FINE ROOT PRODUCTION AND TURNOVER ALONG A FOREST SUCCESSION AFTER SLASH-AND-BURN AGRICULTURE †

[PRODUCCIÓN Y RECAMBIO DE RAÍCES FINAS A LO LARGO DE UNA SUCESIÓN FORESTAL TRAS LA AGRICULTURA DE ROZA TUMBA Y QUEMA]

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SUMMARY

Background. Fine root production and turnover are the fundamental processes of net primary productivity in forest ecosystems. Fine root production and turnover rates can vary with the successional gradients of the forest ecosystems created by land use changes. **Objective.** To evaluate the variations in fine root production and turnover along the successional gradients of tropical secondary forests and compare them with adjacent primary forests. **Methodology.** A total of 256 cylindrical ingrowth bags (of 8 cm diameter and 30 cm depth) were established in 16 forest stands representing four stages of succession. Four ingrowth bags from each stand were collected at an interval of about three months. Live and dead fine roots (≤2 mm diameter) were separated, washed, oven-dried, and weighed. **Results.** There was no significant difference in annual fine root productivity between secondary forests and primary forests but the fine root turnover rates were higher in secondary forests than in primary forests. Fine root production rates varied from 1.9 to 2.8 Mg of dry biomass ha^{-1} yr^{-1} while fine root turnover over rates ranged from 1.1 to 1.5 yr^{-1}. Fine root production was higher in the dry season compared to the wet season. **Implications.** The results on fine root dynamics can be useful in modeling below-ground mechanisms of carbon sequestration in forest ecosystems during succession. **Conclusions**. Fine root productivity did not vary with forest age but the relative turnover rates were higher in secondary forests than in primary forests. Tree basal area was a significant predictor of fine root production.

Key words: Fine root biomass; secondary forests; ingrowth bags; belowground carbon dynamics; Calakmul

RESUMEN

Antecedentes. La producción y renovación de raíces finas son los procesos fundamentales de la productividad primaria neta en los ecosistemas forestales. Las tasas de producción y renovación de raíces finas pueden variar con los gradientes sucesionales de los ecosistemas forestales creados por los cambios en el uso del suelo. **Objetivo**. Evaluar las variaciones en la producción y renovación de raíces finas a lo largo de los gradientes sucesionales de los bosques secundarios tropicales y compararlas con los bosques primarios adyacentes.

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Metodología. Se estableció un total de 256 bolsas cilíndricas de crecimiento interno (de 8 cm de diámetro y 30 cm de profundidad) en 16 rodales forestales que representaban cuatro etapas de sucesión. Se recogieron cuatro bolsas de crecimiento de cada rodal con un intervalo de unos tres meses. Las raíces finas vivas y muertas (≤2 mm de diámetro) se separaron, lavaron, secaron y pesaron. **Resultados:** No hubo diferencias significativas en la productividad anual de raíces finas entre bosques secundarios y primarios, pero las tasas de renovación de raíces finas fueron mayores en los bosques secundarios que en los primarios. Las tasas de producción de raíces finas variaron de 1.9 a 2.8 Mg de biomasa seca ha^{-1} año^{-1} mientras que las tasas de renovación de raíces finas variaron de 1.1 a 1.5 año^{-1}. La producción de raíces finas fue mayor en la estación seca que en la húmeda. **Implicaciones:** Los resultados sobre la dinámica de las raíces finas pueden ser útiles en la modelización de los mecanismos subterráneos de secuestro de carbono en ecosistemas forestales durante la sucesión. **Conclusiones:** La productividad de las raíces finas no varió con la edad del bosque, pero las tasas relativas de renovación fueron mayores en los bosques secundarios que en los primarios. El área basal de los árboles fue un predictor significativo de la producción de raíces finas.

Palabras clave: Biomasa de raíces finas; bosques secundarios; bolsas de crecimiento; dinámica del carbono subterráneo; Calakmul.

INTRODUCTION

Fine root production is a fundamental component of forest productivity because it contributes to 22% – 40% of terrestrial net primary production (Lima *et al.* 2010; Finér *et al.* 2011a; Luke McCormack *et al.* 2013; Pandey *et al.* 2023). Fine root production and turnover is one of the important pathways of carbon and nutrient cycling in forest ecosystems (Nadelhoffer and Raich 1992; Matamala *et al.* 2003; Jourdan *et al.* 2008; Germon *et al.* 2020). Changes in fine root distribution affect mycorrhizal colonization, organic matter, and nutrient allocation to deeper soil profiles (Addo-Danso *et al.* 2020; Cordeiro *et al.* 2020; Cusack and Turner 2021). Along with litterfall, fine root turnover provides detrital carbon to soil organisms, which enhances the overall microbial activity in the soil and is a variable to improve soil water holding capacity and ultimately improve soil quality (Metcalfe *et al.* 2008; Luke McCormack *et al.* 2013; Zheng *et al.* 2021; Sánchez-Silva *et al.* 2022). Fine roots represent a dynamic fraction of belowground biomass and an important nutrient reserve for secondary forest growth, while the turnover is one of the key mechanisms of the forest ecosystem recovery after natural or anthropogenic disturbances (Brunner *et al.* 2013; Hertel *et al.* 2013; Freschet *et al.* 2021). Production and decomposition of fine roots are also related to carbon fluxes from the forest ecosystems since they emit carbon dioxide when they respire and decompose (Chen *et al.* 2004; Luke McCormack *et al.* 2013; Sun *et al.* 2020). Fine root productivity in European broadleaf forests was reported to be 2.5 Mg ha^{-1} yr^{-1} while in tropical forests of the Brazilian Amazon, it was 1.6 Mg ha^{-1} yr^{-1} (Newman *et al.* 2020, Martins *et al.* 2022). However, fine root productivity varies with the changes in forest structural properties and functions.

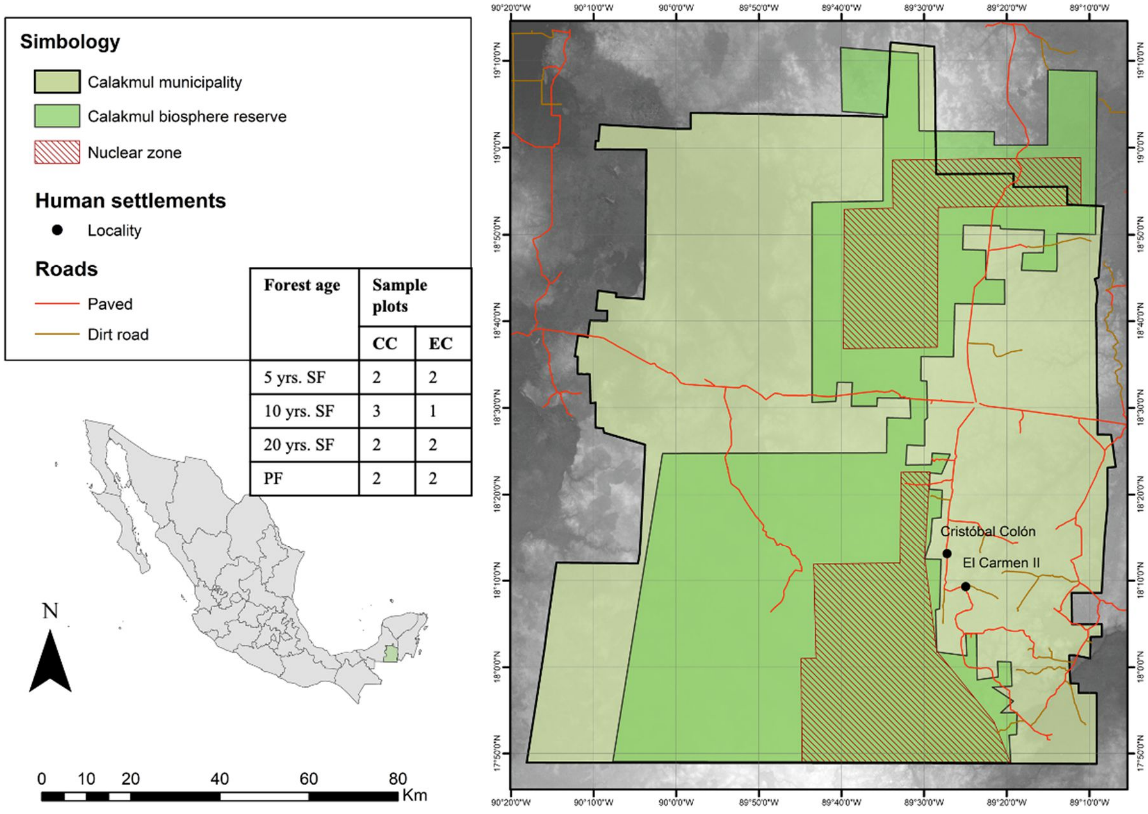
The structure and function of the tropical forests in the world are in a continuous process of change due to different types of anthropogenic disturbances (Marín-Spiotta *et al.* 2008; Chazdon 2014; Poorter *et al.* 2021). Successional forest patches at different stages of growth are the common characteristics of tropical landscapes in southern Mexico because of the recent land use changes (Velasco-Murguía *et al.* 2021; Jakovac *et al.* 2022; Aryal *et al.* 2024). Such successional secondary forest regeneration mostly occurs in the land left fallow after the cessation of farming activities such as slash-and-burn agriculture. During the recovery from younger to older ages, these secondary forests undergo through multiple ecological changes. One of the changes during secondary succession is the productivity and turnover of fine roots. Successional changes in species composition, stand structure, above and belowground biomass stocks, and soil fertility can explain the variation in fine root production during secondary vegetation growth (Riutta *et al.* 2021; Aryal *et al.* 2022). It is fundamental to understand the successional dynamics of fine root growth and turnover because a significant proportion of total biomass stock and production takes place belowground (Neill 1992; Kochsiek *et al.* 2013; Martins *et al.* 2021).

Shifting cultivation is still a common practice in southern Mexico where farmers slash and burn primary as well as secondary forests for milpa, a corn-squash-bean agriculture, for one or few years and they abandon the land for fallowing (Batista *et al.* 2021; Falkowski *et al.* 2023). The fallow period of those forests is getting shorter because the pressure for food production is increasing. Many studies have focused on aboveground carbon dynamics but the belowground carbon dynamics of those successional forests has not been studied widely (Girardin *et al.* 2010; Kochsiek *et al.* 2013). In this study, we tested the following two hypotheses: i) fine root production dynamics are related to forest growth stages, and ii) aboveground parameters of forest structure like basal area can explain the fine root production variation to some extent in tropical secondary forests.

MATERIALS AND METHODS

Study site and experimental plots

The study was conducted in a chronosequence of tropical secondary forests regenerated after the cessation of slash-and-burn agriculture. Secondary forests (SF) of 5, 10, and 20 years of age and old-growth primary forests (PF) were sampled. Slash and burn agriculture in the region comprise of clearing forests, cultivating milpa (corn-squash-bean) for a few years and leaving the land fallow for forest recovery. Sampling sites were located in ejidos El Carmen II and Cristóbal Colon of Calakmul municipality, in the state of Campeche, the southern part of the Yucatan Peninsula, Mexico (Fig. 1). The region is characterized by a sub-humid tropical climate (García 1973) with an average precipitation of 1000-1500 mm per year (with major portions of the rainfall from July to October) and mean annual temperature of 22 - 26ºC (García Gil *et al.* 2002). Rendzic leptosols and vertisols are the dominating soil types (Bautista *et al.* 2011). The dominant forest type in the region is semi-evergreen tropical forest (Rzedowski 1981; Pérez-Salicrup 2004), of which large portions have been converted to slash-and-burn agriculture that created a mosaic of agricultural lands mixed with secondary forests in various stages of development. A total of 16 sampling plots (four plots × four successional categories) were established to evaluate fine root production and turnover (Fig. 1). Successional categories include 1) younger secondary forests of five years old, 2) medium secondary forests of 10 years, 3) advanced secondary forests of 20 years, and 4) old-growth primary forests.



Forest age	Sample plots	
	CC	EC
5 yrs. SF	2	2
10 yrs. SF	3	1
20 yrs. SF	2	2
PF	2	2

Figure 1. Location of the study site and distribution sampling plots according to the forest age class. CC = Cristobal Colon, EC = El Carmen II. SF = secondary forests and PF = primary forests (source: original from authors).

The most common tree species of these successional forests are listed in Table 1 in the order of abundance. The average stand height corresponding to 5-, 10-, and 20-years SF, and PF are found in the range of 3 - 6, 6 - 10, 10 - 15, and 20 - 25 meters respectively. The average diameter at breast height (DBH) of all the inventoried trees were 3.2, 4.6, 5.4, and 7.5 cm respectively for 5-, 10-, and 20-years SF and PF. Tree densities of 7.5, 8.4, 8.4, and 5.0 thousand trees (>1 cm DBH) per hectare were recorded respectively for 5-, 10-, and 20-years SF and PF.

Table 1. The most abundant tree species at different ages of secondary and primary forests of Calakmul, Mexico

5 yrs. SF	**10 yrs. SF**	**20 yrs. SF**	**PF**
Hampea trilobata	*Lonchocarpus guatemalensis*	*Lonchocarpus guatemalensis*	*Pouteria reticulata*
Lonchocarpus guatemalensis	*Hampea trilobata*	*Hampea trilobata*	*Gymnanthes lucida*
Bursera simaruba	*Croton icche*	*Croton arboreus*	*Piper yucatanense*
Piscidia piscipula	*Bursera simaruba*	*Neomillspaughia emarginata*	*Nectandra salicifolia*
Diospyros salicifolia	*Guettarda combsii*	*Eugenia ibarrae*	*Drypetes lateriflora*
Nectandra salicifolia	*Nectandra salicifolia*	*Bursera simaruba*	*Eugenia ibarrae*
Trema micrantha	*Diospyros salicifolia*	*Nectandra salicifolia*	*Eugenia winzerlingii*
Guettarda combsii	*Eugenia ibarrae*	*Lonchocarpus yucatanensis*	*Manilkara zapota*
Neomillspaughia emarginata	*Coccoloba reflexiflora*	*Croton icche*	*Bravaisia berlandieriana*
Esenbeckia berlandieri	*Croton arboreus*	*Guettarda combsii*	*Mosannona depressa*
Allophylus cominia	*Lonchocarpus rugosus*	*Mimosa bahamensis*	*Krugiodendron ferreum*
Muntingia calabura	*Allophylus cominia*	*Allophylus cominia*	*Calliandra belizensis*
Lonchocarpus rugosus	*Neomillspaughia emarginata*	*Thouinia paucidentata*	*Melicoccus oliviformis*
Cecropia peltata	*Piscidia piscipula*	*Dendropanax arboreus*	*Myrciaria floribunda*
Cascabela gaumeri	*Thevetia ahouai*	*Piscidia piscipula*	*Thouinia paucidentata*
Coccoloba reflexiflora	*Esenbeckia berlandieri*	*Croton glabellus*	*Chrysophyllum argenteum*
Dendropanax arboreus	*Coccoloba cozumelensis*	*Cascabela gaumeri*	*Lonchocarpus yucatanensis*
Bauhinia divaricata	*Muntingia calabura*	*Diospyros salicifolia*	*Brosimum alicastrum*
Croton arboreus	*Cascabela gaumeri*	*Coccoloba reflexiflora*	*Lonchocarpus guatemalensis*
Thouinia paucidentata	*Lonchocarpus castilloi*	*Metopium brownei*	*Gymnopodium floribundum*
Croton icche	*Zuelania guidonia*	*Eugenia winzerlingii*	*Neea choriophylla*
Zuelania guidonia	*Eugenia winzerlingii*	*Malpighia glabra*	*Laetia thamnia*
Eugenia ibarrae	*Metopium brownei*	*Lonchocarpus castilloi*	*Croton lundellii*
Lonchocarpus yucatanensis	*Dendropanax arboreus*	*Gymnopodium floribundum*	*Chamaedorea oblongata*
Cedrela odorata	*Thouinia paucidentata*	*Vitex gaumeri*	*Malpighia glabra*
Chrysophyllum mexicanum	*Chrysophyllum mexicanum*	*Cupania belizensis*	*Protium copal*
Trophis racemosa	*Trema micrantha*	*Lonchocarpus rugosus*	*Coccoloba reflexiflora*
Lysiloma latisiliqua	*Lysiloma latisiliqua*	*Trophis racemosa*	*Pimenta dioica*
Thevetia ahouai	*Hamelia patens*	*Zuelania guidonia*	*Croton glabellus*
Astronium graveolens	*Swartzia cubensis*	*Randia aculeata*	*Semialarium mexicanum*
Gymnopodium floribundum	*Machaonia lindeniana*	*Coccoloba cozumelensis*	*Erythroxylum rotundifolium*
Lonchocarpus castilloi	*Randia aculeata*	*Mosannona depressa*	*Croton icche*

5 yrs. SF	**10 yrs. SF**	**20 yrs. SF**	**PF**
Acacia gaumeri	*Gymnopodium floribundum*	*Diospyros anisandra*	*Diospyros salicifolia*
Spondias mombin	*Trophis racemosa*	*Lonchocarpus xuul*	*Amyris elemifera*
Vitex gaumeri	*Caesalpinia gaumeri*	*Lysiloma latisiliqua*	*Sebastiania adenophora*
Swartzia cubensis	*Vitex gaumeri*	*Acacia gaumeri*	*Exothea diphylla*
Coccoloba cozumelensis	*Lonchocarpus yucatanensis*	*Neea choriophylla*	*Randia longiloba*
Sideroxylon salicifolium	*Mosannona depressa*	*Protium copal*	*Bonellia flammea*
Eugenia winzerlingii	*Bauhinia divaricata*	*Sabal mexicana*	*Bursera simaruba*
Platymiscium yucatanum	*Acacia gaumeri*	*Spondias mombin*	*Caesalpinia mollis*
Tabebuia chrysantha	*Cecropia peltata*	*Chrysophyllum mexicanum*	*Coccoloba acapulcensis*

Successional categories: 5 yrs.SF - younger secondary forests of five years old, 10 yrs. SF- medium secondary forests of 10 years, 20 yrs. SF - advanced secondary forests of 20 years, and PF - old-growth primary forests.

Fine root production and turnover

A total of 256 ingrowth bags (16 bags per plot) of 8 cm diameter were installed in the soil to a depth of 30 cm (Fig. 2). Sixteen ingrowth bags were placed in a row at an interval of about 0.5 m taking in to account the minimum distance of 0.5 m from tree trunks in each plot. A metal core (probe) of 8 cm diameter was used to dig the hole and take the soil out. All fine and coarse roots were removed from the soil. The root-free soils were reused to fill up the nylon bags (0.4 mm mesh size) and placed again in the same hole. Bags were filled with the soil after eliminating all living and dead roots from the same hole maintaining approximately the original layer, structure, and soil density (Jourdan *et al.* 2008).

The initial root samples collected from soil cores were transported to the laboratory, washed, and separated into fine (≤2 mm diameter) and coarse root (>2 mm) fragments using different mesh-sized sieves and Vernier calipers (Majdi *et al.* 2005). The fine root biomass samples were oven-dried for 48 hours at 65°C and weighed with the ±0.001 g balance. The sixteen samples of initial fine root biomass weights were then averaged and calculated as megagrams of dry biomass per hectare for each plot. A total of 64 ingrowth bags (four bags from each plot) were collected at three-month intervals up to a year. Live and dead roots were separated using forceps and lenses looking at the differences in the characteristics like color, turgidity, flexibility, and water floating. Fine roots (≤2 mm diameter) were then washed, oven-dried, and weighed.

Fine root production (Mg C ha^{-1}) was estimated as the sum of dead and live root biomass from the positive increments method (eq. 1) (Neill 1992). In the positive increments method, we summed up all the positive increments of biomass and necromass between two or more successive sampling dates and converted them to annual production (Jourdan *et al.* 2008). Mean standing live fine root biomass is the average of live root biomass obtained from different collections during the whole experimental period (eq. 2). Fine root turnover rate (yr^{-1}) was estimated as the ratio between positive increments and mean standing live fine root biomass (eq. 3)

$$\mathrm{PI} = \left(\sum_{i=1}^{12} \mathrm{P_i} - \mathrm{P_{i-1}}\right)\frac{365}{\mathrm{D}} \text{------------------------} \textit{eq. 1}$$

$$\mathrm{MSB} = \frac{\mathrm{LB_1} + \mathrm{LB_2} + \mathrm{LB_3} + \cdots + \mathrm{LB_n}}{12} \text{-------------------} \textit{eq. 2}$$

$$\mathrm{TR}\,(yr^{-1}) = \frac{PI\,(g\,m^{-2}yr^{-1})}{MSB\,(g\,m^{-2})} \text{--------------------} \textit{eq. 3}$$

Where PI is the positive increments of fine roots cumulative over the sampling period (g m^{-2} yr^{-1}), P_i is the fine root production after *i* period of regrowth (where i equals 1, 2 …n), D is the number of days throughout the study period after installation of ingrowth cores, MSB is the mean standing biomass (g m^{-2}) of fine root over the sampling period, LB_1, LB_2, LB, and LB_n indicate the live root biomass of each sampling period, and TR denotes the turnover rate.

Figure 2. Collected ingrowth bag (left) and fine root separation (dead and live) from the soil (right) (source: original from authors).

Tree measurements

All the trees with at least 1 cm diameter at breast height (DBH, 1.3 m above ground level) were measured in a 400 m^2 plot, while trees with 5 cm DBH or more were measured in a 1000 m^2 plot. Smaller and shorter trees that did not reach a diameter of 1 cm at a height of 1.3 m from the ground level were discarded. DBH values were used to calculate basal areas of individual trees and summed to plot level basal area as m^2 ha^{-1}. Tree counts were converted to tree density (numbers of trees per hectare). The coarse root biomass of the trees was estimated using published allometric equations (Cairns *et al.* 1997). The floristic list of the species can be found in Aryal *et al.* (2024).

Statistical analysis

Fine root production and turnover data obtained in grams from 8 cm diameter and 30 cm long cylindrical ingrowth bags were transformed to megagrams per hectare (Mg ha^{-1}). Adjustments to 365 days were made to present the annual productivity where the duration of the experiment differed from the exact one-year period. Four samples of fine root production and turnover from each experimental plot were averaged to obtain the plot-level mean at each collection period. A total of 16 plots (four plots × four forest successional categories) were considered in statistical analysis. The data were tested for normality using the Shapiro-Wilk test. Since all the datasets met or were found near to fulfilling the ANOVA assumptions, no transformations were made. One-way ANOVA was used to test the significant differences between forest successional categories. The repeated measures ANOVA was applied to test the significant differences in fine root production and turnover between forest growth stages (age classes) throughout the sampling period. Tukey´s post hoc test was performed to compare means between forest successional categories. Monthly rainfall data obtained from nearby meteorological stations were plotted in the graph to align with the seasonal variation of fine root production. Multiple regressions as well as simple linear regression analyses were performed to identify the significant predicting variables of fine root production such as basal area and tree density.

RESULTS

Initial fine-root biomass

Initial fine root biomass ranged from 2.7 to 3.9 Mg ha^{-1} which did not change significantly among forest successional categories (Table 1). It is the amount of dry fine root biomass obtained from soil cores before installing the ingrowth bags. Total root biomass estimated by using an allometric equation showed a gradual increase with forest age. The values ranged from 7 to 51 Mg ha^{-1} with primary forest being the highest. Initial fine root biomass contributed 8 to 38 percent of total estimated coarse root biomass which was higher in younger secondary forests and lower in primary forests. The basal area of the trees of ≥1 cm diameter at breast height (DBH) also increased gradually with increasing forest age which ranged from 8 to 33 m^2 per hectare (Table 1).

Fine root production and turnover

Primary forests showed a higher fine root production compared to secondary forests with a slightly increasing trend with forest age. However, there were no significant differences between forest successional classes in fine root turnover. The average fine root production rate ranged from 1.9 to 2.8 Mg of biomass ha^{-1} yr^{-1} while turnover over rate ranged from 1.1 to 1.5 yr^{-1} (Fig. 3). Fine root production reached about 60 - 70% of initial fine root biomass in primary as well as secondary forests. The proportion of fine root turnover rate to fine root production rate ranged from 0.41 to 0.68 with the highest value in the young secondary forest of 5 years and the lowest value in primary forests. This showed that relative fine root turnover is faster in younger forests compared to older ones.

Table 1. Average (± 95% confidence interval) initial fine root biomass, estimated total root biomass, and basal area of trees ≥1 cm DBH measured before the establishment of ingrowth bags at different stages of forest growth in Calakmul, Campeche, Mexico.

Forest age class	Initial fine root biomass, Mg ha^{-1}, estimated by soil coring method	Total root biomass, Mg ha^{-1}, estimated by using allometric equations	Basal area, m^2 (Trees of ≥1 cm DBH)
5 yrs. SF	2.7 ± 0.5^{A}	7.0 ± 1.8^{C}	8.7 ± 1.6^{C}
10 yrs. SF	3.4 ± 0.5^{A}	$16.1\pm4.9A^{B}$	16.2 ± 4.7^{B}
20 yrs. SF	3.3 ± 0.4^{A}	22.3 ± 4.2^{B}	20.9 ± 3.4^{B}
PF	3.9 ± 0.6^{A}	50.7 ± 9.9^{A}	33.2 ± 5.1^{A}

Different letters followed by the numbers indicate significant differences among forest successional classes. SF = secondary forests, PF = primary forests.

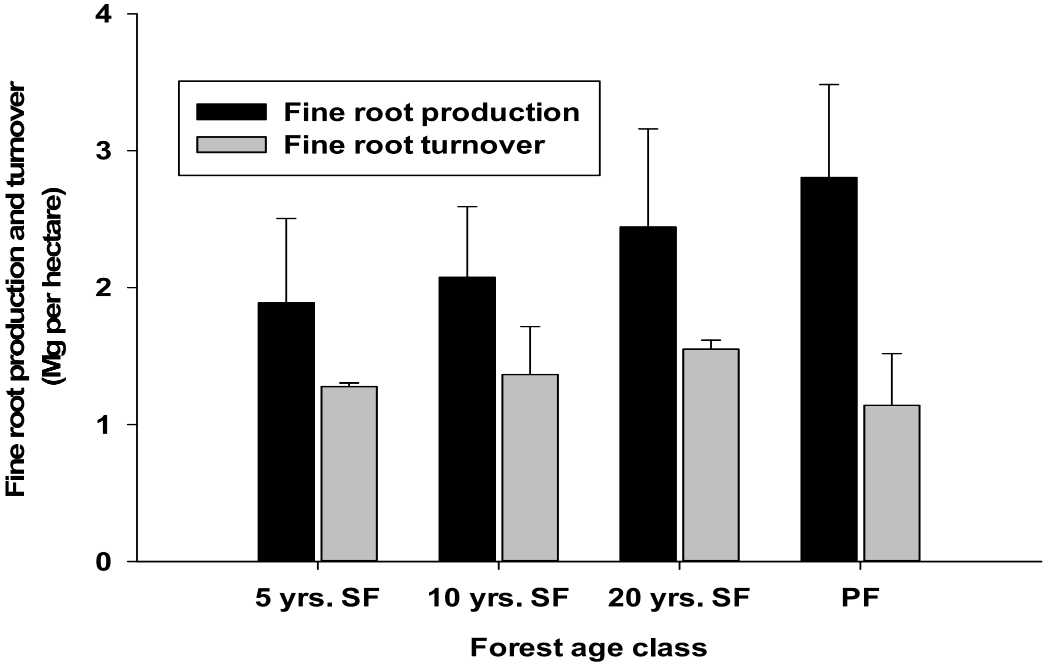


Figure 3. Mean (upper 95% confidence interval) values of fine root production and turnover (Mg C ha^{-1} yr^{-1}) among four stages of forest growth. SF = advanced secondary forest, PF = primary forest.

Among different estimations of fine root production, long-term core values indicate the amount of fine root biomass produced in the final ingrowth bag samples which was of 13 months duration in our experiment. Although the numerical mean value seems to be higher in primary forests, fine root biomass from long-term cores did not change significantly (Table 2). Mean standing biomass is the average of live fine root biomass from all different collections throughout the sampling period. Primary forests showed a significantly higher mean standing biomass compared to secondary forests. This showed that the fine root mortality can be slower in mature forests which were also reflected by lower turnover rates.

Seasonal variation of fine root production

After the establishment of ingrowth bags in February, fine root production increased in May and decreased in August. August was a rainy month and probably the fine root mortality during summer rainy months was higher. Fine root production again increased in December, when the amount of rainfall decreased before reaching to dry season (Fig. 4). Then after, the production trends varied among forest successional stages. Primary forest and younger secondary forest of 10 years showed a slightly decreasing trend while secondary forest of 5 and 20 years showed a slight increase in fine root production.

In a multiple regression analysis, considering tree density and basal area as independent variables and fine root production as a dependent variable, we found that only basal area was the significant predictor of the variation in fine root production ($\beta = 0.5$, $\rho<0.05$). Tree density was not considered a significant predicting variable (Table 3). The linear relationship between basal area and fine root production showed an increasing trend of fine root production with the increase in basal area of the trees of ≥1 cm DBH (Fig. 5). Because of the abundance of outliers in the graph, we assume that other variables also affect fine root production in such forest ecosystems which we did not evaluate in this study.

DISCUSSION

Our results demonstrated that the ratio of fine root biomass to estimated total root biomass decreased gradually with forest age. This trend can be explained by the fact that carbon allocation in coarse root increases with the increase in tree size, aboveground biomass, and forest successional age (Zhou *et al.* 2020). At the same time, the relative fine root turnover rate (ratio between fine root turnover and initial fine root biomass stock) also decreased with forest age providing the basis to accept the hypothesis that younger secondary forests are faster in belowground carbon turnover compared to older secondary and primary forests (Puglielli *et al.* 2021; Titlyanova and Shibareva 2022). However, other factors such as soil fertility, plant species composition, and the changes in aboveground net primary productivity can determine fine root production and turnover (Becknell *et al.* 2021; Ma *et al.* 2022). Younger secondary forests were dominated by soft-wood density species, while older secondary and primary forests were dominated by dense-wood species (Aryal *et al.* 2024). Aboveground litter production and decomposition rates were affected by leaf traits that varied with forest successional ages in these plots (Sánchez-Silva *et al.* 2018). These variations of tree species composition and related changes in plant traits can explain the changes in belowground functioning, including fine root productivity and turnover. A shift from more acquisitive traits to conservative traits on root characteristics can explain our results of lower turnover during older phases of forest succession (Hogan *et al.* 2023). The changes in soil fertility, nutrient availability, and relative abundance of nitrogen-fixing plants along the forest succession also determine the variation in fine root productivity (Figueiredo *et al.* 2024).

Table 2. Average (± 95% confidence interval) fine root production estimated from long-term cores, positive increments, and mean standing biomass at different stages of forest growth in Calakmul, Campeche, Mexico. Different letters in the exponent denote significant differences among forest age classes.

Forest age class	Long-term cores	Positive increments	Mean standing biomass
5 yrs. SF	2.04 ± 1.08^{A}	1.89 ± 1.00^{A}	1.48 ± 0.77^{B}
10 yrs. SF	2.24 ± 0.90^{A}	2.08 ± 0.83^{A}	1.55 ± 0.41^{B}
20 yrs. SF	2.64 ± 1.26^{A}	2.44 ± 1.16^{A}	1.58 ± 0.78^{B}
PF	3.03 ± 1.20^{A}	2.57 ± 0.57^{A}	2.27 ± 0.61^{A}

Different letters followed by the numbers indicate significant differences among forest age classes. SF = secondary forests, PF = primary forests.

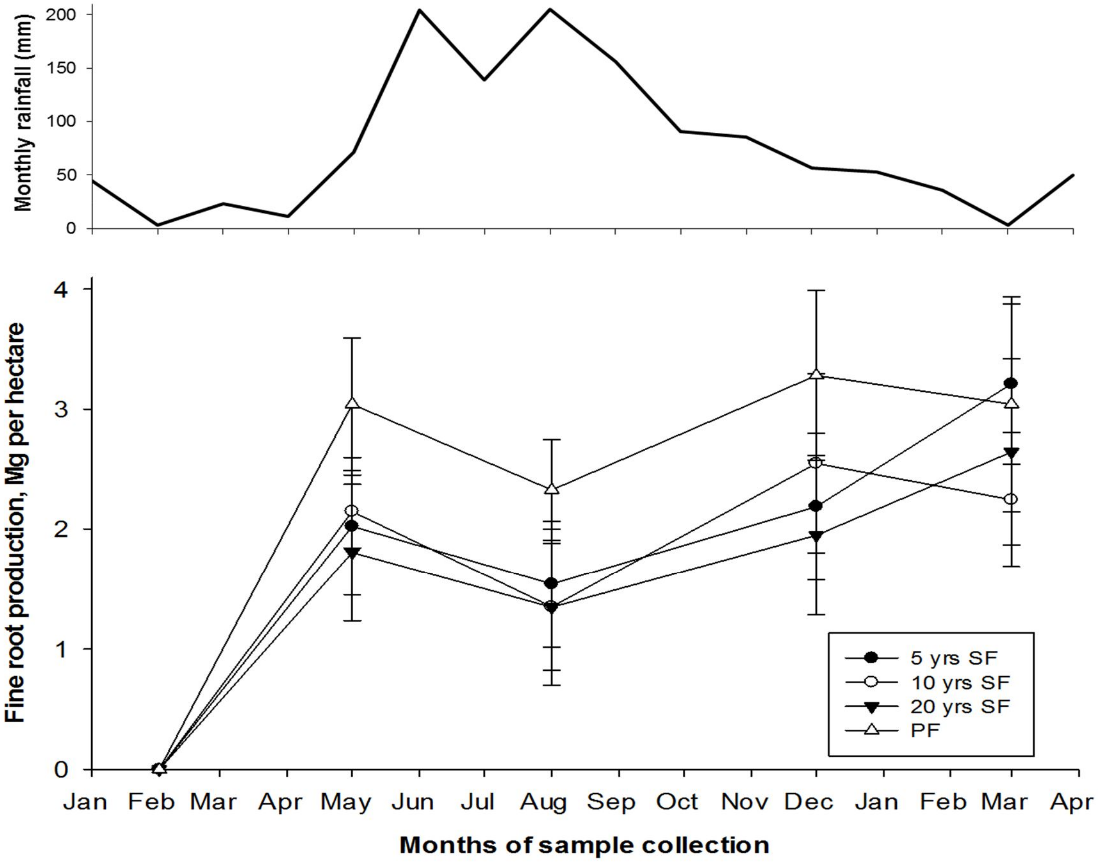


Figure 4. Fine root production (Mg C ha^{-1} yr^{-1}) at different months during the period of sample collections (from February to March). SF = secondary forests, PF = primary forests. Vertical bars represent the 95% confidence intervals. The upper graph shows the monthly rainfall pattern during the study period, recorded in Zoh Laguna metrological station, about 30 km from the study plots.

Table 3. Multiple regression analysis between fine root production and two independent variables (tree density and basal areas). Beta values with less than 0.05 probability of error are considered significant.

Variables	Beta	Std. err.	B	Std. err.	t(13)	p-level
Intercept			1.95	0.81	2.41	0.031
Tree density, trees per hectare	-0.23	0.22	-0.00	0.00	-1.01	0.328
Basal area, m^2 per hectare	0.50	0.23	0.05	0.02	2.2	0.047

Fine root production rates in tropical forests obtained from different published studies varied from 1.8 to 13.6 Mg ha^{-1} yr^{-1} while the stock varied between 0.9 and 24.3 Mg ha^{-1} (Castellanos *et al.* 2001; Finér *et al.* 2011a; Girardin *et al.* 2013; Huaraca Huasco *et al.* 2021). Our results of 1.9 to 2.8 Mg per hectare per year of fine root production and 2.7 to 3.9 Mg ha^{-1} of initial fine root biomass stocks are found within the reported ranges. Castellanos et al (2001) in a study in tropical dry forests of Jalisco, Mexico reported a fine root production rate of 1.8 Mg $ha^{-1}yr^{-1}$ to a depth of 10 cm and stated that burning in slash and burn agriculture decreased the fine root production. The fine-root turnover rate reported in a semi-arid tropical forest of India was 0.65 to 0.97yr^{-1} and was reported to be important to maintain site productivity (Jha and Mohapatra 2010). Although some studies reported an increasing trend of fine root biomass along the successional gradient with the increase in forest age, our results showed that the difference among successional categories was statistically non-significant (Yang *et al.* 2010; Hogan *et al.* 2023).

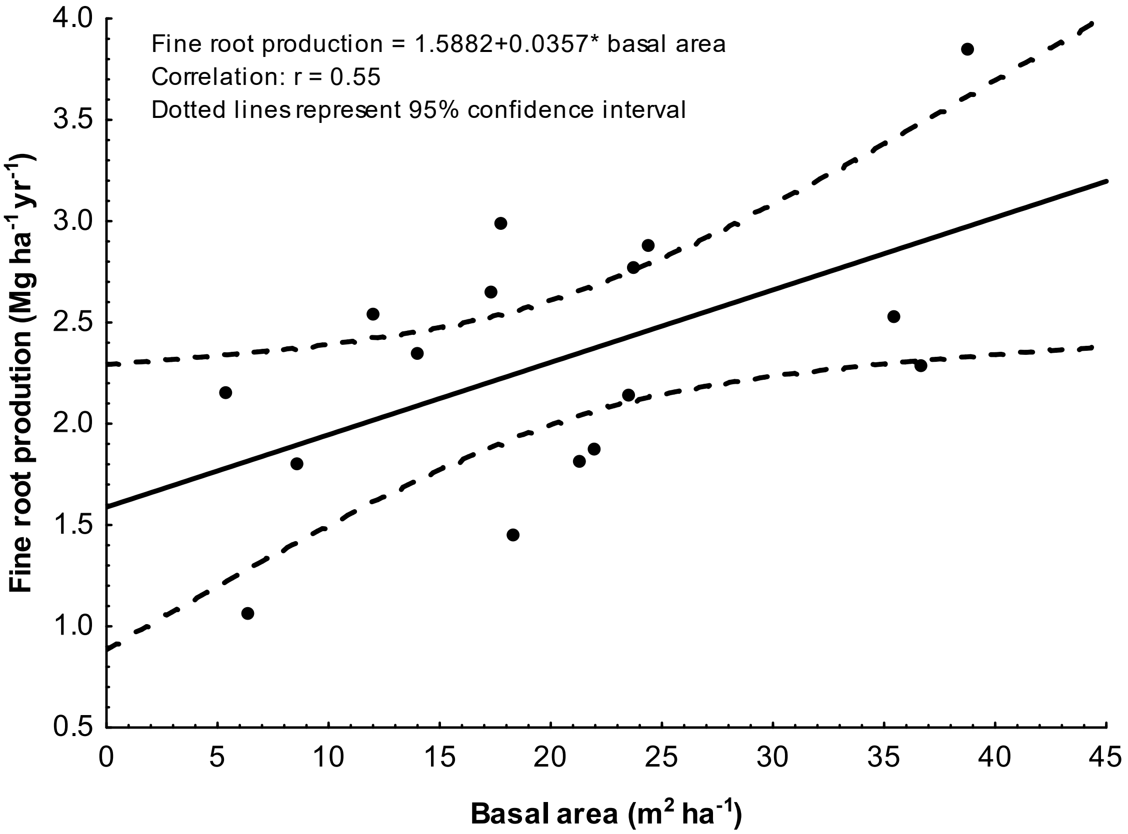


Figure 5. Relationship between fine root production and basal area of the trees with ≥1 cm DBH, measured in tropical secondary forests of Calakmul, Campeche, Mexico.

Seasonal climatic variations also affect fine root production rates (Gill and Jackson 2000; Sánchez-Silva *et al.* 2022). Some studies reported higher fine root production during the wet season (Chen *et al.* 2004; Morales Ruiz *et al.* 2021) but higher fine root production was observed in drier months compared to wet months in our study which was similar to the findings reported in Amazonian forests (Lima *et al.* 2010). This variation can be explained by the fact that plants shift carbon allocation towards roots where photosynthates are used to increase water uptake when water is a limiting resource, resulting in plants with higher fine root production in the dry season (Metcalfe *et al.* 2008; Umaña *et al.* 2021).

Aboveground forest structural parameters like tree size, tree density, basal area, and species composition can be related to fine root production and turnover (Finér *et al.* 2011a; Barbhuiya *et al.* 2012; Weemstra *et al.* 2020; Zeng *et al.* 2020). The basal area of the trees (≥1 cm DBH) explained about 50% of the variation in fine root production in our study. In a global compilation report, it is mentioned that tree basal area predicted 49% of fine root biomass (Finér *et al.* 2011b). However, the correlation between fine root production and aboveground net primary productivity varies with forest type, site conditions, and nutrient distribution at different soil horizons (Nadelhoffer and Raich 1992; Ding *et al.* 2021).

Some studies mention that fine root dynamics depend on soil properties like texture and available nutrients (Hertel *et al.* 2013). In an analysis of some soil parameters, soils in our experimental plots are found relatively homogenous (Aryal *et al.* 2015), thus, we assume that the variation in fine root production caused by soil variation is not significant. Some of the reports mentioned that understory vegetation can contribute to 20 - 30% of the fine root biomass (Finér *et al.* 2011b). However, we could not separate the contribution of tree and understory vegetation in fine root production and turnover due to logistical limitations. We recommend evaluating the role of understory vegetation in future studies of this type.

Implications of plant succession in future estimates of carbon dynamics in tropical environments

Earlier studies showed that the aboveground carbon and species composition recovery period of these secondary forests was more than 100 years after the cessation of slash-and-burn agriculture especially due to the successional shift of softwood species to hardwood species (Aryal *et al.* 2024). The responses of such changes can also be noted in the fine root dynamics of the vegetation. It is interesting to note that the results of the fine root production in our study did not show any statistical difference between secondary and primary forests indicating that fine root production of secondary forests gets near to primary forests from the early stages of succession (Sánchez-Silva *et al.* 2022). However, the relative turnover rates were found higher in secondary forests than in primary forests. This showed that the growth and dieback of the fine roots are faster in secondary forests which, in turn, helps secondary forests to recover their soil organic carbon earlier. However, the durability of belowground biomass carbon can be shorter in secondary forests compared to primary forests. Our results can be considered as one of the important bases regarding fine root production and turnover for modeling carbon dynamics of the tropical secondary and primary forests in the region. If combined with aboveground litterfall monitoring, annual live biomass increments rates, and soil organic carbon estimations (Aryal *et al.* 2017, 2022; Sánchez-Silva *et al.* 2018), this study provides strong evidence regarding the successional changes in tropical forest carbon dynamics useful for carbon measurement, reporting and verification (MRV) as proposed in reduction of emissions from deforestation and degradation plus conservation (REDD+) strategies. Here, we did not analyze the effect of fine root turnover on soil organic carbon storage but a study in the tropical forests of Panama reported that fine root production and turnover contributed to organic matter addition in surface soil but this effect was minimal in the deeper soil horizons, which can be explained by the decline of fine root turnover rates with soil depth (Cusack *et al.* 2021; Cordeiro *et al.* 2020). Fine root biomass production and turnover contributed to increased particulate and readily oxidizable organic carbon in the soil, resulting in total soil organic carbon in a subtropical forest (Xiang *et al.* 2022). Fine root turnover makes a greater contribution to organic carbon accumulation in soil aggregates than aboveground litterfall during the course of forest succession because of the distribution of root biomass in the soil profile (Shi *et al.* 2023).

CONCLUSIONS

Fine root productivity in tropical secondary forests reached near to primary forest level from the early stages of succession (~5 years). However, fine root turnover rates were faster in secondary forests than in primary forests accepting the hypothesis of faster carbon cycling in younger phases of forest growth than in older phases. Aboveground forest structural parameters like tree basal area explained about 50% of the variation in fine root productivity. Fine root production was higher in the dry season than in the wet season in this study. The results of this study can be used for belowground carbon balance modeling of the successional forests. The information also contributes to generating a baseline for future studies on below-ground carbon dynamics in the succession of tree species from the conversion of an agricultural system to forests in tropical environments.

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Conflict of interest statement. The authors declare that there is no conflict of interest.

Compliance with ethical standards. Due to the nature of this work, this research does not require approval from an ethical committee.

Data availability. Data can be available from the corresponding author upon request.

Author contribution statement (CRediT). D. Aryal - conceptualization, methodology, project administration, investigation, data collection, analysis, writing original draft, and visualization. **D. Morales**, **D. Molina**, **J. Venegas**, **F. Casanova**, and **G. Villanueva** – manuscript writing, review, and editing.

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