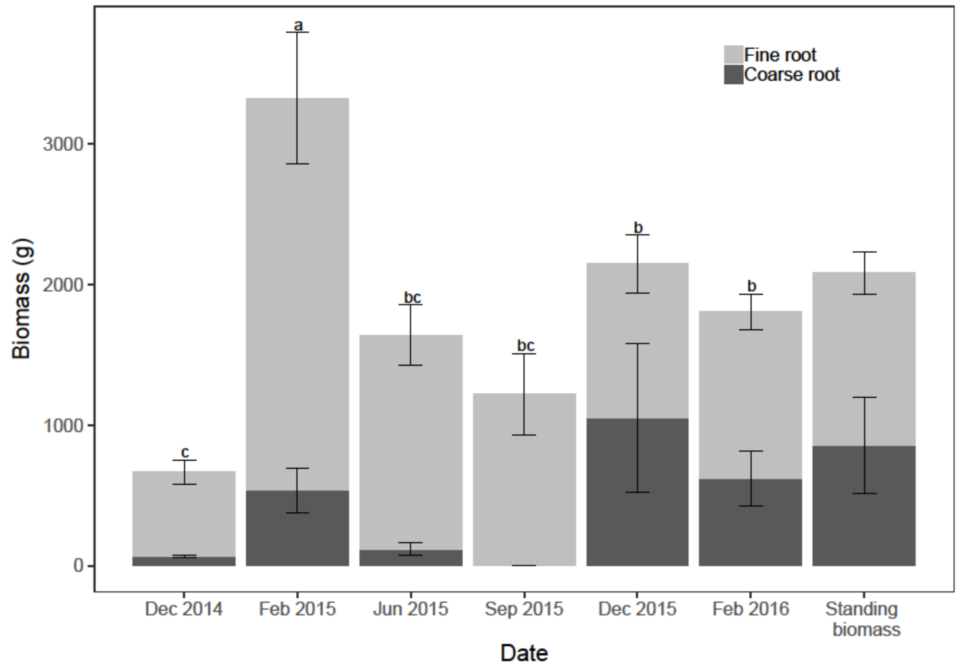

Figure 2. Root biomass from ingrowth cores retrieved at three-month intervals used to derive root production (mean ± SE). Standing root biomass was sampled in February 2016. Bars sharing the same letters indicate no significant difference among total root biomass ($p < 0.05$).

Root depth

Total root stock varied significantly with soil depth ($p < 0.015$). Most of the roots were found below 10 cm in the soil profile (Figure 3). Fine root biomass was significantly higher lower down the soil profile ($p < 0.001$), however, there was no significant difference in coarse root biomass between soil layers. 61% of total root biomass was found in the 20 to 40 cm horizon.

Root production (total roots, fine roots and coarse roots) did not vary significantly with soil depth (Figure 4). In terms of composition of roots in each soil layer, fine root biomass increased with increasing depth and represented 78 % of total root production. In contrast, coarse root production showed a decreasing trend with increasing soil depth.

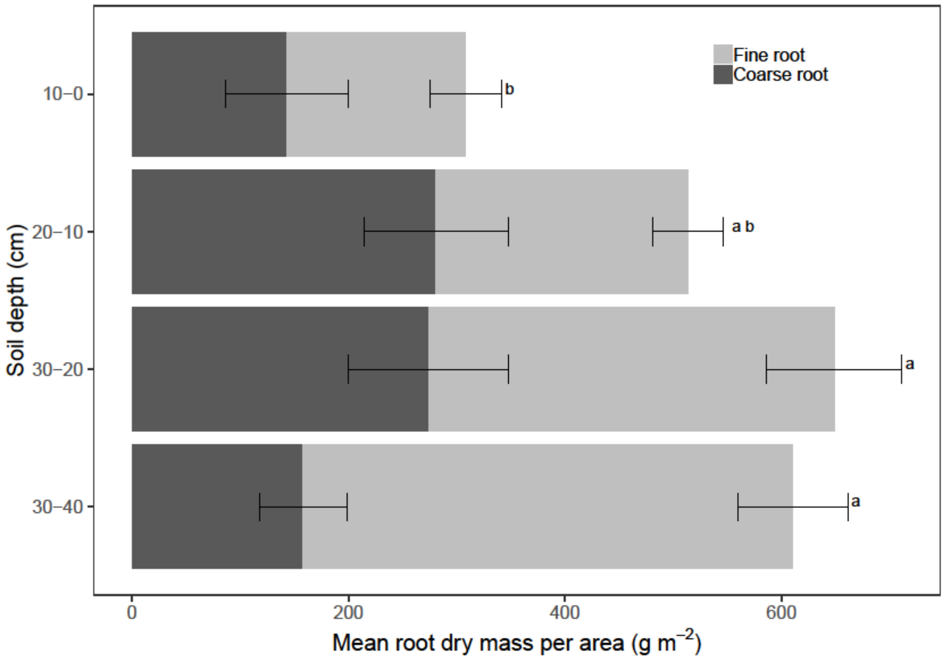

Fig 3. Standing root biomass (root stock) according to soil depth. Bars sharing the same letters indicate no significant difference among soil depth ($p < 0.05$). Mean ± SE

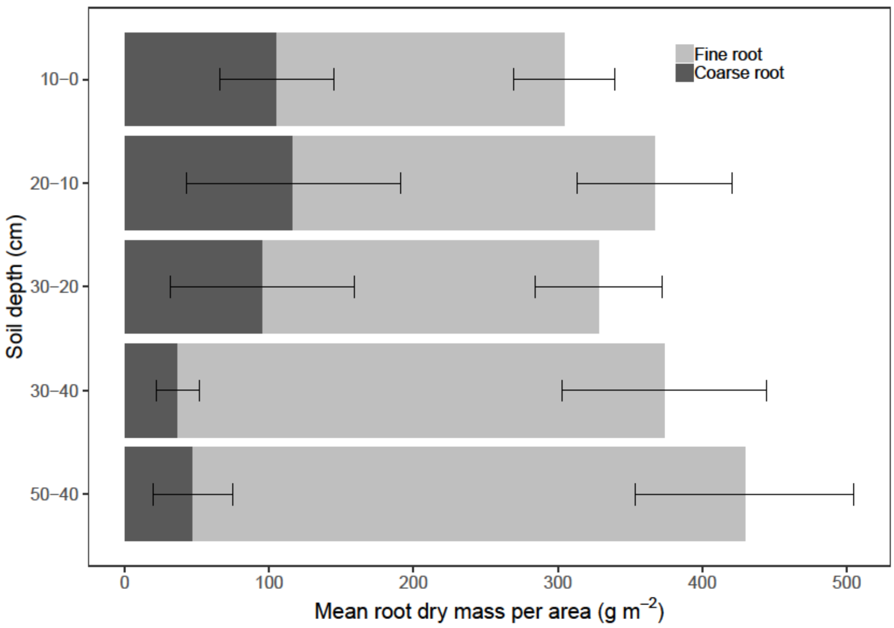

Fig 4. Total root production according to soil depth, over the course of 17 months. Mean ± SE.

Aboveground standing stock and production rate

The initial and final aboveground biomasses were 269.73 t ha^{-1} and 276.54 t ha^{-1} respectively, thus providing an aboveground production increment of 4.8 t $ha^{-1}year^{-1}$.

Above and belowground allocation of biomass and production

The standing stock root to shoot ratio was surprisingly low at 0.075 (Table 3). However, over the course of 17 months, the ratio of below to above ground production was 2.65, thereby greatly favouring allocation to roots. Hence, 93% of standing stock was allocated aboveground and 7% belowground, in comparison with above and below ground production allocation figures of 27% and 73% respectively (Table 3). Similar work to this study is reported in Tables 4, 5 and 6.

Table 3. Summary of above and belowground parameters.

Above and below ground parameter	Standing stock	Production
Aboveground	277 (t ha^{-1})	4.8 (t $ha^{-1}yr^{-1}$)
Belowground	20.81 (t ha^{-1})	12.7 (t $ha^{-1}yr^{-1}$)
Fine root biomass	12.25 (t ha $^{-1}$) (59%)	9.88 (t $ha^{-1}yr^{-1}$) (78%)
Coarse root biomass	8.56 (t ha-^{1}) (41%)	2.81 (t $ha^{-1}yr^{-1}$) (22%)
Based on soil horizon	39.5% total roots in the 0-20 cm soil horizon. 60.5% total roots in the 20-40 cm soil horizon.	55.4% total roots in the 0-30 cm soil horizon. 44.6% total roots in the 30-50 cm soil horizon.

Total root turnover	0.61 (yr^{-1})	
Fine root turnover	0.81 (yr^{-1})	
Coarse root turnover	0.33 (yr^{-1})	
Root:shoot	0.075	2.65
Aboveground allocation	93%	27%
Belowground allocation	7%	73%

Table 4. Comparison of belowground production in mangrove forest of different regions

Forest type/ setting	Dominant species	Below ground biomass (t ha^{-1})	Below Ground production (t ha^{-1} yr^{-1})	Country	Reference
Island	*Sonneratia*	38.5	-	HalmaheraIsland, Indonesia	Komiyama et al. (1988)
Fringe	*Rhizophora*		2.65	Rotatan Island, Honduras	Cahoon et al.(2003)
Basin	*Avicennia*		3.02	Rotatan Island, Honduras	Cahoon et al.(2003)
Fringe	*R. mangle*		3.52	Florida, US	Sanchez (2005)
Basin	*Rhizophora, Avicennia germinans and Laguncularia*		3.14	Florida, US	Sanchez (2005)
Basin	*Avicennia germinans*		3.78	Florida, US	Sanchez (2005)
Scrub	*R. mangle*		3.07	Florida, US	Sanchez (2005)
	R. apiculata, A.alba, Xylocarpus granatum	-	11.02	Eastern Thailand	Komiyama (2006)

Basin	*Rhizophora and Avicennia*		5.25	Twins cays, Belize	McKee et al. (2007a)
Fringe	*Rhizophora*		3.94	Twins cays, Belize	McKee et al. (2007a)
Transition	*Rhizophora*		0.82	Twins cays, Belize	McKee et al. (2007a)
	Sonneratia	75		Gazi Bay, Kenya	Tamooh et al. (2008)
Riverine	*R. mangle*, *Laguncularia racemosa* and *Ceriops erectus*		4.65	Shark River, Florida	Castaneda-Moya et al. (2011)
Riverine	*Rhizophora, Laguncularia* and *Aegiceras*		6.43	Shark River, Florida	Castaneda-Moya et al. (2011)
Riverine	*Rhizophora, laguncularia, Aegiceras*		4.69	Shark River, Florida	Castaneda-Moya et al. (2011)
Scrub	*Rhizophora*		5.61	Taylor River, Florida	Castaneda-Moya et al. (2011)
Scrub	*Rhizophora*		4.07	Taylor River, Florida	Castaneda-Moya et al. (2011)
Fringe	*Rhizophora* and *Ceriops*		4.85	Taylor River, Florida	Castaneda-Moya et al. (2011)

Basin/ landward	*Avicennia marina*	6.03	3.66	Gazi Bay, Kenya	Lang'at (2013)
Scrub	*Ceriops tagal*	0.64	0.65	Gazi Bay, Kenya	Lang'at (2013)
Basin/ interior	*Rhizophora mucronata*		2.54	Gazi Bay, Kenya	Lang'at (2013)
Fringe	*Sonneratia alba*	5.16	5.16	Gazi Bay, Kenya	Lang'at (2013)
		9.47-30.40	0.46-1.85	Celestun lagoon, Mexico	Adame et al. (2014)
Yela River, soil fertility gradient	Mixed mangroves	4.48-26.41	4.6-11.9	Micronesia	Cormier et al. (2015)
	Avicennia alba	68.4	3.40	Trat River, Thailand	Paungparn et al. (2016)
		2.43-18.69	5.7–28.4	Dongzhai Bay, China	Xiong et al. (2017)
Oligohaline zone	*Heritiera fomes*	82.3	-	Sundarbans, Bangladesh	Kamaruzzaman et al. (2018)
Oligohaline zone	Mixed mangroves	84.2	-	Sundarbans, Bangladesh	Kamaruzzaman et al. (2018)

Delta	*Avicennia alba*	20.81	12.7	Kelantan delta, Eastern Malaysian Peninsular	This study (2017)

Table 5. Comparison of aboveground production in mangrove forest of different regions

Forest type/setting	Dominant species	Tree height (m)	Aboveground biomass (t ha^{-1})	Aboveground production (t ha^{-1} year^{-1})	Country	Reference
	Rhizophora apiculata	-	500	6.7	Malaysia	Putz and Chan (1986)
	Rhizophora	3.5	240	6.77	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	Rhizophora and Avicennia	3.5	172	5.62	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	Rhizophora	3.5		4.33	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	Avicennia	3.5	193	1.40	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	Rhizophora apiculata	21.0		12.38	Malaysia	Ong *et al.* (1995)

Basin/landward	*Avicennia marina*	5.1	14.5	4.69	Kenya	Lang'at (2013)
Scrub	*Ceriops tagal*	2.4	11.8	1.97	Kenya	Lang'at (2013)
Basin/interior	*Rhizophora mucronata*	5.4	125.7	11.73	Kenya	Lang'at (2013)
Fringe	*Sonneratia alba*	6.1	112.9	5.93	Kenya	Lang'at (2013)
	Avicennia alba	11.3	169.9	8.1	Thailand	Paungparn *et al.* (2016)
Oligohaline	*Heritiera fomes*	8.9	153.7	-	Bangladesh	Kamaruzzaman et al (2018)
Oligohaline	Mixed mangroves	-	154.8	17.2	Bangladesh	Kamarazzaman et al (2017)
Delta	*Avicennia alba*	14.13	277	4.8	Eastern Malaysian Peninsular	This study (2017)

Table 6. Comparison of root:shoot ratio in mangrove forest of different regions

Study site	Species	Root:shoot for biomass	Root:shoot for production	References
Indonesia	*Sonneratia*	0.23		Komiyama et al. (1988)
	Bruguiera	0.29-0.44		
	Rhizophora	0.53-0.67		
Japan	*Bruguiera*	1.38		Komiyama et al. (1989)
	Rhizophora	1.39		
Thailand	*Ceriops tagal*	1.05		Komiyama et al. (1989)
Greenhouse	*Rhizophora mangle*	0.38		Pezeshki et al. (1990)
	Avicennia germinans	0.42		
Queensland	*Avicennia marina*	0.58		Mackey (1993)
Malaysia	*Rhizophora apiculata*	0.05		Ong et al. (1995)
Greenhouse	*Rhizophora mangle*	0.1		McKee (1995b)
	Laguncularia racemosa	0.4-1.5		

	Avicennia germinans	0.2-0.5		
Australia	*Avicennia marina*	4.1		Saintilan (1997a)
	Avicennia corniculatum	1.9		
Queensland	*Avicennia marina*	0.4-3.1		Saintilan (1997b)
	Avicennia corniculatum	0.4-1.4		
	Rhizophora stylosa	1.2-1.7		
Japan	*Rhizophora stylosa*	0.44		Matsui (1998)
Australia	*Rhziophora*	0.42		
	Ceriops	0.42		
Dominican Republic	*Rhizophora mangle*			Sherman et al. (2003)
	Laguncularia racemosa	< 0.5		
	Avicennia germinans			
Florida/Greenhouse	*Avicennia germinans*		> 0.5-1	Sanchez (2005)

	Rhizophora mangle		> 0.5-1	
Shark River, Florida	*Rhizophora mangle, Laguncularia racemosa* and *Ceriops erectus*			Castaneda-Moya et al. (2011)
Shark River, Florida	*Rhizophora, Laguncularia* and *Aegiceras*			Castaneda-Moya et al. (2011)
Shark River, Florida	*Rhizophora, laguncularia, Aegiceras*			Castaneda-Moya et al. (2011)
Taylor River, Florida	*Rhizophora*			Castaneda-Moya et al. (2011)
Taylor River, Florida	*Rhizophora*			Castaneda-Moya et al. (2011)
Taylor River, Florida	*Rhizophora* and *Ceriops*			Castaneda-Moya et al. (2011)
		0.2-1.1		Lang'at (2012)
Gazi Bay, Kenya	*Avicennia marina*		3.66	Lang'at (2013)
Gazi Bay, Kenya	*Ceriops tagal*		0.65	Lang'at (2013)
Gazi Bay, Kenya	*Rhizophora mucronata*		2.54	Lang'at (2013)
Gazi Bay, Kenya	*Sonneratia alba*		5.16	Lang'at (2013)

Yela, Kosrae Micronesia		0.074		Cormier et al. (2015)
Kelantan delta, Malaysian Peninsular	*Avicennia alba*	0.075	2.65	This study (2017)

Discussion

Root stock, production and turnover

This study showed very high rates of root production and turnover, coupled with relatively low standing stocks with an unusual depth distribution. Estimated annual root production was 12.7 t $ha^{-1}year^{-1}$, the second highest rate reported from a mangrove forest. Most other estimates of root productivity are much lower, typically ranging from 2-6 t $ha^{-1}year^{-1}$ (Table 4.), although another study in Eastern Thailand produced a similar figure of 11.02 t $ha^{-1}year^{-1}$ (Komiyama et al. 2006). The highest reported productivity is 28.4 t $ha^{-1}year^{-1}$, from a *Ceriops tagal* stand in China (Xiong et al., 2017). This very high estimate was made by summing a series of cores, rather than by using the in-growth method as employed here and in most other studies. Hence this large difference may be explained by methodological discrepancies. There was also a high estimated total root turnover of 0.61 yr^{-1}, with fine roots turning over more than twice as quickly as coarse roots (0.81 yr^{-1}in comparison with 0.31 yr^{-1}) (Table 3). This rate of fine root turnover exceeds most other estimates, such as those reported from Florida (0.6 yr^{-1}; Castaneda-Moya et al. 2011), Mexico (0.4 yr^{-1}; Adame et al., 2014) and Micronesia (0.05 yr^{-1}; Cormier et al., 2015). The exception is Xiong et al. (2017) who report rates of up to 5.96, driven by their exceptionally high estimates of production; hence again methodological differences may explain this. The current work was also unusual in finding that roots were more abundant lower down the soil profile. A more typical pattern is described by Castaneda-Moya et al. (2011), who observed that root biomass decreased with soil depth in a Florida mangrove forest. This might be explained by the higher concentration of soil nutrient near the soil surface (Castaneda-Moya et al. 2011).

Explanations for these unusual findings of large productivity, fast turnover rate and abundant deeper roots may lie in the environmental setting of the Kelantan Delta forest. This is a physically sheltered site with high levels of soil oxygen and low salinity and copious freshwater input, which shows a highly seasonal pattern. Investment in roots for structural strength, for example to resist wave buffeting in very muddy soils, is not necessary here. The high salinity conditions known to encourage high root:shoot ratios in *Avicennia* species elsewhere also do not apply here. The very high productivity and turnover rates of fine roots may be driven by seasonal growth to obtain nutrients such as nitrogen and phosphorus. Rapid root production occurred following the installation of the ingrowth cores in September 2014, peaking in March 2015 and with a secondary peak in

December 2015, coinciding with the monsoon season. This suggests a strong seasonal pattern in root production on the east coast of the Malaysian peninsular. In this region, the northeast monsoon brings heavy rainfall, usually from November to March every year. Paungparn et al. (2016) also reported high mangrove root production after the rainy season in Thailand. Terrestrial forests may show a similar pattern, for example belowground production of the rubber tree (*Havea brasiliensis*) exhibited seasonal root production which was highly correlated with rainfall (Maeght et al. 2015). Heavy rainfall reduces the salinity of porewater in mangrove systems which favours root growth and stimulates high root production (Cormier et al. 2015). The mean salinity in this study was only 12.08 ± 1.07 ppt, providing ideal conditions for optimum mangrove production.

It is possible that estimated root production and turnover are inflated by experimental artefacts. Cutting all roots before returning them to the ingrowth cores may have provided unnaturally high levels of nutrients, stimulating root growth (McKee 2001). However, the alternative of removing all dead roots would have risked the opposite artefact of underestimated production, and any boost to growth should be quite limited in duration. Xiong et al. (2017) argue that in-growth core methods usually underestimate productivity since they leave inadequate time for a return to steady state conditions. This seems unlikely here given that root biomass exceeded ambient stocks after six months. Subsequent months saw a reduction in biomass, indicating rapid root turnover. Turnover rates calculated across the whole experiment, for total, fine and coarse root biomass, were 0.61, 0.81 and 0.33 respectively (Table 3.). Root turnover rates in this study decreased with increasing root size, as also found by Castaneda-Moya et al. (2011) in a Florida mangrove forest.

In this study, fine roots were the main component of total root stock, providing 59% of the standing root biomass. In terms of root productivity, fine roots accounted for 78% of total root production. This figure is similar to the 62-75% found in Honduran mangroves (Cahoon et al. 2003). This has been explained by the primary role of fine roots in water and soil nutrient acquisition (Sanchez 2005) particularly during early root growth. However, in contrast in Florida and Mexico Castaneda-Moya et al. (2011) and Adame et al. (2014) found a higher fraction of total root biomass was represented by coarse roots. Lower coarse root biomass was found in this study, reflecting very rapid root turnover in this mangrove system, with fine roots making a major contribution to the belowground components.

The root standing stock found in this study (20.81 t ha^{-1}) was amongst the lowest reported from the literature for mature forests (Table 4). This may be due to the positioning of the cores relatively far away from the tree trunks, which may have led to an underestimation, particularly of coarse root biomass. Further studies of root biomass should pay attention to this issue. Because of the high aboveground biomass in this study (277 t ha^{-1}) the resulting root:shoot ratio is unusually low.

Aboveground biomass and production

Aboveground biomass measured in the present study is high (277 t ha^{-1}), but comparable with results from other studies (Table 5.). The average stem diameter was 17 ± 1.0 cm which represents a young stand. A study conducted 30 years ago on a more mature stand in the Malaysian peninsular found aboveground biomass to be twice as high (500 t ha^{-1} and a mean DBH of 50 cm) as in the present study (Putz and Chan 1986). Aboveground biomass of mature mangrove forests is generally greater at lower latitudes, which can be explained by the variation in temperature (Komiyama et al. 2008).

Annual aboveground production of *Avicennia alba* in this study (4.8 t ha^{-1} year^{-1}) is similar to that of *Avicennia marina* in Kenya (4.69 t ha^{-1} year^{-1}) (Lang'at 2013), but lower than aboveground production of the same species in Thailand (8.0 t ha^{-1} year^{-1}) (Paungparn et al. 2015). Other aboveground studies in a mangrove forest in Sri Lanka also showed low production (1.40 t ha^{-1} year^{-1}) (Amarasinghe and Balasubramaniam 1992) as compared with this study (Table 4).

Correlation between environmental data and roots data

Root production did not significantly correlate with any of the measured soil nutrient concentrations or any of the physiochemical parameters, although there was a trend towards increased root growth with increased soil nitrogen. Previous studies have shown than root production in mangroves might be more dependent on the available phosphorus (P), for example in the Floridian mangroves, (Castaneda-Moya et al. 2011; Adame et al. 2014; Poret et al. 2015). However, root production shows contrasting responses to soil P in other studies, as it has been found to increase with soil P in Celestun Lagoon, Mexico (Adame et al. 2014), while it increases with P deficiency within the Everglades (Florida, USA) (Castaneda-Moya et al. 2011).

Salinity is often an important environmental factor determining root production. The maximum root production recorded here during the monsoon season in March (2015) and December (2015) is likely to be because of reductions in salinity. This finding is similar to the study of Thai mangroves which also had high root production during the monsoon season (Paungparn, 2016), and conforms with the finding of Xiong et al. (2017) that fine root production is higher in less saline areas.

Biomass allocation to above and belowground production

Mangroves growing on soil with poor nutrient content allocate most of their resources to grow belowground biomass as a strategy to optimize limited resources (Castaneda-Moya et al 2013). In this study, the root:shoot ratio for standing stock was 0.075, similar to that measured by Cormier et al. (2015) in the mangroves of Micronesia (Table 6). Root:shoot ratio values from the present study and that of Cormier et al. (2015) are much lower than those of 0.4 to 4.1 reported from other mangrove forests (Saintilan a and b 1997) (Table 6.). These results reflect higher biomass investment aboveground in a productive deltaic mangrove forest and are consistent with the higher allocation of biomass aboveground also observed in a productive riverine mangrove forest (Castaneda-Moya et al. 2013).

The root:shoot productivity ratio was 2.65, much higher than the ratio found for standing stocks (0.075). This high productivity and turn-over of roots probably reflects the good environmental conditions at the study site, with relatively high levels of dissolved oxygen and low salinity in the soil porewater, which stimulate root production. Xiong et al. (2017) also reported highest rates of fine root production and turnover in sites with high nutrients and low salinity.

Conclusion

In this study, a productive riverine mangrove forest allocated a large proportion of total standing biomass to the above ground components, particularly in the tree stems. In contrast, belowground productivity was higher than aboveground, and was one of the highest yet recorded in a mangrove forest, with the difference between high estimated root productivity and low standing stock implying rapid root turnover. The benign conditions at the field site, with low salinity and little wave impact, may explain this unusually high root productivity and turnover.

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