Estimation of probable annual fine-root production and missing dead roots associated with the ingrowth core method: attempt with major mangrove species on Iriomote Island, southwestern Japan, located in the subtropics

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Abstract: To estimate annul fine-root production, an experiment combining the ingrowth core method for two years with the root litter bag method for one year was conducted for two major mangrove species on Iriomote Island, southwestern Japan, located in the subtropics. The combination of the two methods enabled us to create a new procedure to estimate the probable fine-root productivity and the missing dead roots resulting from decomposition processes.

The probable annual fine-root production values up to a 50 cm depth were calculated at 1691 g m^{-2} $year^{-1}$ for a seashore *Rhizophora stylosa* located 4 cm above mean sea level, 1658 g m^{-2} $year^{-1}$ for an interior *R. stylosa* located 30 cm above mean sea level, 1150 g m^{-2} $year^{-1}$ for a seashore *Bruguiera gymnorrhiza* located 22 cm above mean sea level and 962 g m^{-2} $year^{-1}$ for an interior *B. gymnorrhiza* located 43 cm above mean sea level, of which the missing dead roots were estimated at 182 g m^{-2} $year^{-1}$, 239 g m^{-2} $year^{-1}$, 189 g m^{-2} $year^{-1}$ and 172 g m^{-2} $year^{-1}$, respectively. The higher productivity of the fine roots of *R. stylosa*, especially the very fine roots, than those of the other species may have partly contributed to the accumulation of mangrove peat, which is generally distributed in *Rhizophora* forests only. Common trends suggesting shorter turnover time in the lower tidal submergence rate zone than in the higher tidal submergence rate zone, i.e., greater fine-root biomass accumulation in the lower elevation zone and greater mortality in the higher elevation zone, were found for both species.

Introduction

Fine roots, which are generally defined as less than 2 mm in diameter, possibly play a significant role in carbon sequestration in forest ecosystems. Terrestrial forests allocate 4 to 69 % of their total annual photosynthate to fine roots, depending on the various environmental conditions, such as climatic variations (Vogt et al., 1996). However, fine root dynamics are one of the least understood aspects of plant function because of our inability to visibly monitor the dynamics of an entire root system of a plant (Vogt et al., 1998).

Mangrove forests develop in intertidal zones in the tropics and subtropics, covering 152,000 km^2 in over 123 countries (Spalding et al., 2010), and play a significant role as sites for carbon sequestration not only aboveground but also belowground (Twilley et al., 1992; Fujimoto, 2004; Donato et al., 2011; Alongi, 2014).

Generally, forest productivity and biomass vary with differences in climatic conditions. The aboveground biomass and stored carbon of mangrove forests decrease with increasing latitude (Twilley et

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al., 1992). On the other hand, belowground stored carbon (up to 100 cm depth) differs by species, for example 500 to 650 Mg C ha^{-1} is stored in *Rhizophora* communities, approximately 200 Mg C ha^{-1} in *Bruguiera gymnorrhiza* communities and approximately 120 Mg C ha^{-1} in *Kandelia obovata* communities (Fujimoto et al., 1999a; Fujimoto, 2004; Ishihara et al., 2004), although the burial rates are possibly different depending on the climatic conditions. Only *Rhizophora* communities, which have the highest value of belowground stored carbon, can create mangrove peat (Fujimoto et al., 1999b; Mochida et al., 1999). Mangrove peat mainly consists of dead fine roots (Fujimoto et al., 1999b; Ono et al., 2015); thus, *Rhizophora* communities may have relatively higher productivity of fine roots.

Komiyama et al. (1987) reported that the proportion of fine roots to total belowground root biomass in a *Rhizophora apiculata* community reached 46.6 %. The fine roots of mangroves possess a refractory nature (Middleton and McKee, 2001). In addition, anaerobic conditions of the intertidal zone retard the decomposition of roots, which increases the relative proportion of root matter accumulation (McKee and Faulkner, 2000; Krauss et al., 2013).

There are two major methods to estimate fine-root productivity, i.e., the ingrowth core method (Flower-Ellis and Persson, 1980; Vogt and Persson, 1991) and the sequential soil core method (Persson, 1980). The former method can directly obtain the amount of accumulated fine roots. However, the value is always underestimated for production unless the amount of fine roots decomposed during the collection intervals is estimated. We refer to the decomposed dead roots as 'missing dead roots (*MDR*)'. The latter method is considered the decomposed fine roots, but there is the problem of repeatability because the core samples are collected from different sites at each sampling under the assumption that the fine roots are equally distributed in the forest. However, the fine roots of mangroves are distributed heterogeneously depending on the distance from the tree base (Komiyama et al., 2000) and the distribution of stilt roots in the case of the *Rhizophora* forest (Komiyama et al., 1987). The decision-matrix method (Fairley and Alexander, 1985) is generally used to calculate fine-root production using data obtained by the sequential soil core method. As the calculation procedure considers fine-root production, mortality, or decomposition to be 0 under specific conditions, the calculated result is always underestimated (Osawa and Aizawa, 2012).

Most previous studies have estimated fine-root productivity for mangroves by the ingrowth core method without considering decomposition processes (e.g., Castañeda-Moya et al., 2011; Adame et al., 2014; Cormier et al., 2015; Noguchi et al., 2020), except for a few studies using the sequential soil core method (Xiong et al., 2017) and the mass balance approach (Lovelock, 2008). Poungparn et al. (2016) collected data by the ingrowth core method and calculated the productivity by the decision-matrix method. However, the calculated values for annual production were smaller than the values accumulated in ingrowth cores for a year.

Osawa and Aizawa (2012) proposed a method to estimate the amount of dead-root decomposition between two time points by combining the ingrowth core and litterbag methods for an artificial terrestrial forest in Japan. However, they were not successful in estimating the annual fine-root production because the estimated values of decomposition included not only the values to the mortality between the two time points but also the values to the existing dead roots in the ingrowth cores at the first time point.

We propose a new approach to calculate annual fine-root production and the amount of decomposition to the mortality for one year by combining the ingrowth core method for two years and the litterbag method for one year for *Rhizophora stylosa* and *Bruguiera gymnorrhiza* communities on Iriomote Island, southwestern Japan.

The distribution of mangrove species is primarily controlled by microlandforms and tidal environments, such as submergence frequency and duration, which affect soil water chemical and physical properties (Fujimoto and Miyagi, 2016). The productivity of fine roots and decomposition rates may differ depending on the tidal environment. Therefore, we established two experimental sites at different elevations for each species to determine the effect of the tidal environment.

Regional setting

Iriomote Island is located in the subtropics of southwestern Japan (24° 15' N to 24° 25' N, 123° 39' E to 123° 56' E) (Fig. 1). The mean annual temperature, mean warmest month temperature, mean coldest

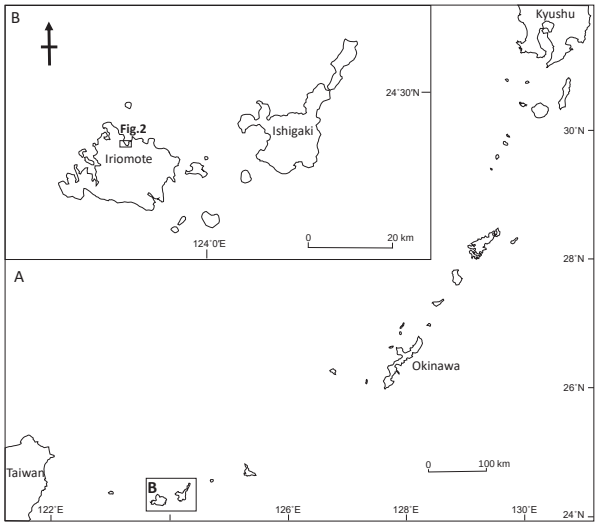

Fig. 1 Map showing the location of Iriomote Island and the study area.

month temperature and mean annual precipitation were calculated as 23.8 ℃ , 28.7 ℃ , 18.4 ℃ and 2254 mm, respectively, between 1990 and 2019 using public data from the Japan Meteorological Agency (http://www.data.jma.go.jp/obd/stats/etrn/index.php). The spring, mean and neap tidal ranges are 129.6 cm, 100.4 cm and 71.2 cm, respectively, at Shirahama Harbor located northwest of the island.

The area of mangrove forests on the island was measured at 503 ha by ISME (2004) using aerial photographs taken between 1994 and 1995. Seven mangrove species, i.e., *R. stylosa, B. gymnorrhiza, Sonneratia alba, Kandelia obovata, Avicennia marina, Lumnitzera racemose*, and *Nypa fruticans*, have been identified on the island. The first two species are the primary species and their communities occupy most of the mangrove area on the island (Nakasuga, 1979).

Methods

Experimental sites and plots

The experiments were conducted in Funaura Bay, in the northeastern part of the island (Fig. 1). A permanent plot, 5 m wide and 50 m long, was established in an *R. stylosa* forest located east of the bay (Fig. 2, plot code: IFR1) to determine the forest structure and dynamics. The *B. gymnorrhiza* plots were established in a forest facing the bay located west of the bay (Fig. 2, IFB1: 5 m wide and 10 m long) and along the Yashi River (Fig. 2, IFB2: 5 m wide and 20 m long).

The species, tree height, stem diameter and location were recorded for all trees over 1.3 m in height in the plots. The diameter was measured at 0.3 m above the highest prop root for *R. stylosa* and at breast height (1.3 m from the ground surface) for *B. gymnorrhiza* and other species. Tree censuses were conducted in March 2013, March 2016 and August 2018 for IFR1 and in March (partly in June) 2014, March 2016 and February 2018 for IFB1 and IFB2.

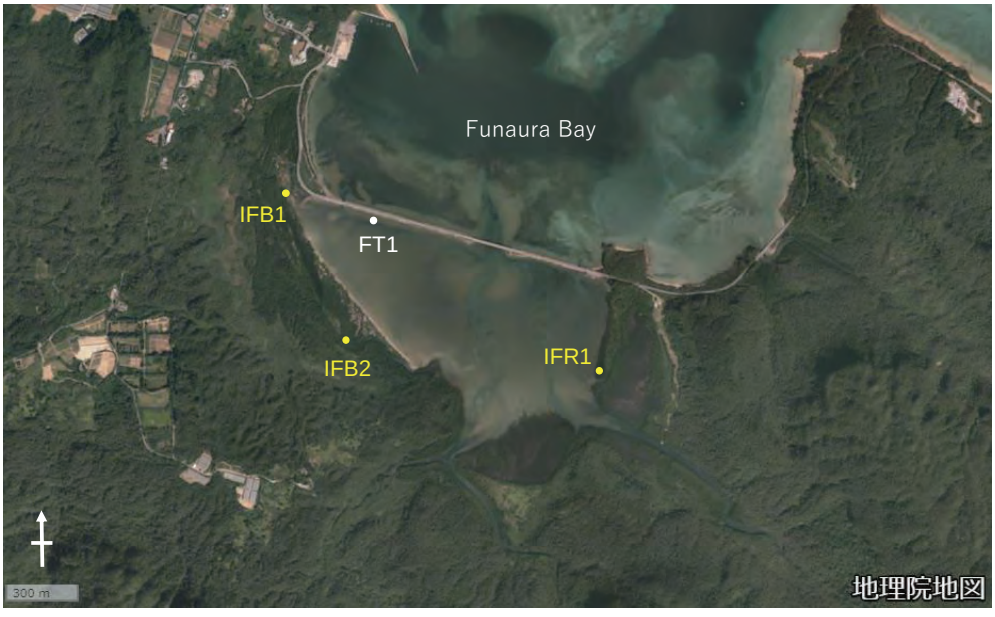

Fig. 2 Map showing the locations of the study plots (IFR1 for *R. stylosa*, IFB1 and IFB2 for *B. gymnorrhiza*) and continuous tide-level observation site (FT1).

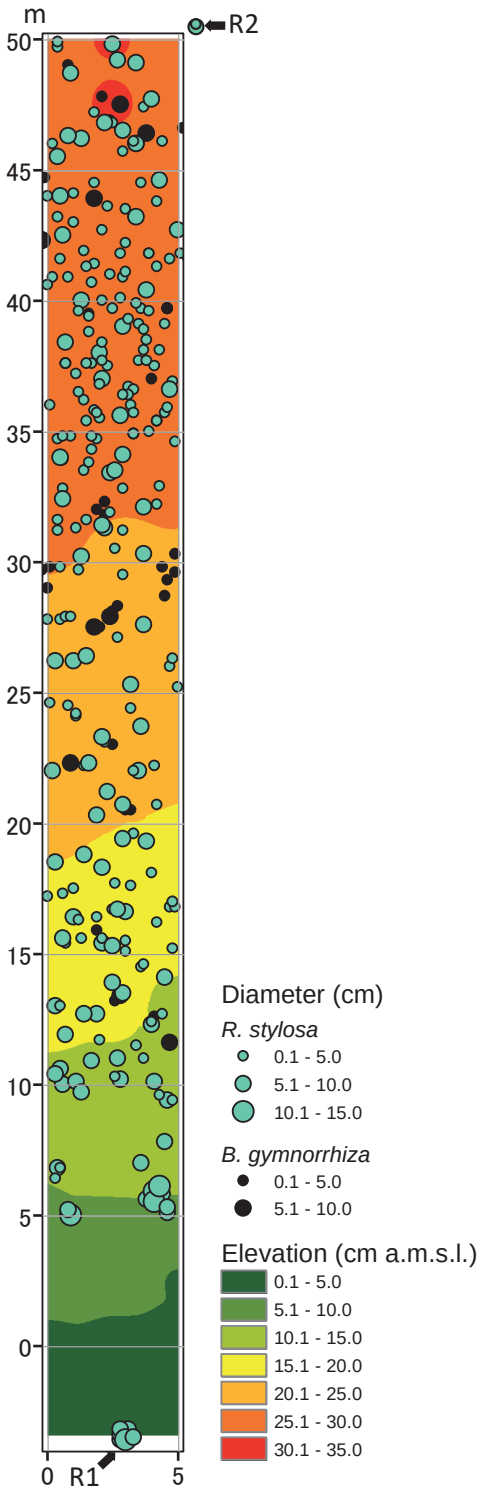

Fig. 3 Topography and species distribution in IFR1 and the experimental sites (R1 and R2).

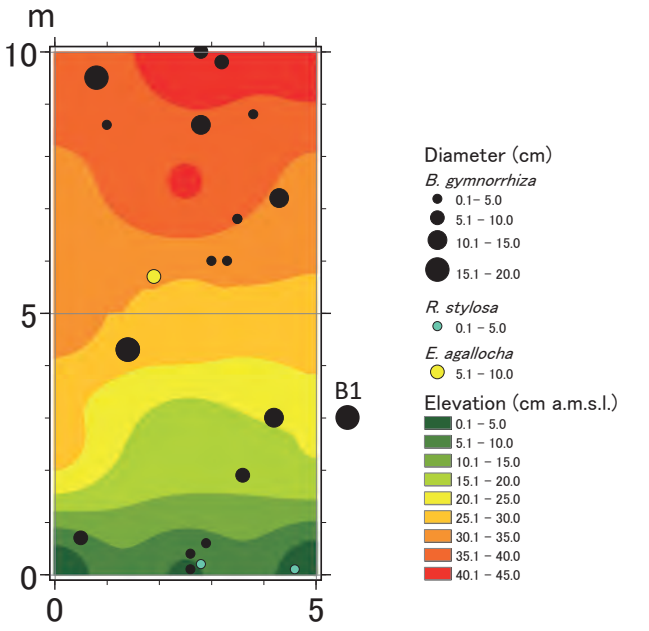

Fig. 4 Topography and species distribution in IFB1 and the experimental site (B1).

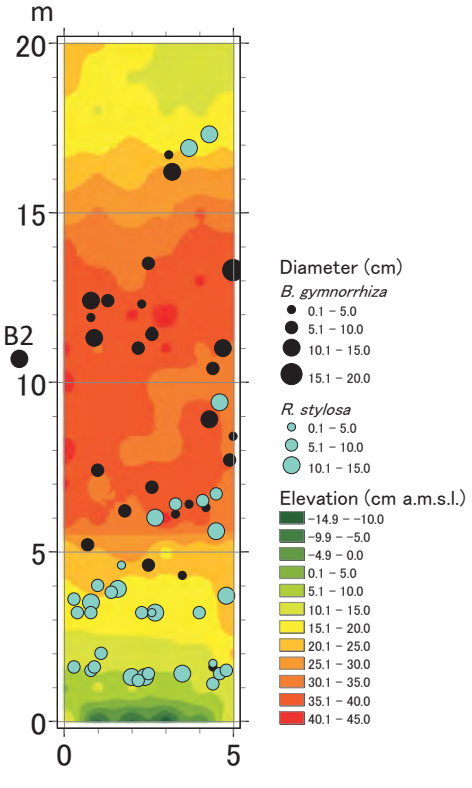

Fig. 5 Topography and species distribution in IFB2 and the experimental site (B2).

The ingrowth core experimental sites for *R. stylosa* were established 3.4 m seaward from the 0 m line (site code: R1) and 0.7 m landward from the 50 m line (site code: R2) of IFR1 (Fig. 3) to investigate the effects of tidal environments, such as submergence rate and time. The experimental sites for *B. gymnorrhiza* were established outside of the 3 m line from the seaward edge of IFB1 (Fig. 4, site code: B1) and at the highest elevation zone next to IFB2 (Fig. 5, site code: B2).

Ground elevation and tidal environment

The elevation of the experimental sites and plots and the amount of submergence time by the tide for a year were estimated based on the continuous tide-level records at an observation point (Fig. 2, site code: FT1). Continuous tide-level observations were conducted at 30-minute intervals from April 8, 2013, to June 1, 2014, using a water level data logger (Cera-Diver DIK-613A-A1, Daiki). The tide level records were adjusted using the atmospheric data observed by an atmospheric data logger (Baro-Diver DIK-611A-E1, Daiki). Tide level at R1 was also observed by a water-level logger and atmospheric data logger (CO-U20-001-04TI and CO-U20-001-04, HOBO, respectively) at 10-minute intervals from April 14, 2014, to May 20, 2014. The relative height between FT1 and R1 was calculated based on the simultaneous tide levels.

The mean tide level in Funaura Bay was identified by the level that inundates for 4380 hours in a year, which means the amount of time in half a year.

The amount of submergence time by the tide for a year for R1, R2, B1 and B2 was calculated using the tide level records for a year starting from April 8, 2013, and the relative height among FT1 and the sites. The elevation of R2 was determined by leveling from R1 using a pocket compass with a bubble level (LS-25, Ushikata). Elevations of the (0, 0) points of IFB1 and IFB2 were determined by the tide-level differences from R1. The tide-level observations were conducted between March 17, 2020, and March 30, 2020, using the water-level logger and atmospheric data logger (CO-U20-001-04TI and CO-U20-001-04, HOBO, respectively). Elevations in B1 and B2 were also identified by leveling from the (0, 0) points of IFB1 and IFB2, respectively.

Ground level in the permanent plots was measured at approximately 2.5 m intervals for IFR1 and IFB1 and 5 m intervals for IFB2 using the pocket compass. Elevation at the (0, 0) point of IFR1 was identified by leveling from R1. Elevation maps for the plots were drawn by spatial interpolation via the IDW method with ArcGIS 3D Analyst.

Ingrowth core and root litterbag methods

A flexible plastic pipe with a 2 mm mesh structure 3 cm in diameter was used for the ingrowth core. The plastic pipes were inserted in holes 60 to 80 cm deep bored by a steel pipe 4 cm in diameter. For B1, we bored only to 40 to 50 cm deep because of the existence of hard layers with rocks. The inside of the plastic pipes was filled with root-free shore sand.

Ten ingrowth cores were set radially from a sample tree between the prop roots for R1 and R2 on March 15, 2013, and between the knee roots for B1 and B2 on March 24, 2014. Five cores were collected approximately one year and two years later, i.e., on March 22, 2014, and February 27, 2015, for R1, respectively; on March 21, 2014, and February 27, 2015, for R2; on February 28, 2015, and March 15, 2016, for B1; and on February 27, 2015, and March 15, 2016, for B2; however, two cores for R1 were not collected during the second collection.

The cores collected were cut into 10 cm lengths. The contents of each cut core were rinsed in water using steel sieves with 1 mm mesh. The roots left on the sieves were divided into live roots and dead roots based on the features of live roots, which are relatively white and tough and float in fresh water. Live roots passing through the sieve were picked up with tweezers as much as possible. Dead roots passing through the sieve were also collected using a 0.4 mm filter. Live roots were classified into three categories, i.e., $\varphi<0.5$ mm (the class of very fine roots), $0.5 \leqq \varphi<2$ mm and $2 \leqq \varphi<5$ mm (the class of small roots). The sorted roots were dried at 95℃ for 48 hours and weighed. Dead roots for B1 were collected for four cores.

The data up to 50 cm deep without contamination by original soils were used to estimate fine-root accumulation.

One mm-mesh polyethylene bags of 15 cm by 20 cm were used for root litterbags. Fresh fine roots were collected from each species, with 3 to 10 g for *R. stylosa* and 4 to 12 g for *B. gymnorrhiza* in dry weight, and the roots were packed in the litterbags.

Three litterbags were set at 10 cm and 30 cm deep for R1 and R2 on March 22, 2014, respectively, and collected on February 28, 2015. Six and five litterbags

Table 1 Average tree diameter, tree height, tree density and basal area for three tree censuses in each plot.

Plot code	Species	Year	Diameter (cm) mean±SD	Height (m) mean±SD	Tree density (stems ha^{-1})	Basal area (m^2 ha^{-1})	zone
IFR1	*R. stylosa*	2013	4.57±2.00	2.30±0.53	11067	21.87	5 to 50 m zone
		2016	4.63±2.00	2.34±0.59	11778	23.80	
		2018	4.92±1.99	2.38±0.57	10933	24.54	
	B. gymnorrhiza	2013	3.70±1.60	2.26±0.44	1911	2.09	5 to 50 m zone
		2016	3.77±1.03	2.27±0.38	1689	2.02	
		2018	3.86±1.25	2.44±0.48	1244	1.61	
IFB1	*B. gymnorrhiza*	2014	8.69±4.80	4.66±1.30	3400	25.94	all
		2016	8.81±5.12	4.53±1.42	3200	25.67	
		2018	8.86±5.16	4.54±1.59	3200	26.00	
IFB2	*B. gymnorrhiza*	2014	7.75±4.18	4.86±1.83	3833	23.10	5 to 17 m zone
		2016	7.68±4.40	4.80±1.68	4000	24.39	
		2018	7.86±4.42	4.69±1.65	4000	25.27	
	R. stylosa	2014	7.13±3.03	4.39±1.22	10800	50.66	0 to 5 m zone
		2016	7.33±2.75	4.65±1.24	10400	49.90	
		2018	7.78±2.86	4.63±1.10	10000	53.77	

SD: standerd deviation

were set at 10 cm and 30 cm deep for B1 and B2, respectively, on March 1, 2015, and collected on March 15, 2016. The dry weight of the residual roots in each litterbag was measured, and the residual rate was calculated.

Statistical tests for significant differences were carried out using Excel for two sites with the same species and EZR (Kanda, 2013) among all sites.

Results

Stand structure of permanent plots

Table 1 shows the average tree diameter, tree height, tree density and basal area for the three censuses for each plot. In IFR1, *R. stylosa* dominated, and *B. gymnorrhiza* was sparsely distributed (Fig. 3). The tree densities of *R. stylosa* and *B. gymnorrhiza* in 2013, 2016 and 2018 were 11,067 stems ha^{-1} and 1,911 stems ha^{-1}; 11,778 stems ha^{-1} and 1,689 stems ha^{-1}; and 10,933 stems ha^{-1} and 1,244 stems ha^{-1}, respectively. The average diameter and tree height were 4.6 cm and 2.3 m in 2013 and 4.9 cm and 2.4 m in 2018 for *R. stylosa* and 3.7 cm and 2.3 m in 2013 and 3.9 cm and 2.4 m in 2018 for *B. gymnorrhiza*, respectively. The basal area of *R. stylosa* increased from 21.9 m^2 ha^{-1} in 2013 to 24.5 m^2 ha^{-1} in 2018, while that of *B. gymnorrhiza* decreased from 2.1 m^2 ha^{-1} in 2013 to 1.6 m^2 ha^{-1} in 2018.

The average diameter and tree height of the *R. stylosa* sample trees for the ingrowth core experiment were 8.2 cm and 3.0 m, which are an average of seven stems, for R1, respectively, and 6.1 cm and 2.5 m, which are an average of two stems, for R2.

In IFB1, *B. gymnorrhiza* dominated, and two *R. stylosa* existed at the seaward edge (Fig. 4). One *Excoecaria agallocha* was also found. The tree density of *B. gymnorrhiza* was 3400 stems ha^{-1} in 2014 and 3200 stems ha^{-1} in 2018. The average diameter and tree height of *B. gymnorrhiza* were 8.7 cm and 4.7 m in 2014 and 8.9 cm and 4.5 m in 2018, respectively. The decrease in tree height was possibly caused by the effects of typhoons. The basal area of *B. gymnorrhiza* in 2018 was 26.0 m^2 ha^{-1}.

In IFB2, *B. gymnorrhiza* dominated on the natural levee, which is a relatively high-elevation zone between the 5 m and 17 m lines, while *R. stylosa* dominated at the relatively low-elevation zone between 0 m and 5 m along the river (Fig. 5). The tree density of *B.*

Table 2 Dry weight of fine root biomass and necromass up to 50 cm deep for all ingrowth cores collected (unit: g m^{-2} 0.5 m^{-1} experimental $days^{-1}$).

site code	first collection							second collection						
	experimental days	biomass				necromass N_i	B_i+N_i	experimental days	biomass				necromass N_j	B_j+N_j
		< 0.5 mm	0.5-2.0 mm	2.0 mm ≦	fine roots B_i				< 0.5 mm	0.5-2.0 mm	2.0 mm ≦	fine roots B_j		
R1	372	482	106	40	588	74	663	714	1435	231	115	1667	929	2596
		258	21	0	279	156	435		986	155	196	1141	433	1574
		363	129	0	492	80	572		1057	248	60	1305	465	1770
		404	30	0	434	184	618		-	-	-	-	-	-
		529	92	96	620	147	767		-	-	-	-	-	-
	mean	407	76	27	483	128	611		1160	211	124	1371	609	1980
	SD	106	48	42	136	49	122		242	50	68	269	278	543
R2	371	374	23	0	397	546	943	714	676	110	76	785	471	1256
		386	63	99	449	257	706		903	34	0	937	1191	2128
		305	5	0	310	180	490		692	145	155	836	883	1720
		339	44	40	383	569	952		755	162	126	917	1217	2134
		382	7	0	389	671	1060		1431	132	218	1563	1148	2711
	mean	357	28	28	386	445	830		891	116	115	1008	982	1990
	SD	35	25	43	50	214	230		315	50	82	317	315	541
B1	341	118	13	0	131	524	655	721	626	112	0	738	821	1559
		295	92	91	387	525	912		810	223	663	1033	1576	2609
		131	52	7	183	632	815		498	130	0	628	409	1037
		210	57	0	267	444	711		416	121	128	536	365	901
		245	81	52	326	636	962		-	-	-	-	-	-
	mean	200	59	30	259	552	811		587	147	198	734	793	1527
	SD	75	31	40	104	82	130		172	51	316	216	561	775
B2	340	165	154	57	319	443	762	721	305	104	0	408	1182	1590
		99	51	0	150	642	792		538	218	62	756	273	1029
		205	94	0	299	289	588		412	201	190	613	911	1524
		156	209	130	365	65	430		247	234	0	481	956	1437
		288	129	0	417	-	417		122	22	54	143	975	1118
	mean	182	127	37	310	360	598		325	156	61	480	859	1340
	SD	70	60	57	100	244	177		159	90	78	230	344	251

SD:standard deviation

gymnorrhiza increased from 3833 stems ha^{-1} in 2014 to 4000 stems ha^{-1} in 2018, while *R. stylosa* decreased from 10,800 stems ha^{-1} to 10,000 stems ha^{-1} between 2014 and 2018. The average diameter and tree height were 7.8 cm and 4.9 m in 2014 and 7.9 cm and 4.7 m in 2018 for *B. gymnorrhiza* and 7.1 cm and 4.4 m in 2014 and 7.8 cm and 4.6 m in 2018 for *R. stylosa*, respectively. The basal area in 2018 was 25.3 m^2 ha^{-1} for *B. gymnorrhiza* and 53.8 m^2 ha^{-1} for *R. stylosa*.

Ground elevation and tidal environment of the experimental sites and plots

The elevation of IFR1 gradually increased seaward to landward (Fig. 3). The elevations (above mean sea level) of sites R1 and R2 were +4 cm and +30 cm, respectively. The elevations of IFB1 and IFB2 were between 0 cm and +44 cm and between -12 cm and +43 cm, respectively (Figs. 4 and 5). The elevations of sites B1 and B2 were +22 cm and +43 cm, respectively.

The amount of submergence time by tide for a year was calculated as 4032 hours for site R1, 2095 hours for site R2, 2651 hours for site B1 and 1268 hours for site B2, which means that the submergence rate to the total number of hours for a year was 46 %, 24 %, 30 % and 14 %, respectively.

Accumulated fine roots

Table 2 shows the dry weight of accumulated live and dead roots, i.e., biomass and necromass, respectively, up to 50 cm deep for all ingrowth cores collected. The average value of the distribution ratio of fine-root biomass up to 50 cm deep at the points collected up to 70 cm deep or more was 92 % for *R. stylosa* and 88 % for *B. gymnorrhiza*.

The accumulated mean fine roots, including necromass, for the first collection (B_i + N_i) and the second collection (B_j + N_j) were 611 g m^{-2} (for 372 days) and 1980 g m^{-2} (for 714 days) for R1, 830 g m^{-2} (for 371 days) and 1990 g m^{-2} (for 714 days) for R2, 811 g m^{-2} (for 341 days) and 1527 g m^{-2} (for 721 days) for B1 and 598 g m^{-2} (for 340 days) and 1340 g m^{-2} (for 721 days) for B2, respectively. These results suggest that the accumulated fine roots, including necromass, in the second year were possibly larger than those in the first year for *R. stylosa*.

Fine-root biomass for the first collection (B_i) and the second collection (B_j) were 483 and 1371 g m^{-2} for R1, 386 and 1008 g m^{-2} for R2, 259 and 734 g m^{-2}

Table 3 Daily fine root biomass accumulation up to 50 cm deep for all ingrowth cores collected (unit: g m^{-2} 0.5 m^{-1} day^{-1}).

	First collection			Second collection		
	< 0.5 mm	0.5-2.0 mm	total	< 0.5 mm	0.5-2.0 mm	total
R1	1.30	0.29	1.58	2.01	0.32	2.33
	0.69	0.06	0.75	1.38	0.22	1.60
	0.98	0.35	1.32	1.48	0.35	1.83
	1.09	0.08	1.17	-	-	-
	1.42	0.25	1.67	-	-	-
mean	1.09	0.20	1.30	1.62	0.30	1.92
SD	0.28	0.13	0.37	0.34	0.07	0.38
R2	1.01	0.06	1.07	0.95	0.15	1.10
	1.04	0.17	1.21	1.26	0.05	1.31
	0.82	0.01	0.84	0.97	0.20	1.17
	0.91	0.12	1.03	1.06	0.23	1.28
	1.03	0.02	1.05	2.00	0.19	2.19
mean	0.96	0.08	1.04	1.25	0.16	1.41
SD	0.09	0.07	0.13	0.44	0.07	0.44
p-value: R1 vs R2	0.370[1)]		0.198[1)]	0.256[2)]		0.150[2)]
B1	0.35	0.04	0.39	0.87	0.16	1.02
	0.86	0.27	1.14	1.12	0.31	1.43
	0.38	0.15	0.54	0.69	0.18	0.87
	0.62	0.17	0.78	0.58	0.17	0.74
	0.72	0.24	0.96	-	-	-
mean	0.59	0.17	0.76	0.81	0.20	1.02
SD	0.22	0.09	0.30	0.24	0.07	0.30
B2	0.49	0.45	0.94	0.42	0.14	0.57
	0.29	0.15	0.44	0.75	0.30	1.05
	0.60	0.28	0.88	0.57	0.28	0.85
	0.46	0.62	1.07	0.34	0.32	0.67
	0.85	0.38	1.23	0.17	0.03	0.20
mean	0.54	0.37	0.91	0.45	0.22	0.67
SD	0.21	0.18	0.30	0.22	0.13	0.32
p-value: B1 vs B2	0.722[2)]		0.447[2)]	0.049[2)]		0.136[2)]
p-value: for all sites	0.001[3)]		0.055[3)]	0.001[3)]		0.002[3)]

SD: standerd deviation, 1): Welch's t-test, 2): Student's t-test, 3): one-way ANOVA

for B1 and 310 and 480 g m^{-2} for B2, respectively, of which 407 and 1160 g m^{-2} for R1, 357 and 891 g m^{-2} for R2, 200 and 587 g m^{-2} for B1 and 182 and 325 g m^{-2} for B2 were very fine roots. The ratios of very fine roots to total fine-root biomass for the first and second collections were 84 and 85 % for R1, 93 and 88 % for R2, 77 and 80 % for B1 and 59 and 68 % for B2, respectively. Namely, the ratio for *R. stylosa* was obviously higher than that for *B. gymnorrhiza*.

The necromass for the first collection (N_i) and the second collection (N_j) were 128 and 609 g m^{-2} for R1, 445 and 982 g m^{-2} for R2, 552 and 793 g m^{-2} for B1 and 360 and 859 g m^{-2} for B2, respectively.

We tested the difference between the sites for the fine-root biomass by converting the observed values to the daily values by dividing the observed values by the experimental days, but this method would not work for necromass because decomposition processes progress exponentially. Table 3 shows the daily values of fine-root biomass up to 50 cm deep for all ingrowth cores collected.

Between the sites for the same species, a significant difference was found in the second collection for the very fine roots of *B. gymnorrhiza* (B1>B2: $p<0.05$, Student's t-test), while there was no significant difference for *R. stylosa*.

Among all four sites, a significant difference was found for very fine roots at both the first and second collections ($p<0.01$, one-way ANOVA) and total fine roots at the second collection ($p<0.01$, one-way ANOVA). The p value for total fine roots on the first collection was 0.055 (one-way ANOVA).

For the first collection, the very fine roots of R1 were significantly larger than those of B1 and B2 ($p<0.01$, Tukey's HSD test), and those of R2 were also significantly larger than those of B2 ($p<0.05$, Tukey's HSD test). The very fine roots of R2 showed a larger tend than those of B1 ($p<0.1$, Tukey's HSD test). For the total fine roots, R1 was significantly larger than B1 ($p<0.05$, Tukey's HSD test).

Table 4 Observed residual ratio of root litter by the litter bag method and the converted values per day.

site	R1				R2				B1				B2			
period (days)	343		1		343		1		379		1		379		1	
depth (cm)	10	30	10	30	10	30	10	30	10	30	10	30	10	30	10	30
Residual ratio for each litter bag (wt %)	74.64	39.50	99.91	99.73	51.16	64.11	99.80	99.87	50.40	48.40	99.82	99.81	57.65	72.68	99.85	99.92
	64.48	63.03	99.87	99.87	53.15	58.24	99.82	99.84	48.64	49.57	99.81	99.82	51.16	58.32	99.82	99.86
	48.15	54.84	99.79	99.82	67.68	54.97	99.89	99.83	47.80	48.40	99.81	99.81	50.99	52.03	99.82	99.83
	-	-	-	-	-	-	-	-	50.91	49.34	99.82	99.81	60.43	67.83	99.87	99.90
	-	-	-	-	-	-	-	-	50.44	45.66	99.82	99.79	50.86	59.63	99.82	99.86
	-	-	-	-	-	-	-	-	56.58	-	99.85	-	68.08	-	99.90	-
mean	62.42	52.46	99.86	99.81	57.33	59.11	99.84	99.85	50.80	48.28	99.82	99.81	56.53	62.10	99.85	99.87
SD	13.36	11.95	0.06	0.07	9.02	4.63	0.04	0.02	3.08	1.56	0.02	0.01	6.95	8.16	0.03	0.03
mean	57.44		99.83		58.22		99.84		49.65		99.82		59.06		99.86	
SD	12.58		0.07		6.49		0.03		2.73		0.01		7.70		0.03	

SD: standerd deviation

For the second collection, the very fine roots of R1 were significantly larger than those of B1 and B2, and those of R2 were also significantly larger than those of B2 ($p<0.05$, $p<0.01$ and $p<0.01$, respectively, Tukey's HSD test). The total fine roots of R1 were significantly larger than those of B1 and B2, and those of R2 were also significantly larger than those of B2 ($p<0.05$, $p<0.01$ and $p<0.05$, respectively, Tukey's HSD test).

Residual ratio of root litter

Table 4 shows the residual ratio of root litter based on the litter bag experiment for all four sites and at two depths. There was no significant difference between 10 cm deep and 30 cm deep for all sites. To test the difference between the species, we converted the observed results to the residual ratio per day because the examination period was different between the species. Let r and R_n be the residual ratio of root litter per day and the residual ratio of root litter after n days, respectively, as $r^n=R_n$, $r=\sqrt[n]{R_n}$. As the period of litterbag experiment for each site was nearly one year, i.e., 343 days for R1 and R2 and 379 days for B1 and B2, we approximated the daily residual ratio of root litter using the values of R_n indicated in Table 4.

The mean residual ratio per day for each site was calculated at 99.83 % for R1, 99.84 % for R2, 99.82 % for B1 and 99.86 % for B2. The results of the Steel-Dwass test indicated that B1 was significantly smaller than B2 ($p<0.01$), although there was no significant difference between the sites for the other combinations.

Discussion

Estimation of fine-root productivity

Live trees continuously produce fine roots, while fine roots die after a certain period of time. Assuming that the fine-root production and dead-root generation rates are constant, fine roots accumulate at a constant rate. However, this assumption can be applied when we discuss annual production only for the climate zones with seasons because these rates seem to vary with season.

Let p, b, and m be average daily fine-root production, average daily fine-root biomass accumulation, and average daily fine-root mortality, respectively, and $p = b + m$. Therefore, let P_n be fine-root production for n days, which can be calculated by the following equation:

$$P_n=n(b+m) \quad (1)$$

Thus, annual fine-root production (P_{365}) is calculated by substituting 365 for n of Eq. 1. That is, we need to estimate the average daily fine-root biomass accumulation and mortality to calculate the annual fine-root production.

Let B_t be fine-root biomass at a certain point in time (t is the number of days after installing the ingrowth core), and b is calculated by the following equation using the values of fine-root biomass at two time

points, i.e., first collection: $t = i$ and second collection: t = j:

$$b=(B_j-B_i)/(j-i) \quad (2)$$

For m, necromass at the second collection (N_j) is expressed by the following equation:

$$N_j=N_i r^{j-i}+m\int_0^{j-i} r^n dn \quad (3)$$

where N_i is the necromass at the first collection and r is the residual ratio of root litter per day. Transforming Eq. 3, m is calculated by the following equation:

$$m=(N_j-N_i r^{j-i})\ln r/(r^{j-i}-1) \quad (4)$$

As the interval between i and j for each site was nearly one year in this study, i.e., 342 days for R1, 343 days for R2, 380 days for B1 and 381 days for B2, we can approximate the average daily fine-root biomass accumulation and fine-root mortality by the values calculated by Eq. 2 and Eq. 4, respectively.

Let MDR_n be missing dead roots for n days, i.e., amount of decomposition to the mortality for n days, which can be calculated by the following Equation.

$$MDR_n=nm-m\int_0^n r^n dn=m(n-\frac{r^n-1}{\ln r}) \quad (5)$$

Thus, annual missing dead roots (MDR_{365}) are calculated by substituting 365 for n in Eq. 5.

Table 5 shows the daily fine-root biomass accumulation (b), daily mortality (m), daily fine-root production (p), annual fine-root production (P_{365}) and annual missing dead roots to the annual production (MDR_{365}) for each site.

The daily fine-root biomass accumulation and daily mortality for each site were calculated at 2.60 g m^{-2} 0.5 m^{-1} day^{-1} and 2.04 g m^{-2} 0.5 m^{-1} day^{-1} for R1, 1.81 g m^{-2} 0.5 m^{-1} day^{-1} and 2.73 g m^{-2} 0.5 m^{-1} day^{-1} for R2, 1.25 g m^{-2} 0.5 m^{-1} day^{-1} and 1.90 g m^{-2} 0.5 m^{-1} day^{-1} for B1 and 0.45 g m^{-2} 0.5 m^{-1} day^{-1} and 2.19 g m^{-2} 0.5 m^{-1} day^{-1} for B2 by Eq. 2 and Eq. 4, respectively. The annual fine-root production and annual missing dead roots for each site were calculated at 1691 g m^{-2} 0.5 m^{-1} $year^{-1}$ and 182 g m^{-2} 0.5 m^{-1} $year^{-1}$ for R1, 1658 g m^{-2} 0.5 m^{-1} $year^{-1}$ and 239 g m^{-2} 0.5 m^{-1} $year^{-1}$ for R2, 1150 g m^{-2} 0.5 m^{-1} $year^{-1}$ and 189 g m^{-2} 0.5 m^{-1} $year^{-1}$ for B1, and 962 g m^{-2} 0.5 m^{-1} $year^{-1}$ and 172 g m^{-2} 0.5 m^{-1} $year^{-1}$ for B2 by Eq. 1 and Eq. 5, respectively.

Osawa and Aizawa (2012) proposed a calculation procedure to estimate fine-root production considering the decomposition processes of dead fine roots between two time points using the data obtained by ingrowth core and litterbag experiments. However, as their procedure was based on the assumption that the periods of both experiments were equivalent, the equation to estimate the dead-root decomposition (Eq. 4 of Osawa and Aizawa, 2012) was not directly applied to the case of different experimental periods, as in this study, without correcting the decomposition rate. Moreover, as the equation was for the estimation of dead-root decomposition not only for the dead-root mortality between the two time points but also for the necromass at the first collection of ingrowth core, it is impossible to use the equation to calculate the annual decomposition to the annual dead-root mortality, which is an essential value to estimate the annual fine-root production. Osawa and Aizawa (2012) calculated the daily decomposition by simply dividing the value obtained from their Eq. 4 by experimental days, which was obviously incorrect because decomposition processes progress exponentially. Based on these issues, we conclude that their method did not lead to an estimate of annual fine-root production.

Appropriate period for the first collection of ingrowth core

Observed values of the accumulated fine roots, including necromass, for the first collection, i.e., 611 g m^{-2} 0.5 m^{-1} 372 $days^{-1}$ for R1, 830 g m^{-2} 0.5 m^{-1} 371 $days^{-1}$ for R2, 811 g m^{-2} 0.5 m^{-1} 341 $days^{-1}$ for B1 and 598 g m^{-2} 0.5 m^{-1} 340 $days^{-1}$ for B2, were lower than the theoretical values calculated by subtracting MDR_n from P_n, i.e., 1536 g m^{-2} 0.5 m^{-1} 372 $days^{-1}$ for R1, 1439 g m^{-2} 0.5 m^{-1} 371 $days^{-1}$ for R2, 907 g m^{-2} 0.5 m^{-1} 341 $days^{-1}$ for B1 and 745 g m^{-2} 0.5 m^{-1} 340 $days^{-1}$ for B2, which suggest that the observed values were underestimated and that it takes a certain period for the fine roots to penetrate into the ingrowth core at a constant rate. The difference between the observed value and the theoretical value was obviously larger in *R. stylosa* than in *B. gymnorrhiza*. The reason for this result is possibly related to the high proportion of very fine roots for *R. stylosa* (Table 2). Since the very fine roots are the most terminal of the root system, their breakout may occur after the invasion of the source roots. The underestimated value for each site, which was estimated by the combination of Eqs. 1 and 5, corresponded to the live- and dead-root accumulation of 215 days for R1, 114 days for R2, 31 days for B1 and 58 days for B2. The first collection of ingrowth cores

Table 5 Estimation of probable fine-root productivity and missing dead roots.

	R1	R2	B1	B2
Daily fine-root biomass accumulation: b (g m^{-2} 0.5 m^{-1} day^{-1})	2.60	1.81	1.25	0.45
Daily fine-root mortality: m (g m^{-2} 0.5 m^{-1} day^{-1})	2.04	2.73	1.90	2.19
Daily fine-root production: p (g m^{-2} 0.5 m^{-1} day^{-1})	4.64	4.54	3.15	2.64
Annual fine-root production: P_{365} (g m^{-2} 0.5 m^{-1} $year^{-1}$)	1691	1658	1150	962
Missing dead roots to annual production: MSD_{365} (g m^{-2} 0.5 m^{-1} $year^{-1}$)	182	239	189	172

must be conducted after enough time has passed the number of days mentioned above.

Differences between the two species and the effect of the tidal environment

The calculated results for fine-root production (Table 5) show that the fine-root productivity of *R. stylosa* was visibly greater than that of *B. gymnorrhiza*, while there was little difference between the two species in terms of missing dead roots, though the differences could not be tested statistically because the values were calculated using the mean values obtained by the ingrowth core and litterbag methods. On the other hand, the very fine-root biomass of *R. stylosa* was significantly greater than that of *B. gymnorrhiza* in both the first and second collections except in R2 vs B1, although a larger trend occurred in R2 than B1 for the first collection (Table 3). Mangrove peat on Iriomote Island is distributed in the *R. stylosa* forest only (Fujimoto and Ohnuki, 1995). The greater productivity of the fine roots of *R. stylosa*, especially very fine roots, possibly contributes to the accumulation of mangrove peat.

Between the sites for the same species, there was little difference in the fine-root production for *R. stylosa*, while fine-root production was greater at the site located in the lower elevation zone (B1) than at the site located in the higher elevation zone (B2) for *B. gymnorrhiza* (Table 4). The very fine-root biomass of B1 was significantly greater than that of B2 for the second collection (Table 3). These trends suggest that the submergence rate by tide possibly affects fine-root production for *B. gymnorrhiza*, especially for very fine roots. On the other hand, the common trends, i.e., the greater daily fine-root biomass accumulation in the lower elevation zone and the higher daily mortality in the higher elevation zone, were found for both species (Table 5). The trends suggest that the fine-root turnover time is possibly shorter in the higher elevation zone, i.e., the lower submergence rate zone, than in the lower elevation zone.

The significantly larger value of the residual ratio of root litter in B2 than in B1 suggests that the root decomposition rate of *B. gymnorrhiza* is possibly slower under the low submergence rate condition. Generally, a low submergence rate condition accelerates the decomposition rate because of the aerobic environment. The opposite result between B1 and B2 suggests that some local conditions, such as the particle size composition of sediments and soil temperature, possibly affect the decomposition rate.

Evaluation of previous studies on fine-root production

Castañeda-Moya et al. (2011) compiled existing data on the fine-root productivity of mangroves, most of which were obtained by the ingrowth core method except for one study (Lovelock, 2008) calculated by using the indirect mass balance approach. The values obtained by the ingrowth core method ranged from 43 g m^{-2} $year^{-1}$ (depth: 30 cm, species: *Rhizophora mangle* scrub, place: Belize, source: Mckee et al., 2007) to 750 g m^{-2} $year^{-1}$ (depth: 30 cm, species: *Sonneratia alba*, place: Kosrae Island, Micronesia, source: Gleason and Ewel, 2002).

In addition, Adam et al (2014) reported values of 40 g m^{-2} $year^{-1}$ for tall trees (8 to 13 m height) of *Laguncularia racemosa and R. mangle* mixed forest, 95 g m^{-2} $year^{-1}$ for medium sized trees (5 to 8 m height) of *R. mangle* and *Avicennia germinans* mixed forest and 146 g m^{-2} $year^{-1}$ for smaller (< 5 m height) *R. mangle* and *A. germinans* mixed forest (depth: 35 cm, place: the northwestern coast of the Yucatan Peninsula, Mexico), and Cormier et al. (2015) reported values between 46 and 119 g m^{-2} $year^{-1}$ (depth: 45 cm, species: mixed forest consisting of *S.*

alba, B. gymnorrhiza and *R. apiculata*, place: Kosrae and Pohnpei Islands, Micronesia). Poungparn et al. (2016) estimated 340 g m^{-2} $year^{-1}$ for the *Avicennia alba* zone, 408 g m^{-2} $year^{-1}$ for the *R. apiculata* zone and 344 g m^{-2} $year^{-1}$ for the *Xylocarpus granatum* zone calculated by the decision-matrix method (depth: 30 cm, place: Trat, eastern Thailand). Noguchi et al. (2020) reported values of 450 g m^{-2} $year^{-1}$ for *A. alba* and 740 g m^{-2} $year^{-1}$ for *R. apiculata* (depth: 40 cm, place: Ranong, southern Thailand).

Previous studies have not estimated missing dead roots. Namely, these values were underestimated as fine-root productivity. Most estimated values in the previous studies were obviously lower than the values obtained in our study, despite the values obtained in the tropics.

On the other hand, in comparison to our study, Xiong et al. (2017) estimated greater fine-root productivity with the decision-matrix method using the data obtained by the sequential soil core method at 3011 g m^{-2} $year^{-1}$ for a riverine *Ceriops tagal* forest, 1056 g m^{-2} $year^{-1}$ for a seashore *C. tagal* forest, 2064 g m^{-2} $year^{-1}$ for a *Bruguiera sexangula* forest, 1873 g m^{-2} $year^{-1}$ for an *R. stylosa* forest and 576 g m^{-2} $year^{-1}$ for an *Avicennia marina* forest (depth: 1 m, place: Hainan Island, China) and found that approximately 90 % of fine-root biomass was distributed up to 60 cm in depth. It is notable that they obtained a slightly larger value than our estimation for *R. stylosa* from a climatic environment similar to Iriomote Island, although the decision-matrix method usually produces underestimations.

Conclusion

Previous studies using the ingrowth core method to estimate fine-root productivity have not considered missing dead roots resulting from decomposition processes, so the estimated values have been underestimated. This study succeeded in estimating probable fine-root productivity, including missing dead roots resulting from decomposition processes by combining ingrowth core experiments for two years with a litter bag experiment for one year.

The probable fine-root productivities were calculated at 1691 g m^{-2} 0.5 m^{-1} $year^{-1}$ for *R. stylosa* located at the seaward forest margin (elevation: +4 cm, submergence rate in time: 46 %), 1658 g m^{-2} 0.5 m^{-1} $year^{-1}$ for interior *R. stylosa* (+30 cm, 24 %), 1150 g m^{-2} 0.5 m^{-1} $year^{-1}$ for seashore *B. gymnorrhiza* (+22 cm, 30 %) and 962 g m^{-2} 0.5 m^{-1} $year^{-1}$ for interior *B. gymnorrhiza* (+43 cm, 14 %), of which missing dead roots were estimated at 182 g m^{-2} 0.5 m^{-1} $year^{-1}$, 239 g m^{-2} 0.5 m^{-1} $year^{-1}$, 189 g m^{-2} 0.5 m^{-1} $year^{-1}$ and 172 g m^{-2} 0.5 m^{-1} $year^{-1}$, respectively. Namely, the fine-root productivity was obviously greater for *R. stylosa* than for *B. gymnorrhiza*, while there was little difference in the missing dead-root values, although the value at the site with a lower submergence rate for *R. stylosa* was relatively large. The greater productivity in the fine roots for *R. stylosa*, especially very fine roots, potentially explains why mangrove peat is distributed in *Rhizophora* forests only.

The common trends for both species, i.e., greater fine-root biomass accumulation in the lower elevation zone and greater mortality in the higher elevation zone, suggest shorter turnover time in the lower submergence rate zone than in the higher submergence rate zone.

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