

Temporal changes of fine root overyielding and foraging strategies in planted monoculture and mixed forests

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10 **Abstract:** Mixed forests are believed to enhance ecosystem functioning and sustainability due to
complementary resource use, environmental benefits and improved soil properties. The facilitation
between different species may induce overyielding. Meanwhile, the species-specific fine root foraging
strategies and tradeoff would determine the structure and dynamics of plant communities. Here the
fine-root biomass, vertical distribution and morphology were investigated in *Pinus massoniana* and
15 *Cinnamomum camphora* pure and mixed plantations at 10-yr, 24-yr and 45-yr old stands. The results
showed that the fine root biomass in the *Pinus* -*Cinnamomum* mixed forest exerted a certain degree of
overyielding effect. These positive admixing effects, however, did not enhance with forest stand
development. Instead, the magnitude of fine root overyielding in mixed forests showed a high degree of
consistency with fine root biomass itself, suggesting the overyielding effects in mixed forests were
20 correlated with the degree of belowground interaction and competition degree involved. The overall
relative yield total (RYT) ranged from 1.83, and 1.51 to 1.33 in 10-yr-old, 24-yr-old and 45-yr-old
stand, respectively. The overyielding were mainly attributed to the over-performance of conservative
species, *Cinnamomum*, in mixed stands, as *Cinnamomum* accounted to the total fine root biomass
81.2%, 81.3% and 53.2% in 10, 24 and 45-yr-old *Pinus*-*Cinnamomum* mixed stands. In contrast, the
25 pioneer species, *Pinus*, adapted to the presence of the species *Cinnamomum* by modification of vertical
distribution and root morphological plasticity in the mixtures. The vertical fine root biomass
distribution model showed *Pinus* roots shifted to the superficial layer when mixed with *Cinnamomum*.
Furthermore, the specific root length (SRL) were significantly higher in *Pinus*-*Cinnamomum* mixed
stands than that in *Pinus* monocultures, and the magnitude of differences increased over time. However,
30 the vertical fine-root distribution and SRL for *Cinnamomum* did not show significant differences
between monoculture and mixtures. These species-specific fine root foraging strategies might imply the
differences of forest growth strategies of co-occurring species and contribute to the success and failure
of particular species during the succession over time.

1 Introduction

In the global carbon cycle, roots of forest trees are an important reservoir of carbon, which is an important component of C pool in terrestrial ecosystem and plays a vital role on global carbon flux and carbon library (Vogt et al., 1998; Claus and George, 2011). In this context, in the past few decades, a lot of interests have been arosed with fine root biomass and production in forest, since fine roots accounted for as much as one-third of global net primary productivity (Jackson and Schulze, 1997) and are primary responsible for water and nutrient uptake by trees (Wells and Eissenstat, 2001; Zeng et al., 2015).

Belowground interactions among co-occurring species play critical roles on the community structure and distribution of plants. The plants are even capable of recognizing non-self neighbours and tend to proliferate more roots into substrate shared with coexisting species, and likely resulting in rooting aggregation and overyielding (de Kroon, 2007). Mixed forests are considered to be less susceptible to abiotic hazards like wind throw and snow break than pure stands (Schmid and Kazda, 2002; Reyer et al., 2010). Most studies investigating tree species diversity effects on aboveground and belowground productivity in forests, however, were based on comparisons between two species mixtures with monocultures. For example, a number of studies found a higher fine root biomass and production in mixtures (Schmid, 2002; Meinen et al., 2009b; Brassard et al., 2011; Lei et al., 2012), although other studies showed otherwise (Bolte and Villanueva, 2006; Mainen et al., 2009a). Recently, more studies were carried out to disentangle the effects of species diversity on the fine root biomass and production in mixed forests containing four to five tree species and the results were still equivocal (Rewald et al., 2009; Lei et al., 2012). However, all these studies on the relationship between diversity and productivity were based on one particular growth stage, or one static stand age. To our knowledge, recently only one study has been conducted comparing the effects on tree species on fine root productivity at 8 and 34 years old (Ma and Chen, 2016). Data on how fine root biomass, spatial distribution and morphology change in relation to stand age at pure and mixed forests, are comparatively few.

Fine root proliferation is greatly determined by environment conditions, such as nutrient supply in the soil, temperature and water. For example, Fine root vertical distribution is impacted by the spatial distribution of soil nutrients and moisture (Zhou and Shangguan, 2007), as well as soil structure and bulk density (Schenk, 2004). Besides, with increasing forests development, the proportion of fine root biomass was prone to increase in the top soil (Bouillet et al., 2002) or indicate no change (Claus and George, 2011). Furthermore, competition among individuals of the same species (intraspecific competition), as well as among different species populations (inter-specific competition), affects the process of tree root growth. Generally belowground competition depends on the soil exploitation capacity and exploitation efficiency of the fine-root systems of each plant, which were determined by the fine root biomass, surface area, root distribution within the soil horizons and specific root length (SRL) (Bausch et al., 2000; Makkonen and Helmisaari, 2001). Different plants within the community, in order to minimize competition for soil nutrients and moisture, may adjust the C investment to fine

roots and distribution, and/or morphological traits to adapt to the competition. Previous studies showed that beech developed a more dynamic and adaptive fine root foraging strategies, including biomass and vertical distribution, comparing to competitive species in mixed stands (Curt and Prevosto, 2003; Bolte et al., 2004). However, how the belowground interactions may shift with forest development is not clear, which may mirror the aboveground competition.

Here the temporal changes of fine root biomass, vertical distribution and fine root morphology were investigated in *Pinus massoniana* and *Cinnamomum camphora* mixed plantations and corresponding single species plantations at age of 10 years, 24 years and 45 years at 0-10 cm, 10-20 cm and 20-30 cm soil depth. Our objectives were to determine the magnitude of admixing effects on fine root biomass over time and to assess the possible shifts of foraging strategies for pioneer species (*P. massoniana*) and conservative species (*C. camphora*) along forest development. In this study we specifically tested the hypotheses that: (i) the total standing fine root biomass are higher in the mixed stands than those in corresponding monocultures, and the magnitude of positive admixing effect increases with forest development; (ii) the fine root foraging strategies of co-existing species, including fine root biomass, vertical distribution and morphological traits, in mixed forests mirrors the growth strategies of different species with forest development.

2 Materials and methods

2.1 Field sites and experimental design

This study was carried out in two different sites in Hunan province, China. One area is located in the Botanical Garden in Changsha (28°06'N, 113°02'E). The annual rainfall on this site is 1422 mm and the mean annual temperature is 17.2 °C, belonging to typical subtropical monsoon climate. The altitude ranges from 50 m to 100 m. The soil type is Alliti-Udic Ferrosols with well-drained clay-loam red soil developed from slate parent rock, and total N concentrations ranging from 0.57 g kg⁻¹ to 1.56 g kg⁻¹ in top 30 cm depth of the soil profile (Wen et al., 2014). Single species and two species mixed patches, consisting of 24-year and 45-year old *P. massoniana* were selected. In monocultures and mixed stand, few *Pinus Elliotii* were also admixed here. Considering the similarity of growth characteristics and the difficulty of root separation between *P. massoniana* or *P. elliotii*, we treated them one group (thereafter called “*Pinus*”). Three plots of size 20m×20m were established in mixed *Pinus-Cinnamomum* stands at age of 24 and 45 years old and corresponding pure species stands (*Pinus* and *Cinnamomum*) at each age, amounting to 18 plots. The another site is located in Taolin forestry station (28°55'N, 113°03'E) in Miluo county, approximate 200 km from the main site with similar climate and parent soil type. The mean annual precipitation is about 1353.6 and mean annual temperature is 16.9 °C. Here, only the smaller patches of mixed and pure species stands with 10 years old pinus and cinnamomum were found. Therein three plots of 12m×12m in mixed forests stands and corresponding pure stands were set up as conducted above. Thereby our study consisted of 27 plots of mixed *Pinus-Cinnamomum* plantations and corresponding monocultures at age of 10, 24 and 45 years old. All the stems were recorded and selected site characteristics are presented in Table 1. More detailed information about the experimental site and soil condition referred to Wen et al. (2014).

2.2 Fine root sampling and processing

The root sampling was carried out in April 2013. Six soil cores in each plot were taken randomly in each square plot by using soil steel auger (diameter of 10 cm) to the soil depth of 30 cm and sliced to three layers (0-10, 10-20, and 20-30 cm). A preliminary survey had shown that very few fine roots occurred below 30 cm soil depth here. All the samples were labeled and transferred to plastic bag, sealed, and transported to the laboratory in 4 °C refrigerator.

In the laboratory, the processes of root separation off the soil were conducted with floatation method (Böhm, 1979; Lei et al., 2012a; 2012b). All the roots were collected with sieve of 0.65 mm aperture. The washed fine roots were poured and suspended in water, then sorted to *Pinus* and *Cinnamomum*, live and dead ones visually according to morphological traits, turgescence, root elasticity, colour, periderm surface structure, and exposure degree of steles. Living roots of *Pinus* and *C. Camphora* are intact, tough, and flexible. In contrast to that, dead roots were brittle and fractured easily and were distinguished by a dark to grey cortex and stele, or the complete loss of the stele and cortex. Only data on living fine roots (≤ 2.0 mm in diameter) are reported in this study.

Live fine-root samples of each species were suspended in a water filled transparent tray on a scanner to facilitate samples dispersing. The morphological characteristics of fine roots were analyzed using the root scan analysis system WinRHIZO 2013 (Regent Instruments Inc., Quebec, Canada) by using images obtained. Thereafter, the root samples were oven-dried at 60 °C to constant weight. The specific root length (SRL) (m g^{-1}) was determined with the total root length by divided root dry weight.

2.3 Data analysis

All data were tested for a normal distribution with the Shapiro-Wilk test. Analysis of variance (ANOVA) or a non-parametric Mann–Whitney U test was used to detect significant differences among three forest types. Differences between means were evaluated by Tukey’s test of honestly significant difference. To examine whether overyielding occurred, the relative yield total (RYT) was calculated based on fine root biomass per basal area, as suggested by Lei (Lei et al., 2012b). The contributions of the different species, i.e. *Pinus* and *Cinnamomum*, to the relative yield total were calculated as the quotient of the fine-root biomass per basal area of each species at a particular stand age in the mixture to the counterpart value in the monoculture. $\text{RYT} > 1$ indicates overyielding, significant difference from 1 were analyzed using t tests or the Mann–Whitney U test.

To calculate the fine root vertical distribution, we adopted a commonly used equation developed by Gale and Grigal (1987):

$$Y=1-\beta^d$$

Therein, Y indicates the cumulative proportion of fine root biomass in the soil depth d (in cm). High values of β were indicate a large proportion of fine root at deeper soil depths, while low values indicate a large proportion of fine roots near the soil surface. Here we Used β as criterion to compare fine root vertical distribution of *Pinus* and *Cinnamomum* in *Pinus*–*Cinnamomum* mixed forests and corresponding monocultures as different ages. All data analyses were conducted with R (R 3.0.3, R development Core Team, Vienna, Austria).

3 Results

3.1 Fine root biomass and overyielding

As the forests grows, the standing fine root biomass tended to decrease with stand ages, averaged as 388.45 g m⁻², 269.27 g m⁻² and 138.59 g m⁻² in 30 cm soil depth in 10-yr-old, 24-yr-old and 45-yr-old stands, respectively. The standing fine root biomass was the highest in *Pinus–Cinnamomum* mixed stands compared to corresponding monocultures at 10- and 24-yr stands in 30 cm depth soil profile (Fig.1). In 45-yr-old stands, single *Pinus* stands showed highest fine root biomass than that in *Cinnamomum* stands and mixed *Pinus–Cinnamomum* stands, but significant differences were only detected in 10-yr-old forest stands. In mixed stands, *Cinnamomum* overperformed in fine root biomass contributions when compared with the aboveground abundance of mixed tree species. *Cinnamomum* accounted for the total fine root biomass 81.2%, 81.3% and 53.2% in 10, 24 and 45-yr-old *Pinus–Cinnamomum* mixed stands. Total fine root necromass showed lower values than fine root biomass and ranged from 17.84 g m⁻² to 96.54 g m⁻² in the pure *Pinus*, *Cinnamomum* and mixed *Pinus–Cinnamomum* stands at differ ages (Fig.1). The standing fine root necromass was the highest in the pure *Cinnamomum* stands at 10- and 45-yr stands compared with mixed stands at the corresponding age in 30 cm depth soil profile, which differed significantly from each stands ($p < 0.05$). In 24-yr-old stands, however, the mixed stands showed the highest fine root necromass, although differences were not significant ($p > 0.05$).

Relative yield total (RYT) for each species in mixed plantations were calculated with adjusted fine root biomass per basal area. The results showed RYT of *Cinnamomum* were bigger than one in mixed plantations in all stand ages. Among them, only 45-yr-old forest stands showed an relative yield total value for fine root biomass that was not significantly different from one ($p > 0.05$). For *Pinus*, the RYT showed inconsistent pattern that RYT was higher than one in 10-yr-old and 45-yr-old mixed stands, while the RYT was marginally lower than one in 24-yr-old stand (Fig. 2a). On the stand level, the overall RYT were bigger than one in all the three development stages, but the values of RYT seemed to decline with increasing stand ages, averaged as 1.83, 1.51 and 1.33 in 10-yr-old, 24-yr-old and 45-yr-old stand, respectively (Fig. 2b).

3.2 Vertical fine root distribution

The standing fine root biomass decreased gradually with soil depth, and fine root biomass was highest in 0-10cm for almost all the cases in the whole stand ages, which accounted for 56.0%, 51.7% and 47.2% in 10-yr-old, 24-yr-old and 45-yr-old stands. When compared with parallel forest stand within the same soil profiles, the fine root biomass was highest in the *Pinus–Cinnamomum* mixed stands in all the three soil layers in 10-yr-old stands and in the top soil layer in 24-yr-old stands. But the significant differences were detected only in 10-year-old stands ($P < 0.05$) (Fig. 3). The abundance of species fine roots declined exponentially with increasing soil depth in the pure and mixed stands. Furthermore, the simulated rooting vertical distribution model of β value for for *Pinus* and *Cinnamomum* growing in pure stands at different stand ages showed the similar patterns that both species allocated more fine roots to the deeper layer with increasing stand ages. Compared the β values for *Pinus* and

Cinnamomum in the pure and mixed stands, however, the results showed that the adjusted β value For *Pinus* in pure stands were significantly higher than that in the mixed stands at all forest ages (see Fig 4), indicating fine roots of *Pinus* were more concentrated in the top soil when mixed with *Cinnamomum*. The β value was 0.915, 0.937, 0.939 in pure stands, and 0.911, 0.914, 0.925 in mixed stands in forests age of 10-yr old, 24-yr old, and 45-yr old, respectively. For *Cinnamomum*, the β values did not show consistent pattern along the stand age as it increased in the pure stands, but decreased in the mixed stands along chronosequence.

3.3 Specific root length

The comparison of specific root length (SRL) in the pure and mixed stands revealed striking differences for *Pinus* and *Cinnamomum*. The SRL_{*Pinus*} in mixed stands were significantly higher than those of corresponding pure stand, and the differences becomes more pronounced over time. For *Cinnamomum*, however, structural trait did not show regular pattern in pure and mixed stand plots. Result from one-way ANOVA revealed that both plantation type and stands age had significant effects on morphology. At in the pure *Pinus* stand, the SRL changed along the chronosequence, decreasing from 8.84 m g⁻¹ in the 10-yr old stands to 6.72 m g⁻¹ in the 24-yr old stands and 6.29 m g⁻¹ in the 45-yr old stands. However, the SRL of mixed stands increased along chronosequence. And significant differences were only detected between the 24-yr and 45-yr old stands ($p < 0.05$) (Fig 5a). For species *Cinnamomum*, the SRL of *Cinnamomum* fine root in the pure stands and mixed stands was basically similar, ranging from 5.24 m g⁻¹ to 8.90 m g⁻¹, and its value did not significantly differ within the same ages ($p > 0.05$) (Fig. 5). Comparing with different age stages, the results showed that SRL of *Cinnamomum* was increased with increase stand age in the pure stands, but no significant differences were detected. However, this kind of phenomenon does not show in the *Pinus*–*Cinnamomum* mixed stands.

4 Discussion

In this study, the fine root biomass seemed to decrease in pure and mixed stands with increase stand age. The stand density decreased with development stages here. The high tree density may have accounted for the higher root biomass, which is in agreement with a previous report described for 13-year-old postfire lodgepole *pine* forests, where the fine root biomass increased with tree density (Creighton M Litton, 2003). When compared with three types of plantations, the fine root biomass was higher in the *Pinus*–*Cinnamomum* mixed stands than those in the pure *Pinus* and *Cinnamomum* stands in 30 cm soil depth in 10-yr-old and 24-yr-old stands. Many previous studies reported the similar pattern that species-rich forests exhibited higher fine root biomass than species-poor stands (Brassard et al., 2011; Liu et al., 2011). Although the absolute fine root biomass in the *Pinus*–*Cinnamomum* mixed forests were not significantly higher than that the counterpart monocultures in 24-yr-old, and even lower than that in monocultures in 45-yr-old stands, the RYT was higher than one, suggesting overyield when comparing the adjusted fine root biomass per basal area in mixed forest with monocultures (Fig. 2b) (Hector, 2006). Likewise, fine root overyielding was reported in mixed forests of *Eucalyptus grandis*

and *Acacia mangium* stands (Laclau et al., 2013), as well as in European beech, sessile oak, Norway spruce and Douglas fir mixed stands at two-, three-, and four-species neighbourhoods in comparison to monocultures (Lei et al., 2012b).

Here we primarily attempted to assess the variations of these admixing effects over time and expected that the admixing effect would be more pronounced over time, as the interactions between different species become more intense over time. On the contrary, in this study, the magnitude of over-yielding in the *Pinus–Cinnamomum* mixed forests declined with stand development as shown in Fig. 1 and Fig. 2. The significant differences between the *Pinus–Cinnamomum* mixed forests and corresponding monocultures were only detected in 10-yr-old forests. Besides, the direct evidence showed that relative yield total decreased from 1.83, and 1.51 to 1.33 in 10-yr-old, 24-yr-old and 45-yr-old stand, respectively. This pattern is consistent the trend that the standing fine root biomass decreased with stand. Therefore, it is likely that the magnitude of fine root overyielding in mixed forests was correlated with fine root biomass and the belowground competitive degree involved.

Here we calculated the RYT for the component species in the mixtures to estimate the specific performance and dynamics of each species to the overyielding in the mixtures over time, and foraging strategies as well. In the mixtures, the RYT of conservative species, *Cinnamomum*, was higher than one for all the stand development stages and the differences were significant from one in 10-yr-old and 24-yr-old stands. This pattern was supported by data on fine root biomass, which *Cinnamomum* accounted for 81.2%, 81.3% and 53.2% in 10, 24 and 45-yr-old *Pinus–Cinnamomum* mixed stands, respectively. (Fig. 1), suggesting *Cinnamomum* invested more carbon to belowground fine roots when co-occurring species presents. In contrast, the pioneer species, *Pinus*, showed significant higher RYT only in 10-yr-old stand and then fluctuated from one thereafter.

In our study, we compared the vertical distribution of fine root biomass with the exponential model of Gale and Grigal (Gale and Grigal 1987) and found very similar patterns for the overall distribution in pure stands along chronosequence. Two species showed the exponential indicator (β values) increased with stand development. The β data indicated that there was clear spatial separation of the fine root systems of the *Pinus* within 0–30 cm of the soil profile. The *Pinus* roots occupied the deeper soil layers in the pure stand whereas it shifted to the superficial layers when mixed with *Cinnamomum*. Many researches revealed previously significant effect of mixed stand on fine root distributions. Bolte and Villanueva (Bolte and Villanueva, 2006) suggested that fine root of *P. abies* distributed deeper in mixed stands than pure stands. Moreover, in mixed stand of beech and *Quercus Petraea*, fine roots of beech grew more deeper than fine roots of *Quercus Petraea* (Büttner and Leuschner, 1994). The presence of *Cinnamomum* in the mixed stands could have pushed the fine root system of *pinus* towards the soil surface where the water and nutrient were more enriched. In mixed stand fine roots tend to proliferate and compete with neighbors for nutrients and water (Leuschner et al., 2000; Schenk and Jackson, 2005) by developing a more flexible fine root system when there is more intense belowground competition. However, the fine-root distribution data indicated that there was no obvious regularity spatial separation of the fine-root systems for *Cinnamomum* within 0-30 cm of the soil profile. Therefore, different tree species may have different strategies for the presence of neighbor species in terms of vertical niche separation.

The specific root length (SRL) was used as indicator for nutrient uptake efficiency and responses to environmental changes or competition (Ostonen et al., 2007). SRL can response that plants were in root

growth the efficiency of consumption photosynthetic primary product, high SRL indicate high efficiency of using photosynthetic primary product of plant root systems (Pregitzer et al., 1998). Our studies showed that SRL of *Pinus* decreased slightly with increase forest age in monocultures, but increased with stand age in mixtures. In 45-yr-old stand, the SRL of *Pinus* in the *Pinus-Cinnamomum* mixed stand was up to two-fold higher than that in monocultures, suggesting *Pinus* exploited water and nutrient resources more efficiently when growing admixed to *Cinnamomum*. It is likely that pioneer species, *Pinus*, was stressed by the competition from the later successional conservative species, *Cinnamomum*. The results were consistent with of previous study showing that compared to pure beech, the higher specific root length (SRL) and specific surface area (SSA) were found for beech admixed with spruce (Bolte and Villanueva 2006). For *Cinnamomum*, in contrast, fine root morphology was rather similar in pure and mixed stands. The SRL of *Cinnamomum* seemed to increase along chronosequence, but no significant differences were detected, in agreement of previous study that mean SRL was not significantly different among the beech, oak and alder chronosequences (Jagodzinski et al., 2016). The contrast performances between early and late successional species, for example, higher carbon input into fine root biomass for conservative species *Cinnamomum*, and shallower fine root distribution and higher SRL in mixtures for pioneer species *Pinus* may suggest that the rooting strategies for competition from co-occurring species was species-specific.

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Table 1 Stand characteristics in pure species *Pinus* stands, pure *Cinnamomum* stands and mixed *Pinus-Cinnamomum* stands at the age 10, 24 and 45 years old.

stand	age	species	Density (n ha ⁻¹)	diameter at breast height (cm)	Height (m)	Basal area (m ² ha ⁻¹)
<i>Pinus stands</i>	10	<i>Pinus</i>	2592	9.38	5.28	20.06
	24	<i>Pinus</i>	2050	14.18	12.86	35.37
	45	<i>Pinus</i>	600	21.40	12.47	22.84
<i>Cinnamomum stands</i>	10	<i>Cinnamomum</i>	2708	7.77	5.99	14.26
	24	<i>Cinnamomum</i>	900	17.02	13.71	23.46
	45	<i>Cinnamomum</i>	800	21.06	13.24	30.63
Mixed <i>Pinus-Cinnamomum stands</i>	10	<i>Pinus</i>	902	7.64	4.73	4.37
		<i>Cinnamomum</i>	1689	8.14	7.20	9.83
	24	<i>Pinus</i>	267	18.88	12.35	7.80
		<i>Cinnamomum</i>	592	15.27	11.41	12.45
	45	<i>Pinus</i>	250	19.69	12.37	7.91
		<i>Cinnamomum</i>	325	21.94	13.75	12.91

Figure captions

Fig. 1 Live fine root biomass and fine root necromass in pure *Pinus* stand (P), *Cinnamomum* stand (C) and mixed *Pinus-Cinnamomum* stand (PC) in 0-30 cm soil depth at the age of 10, 24 and 45 years. Error bars indicate standard errors. Different letters indicate significant differences among different stands within the same ages ($p < 0.05$).

Fig.2 Relative yield total for each species (a) and Relative yield total for total standing fine root biomass (b) and in *Pinus-Cinnamomum* mixed stands at ages of 10, 24, and 45 years old stand age in comparison to monocultures (reference level = 1). Asterisks denote significant differences from 1 with t test or Mann–Whitney *U* test, $P < 0.05$. Each datum shows the mean \pm SE.

Fig. 3 Fine root biomass in pure *Pinus*, *Cinnamomum* and mixed *Pinus-Cinnamomum* stands in 0-10 cm, 10-20 cm and 20-30 cm soil depth at the age of 10, 24 and 45 years. Error bars indicate standard error. Different letters indicate significant differences among different stands within the same soil profile and age stages ($p < 0.05$).

Fig.4 Cumulative fine root biomass along the soil profiles and the coefficients of the rooting distribution (β) for *Pinus* (a) and *Cinnamomum* (b) in the pure and mixed stands at ages of 10, 24 and 45 years. The β value indicates the degree of fine root biomass decreases with soil depth.

Fig.5 Specific root length for live fine root in pure *Pinus*, *Cinnamomum* and *Pinus-Cinnamomum* mixed stands at the age of 10, 24 and 45 years. Error bars indicate standard errors. Asterisks indicates significant differences between pure and mixed stands for *P. massoniana* or *C. camphora* within the same age stages ($p < 0.05$).

Fig. 1

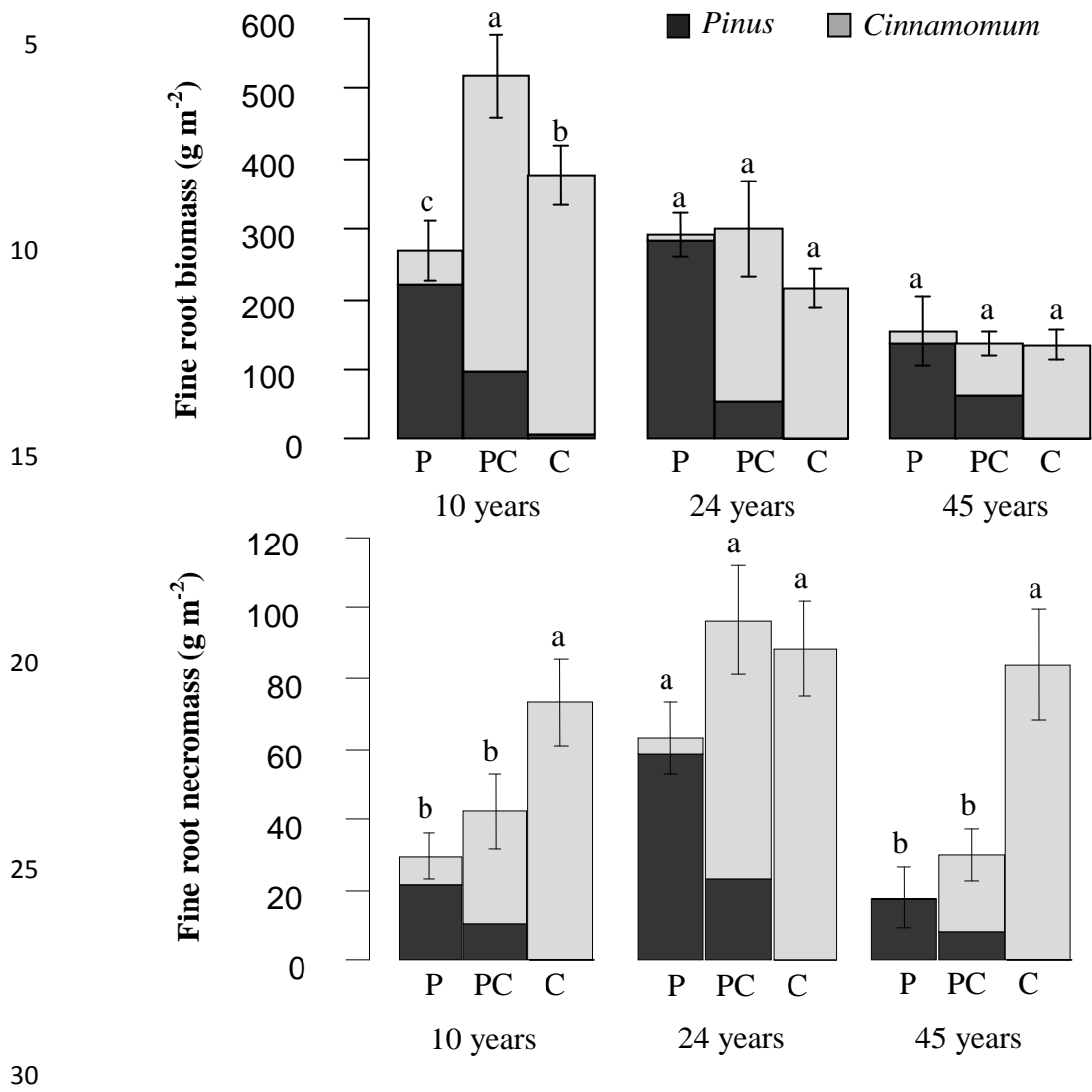
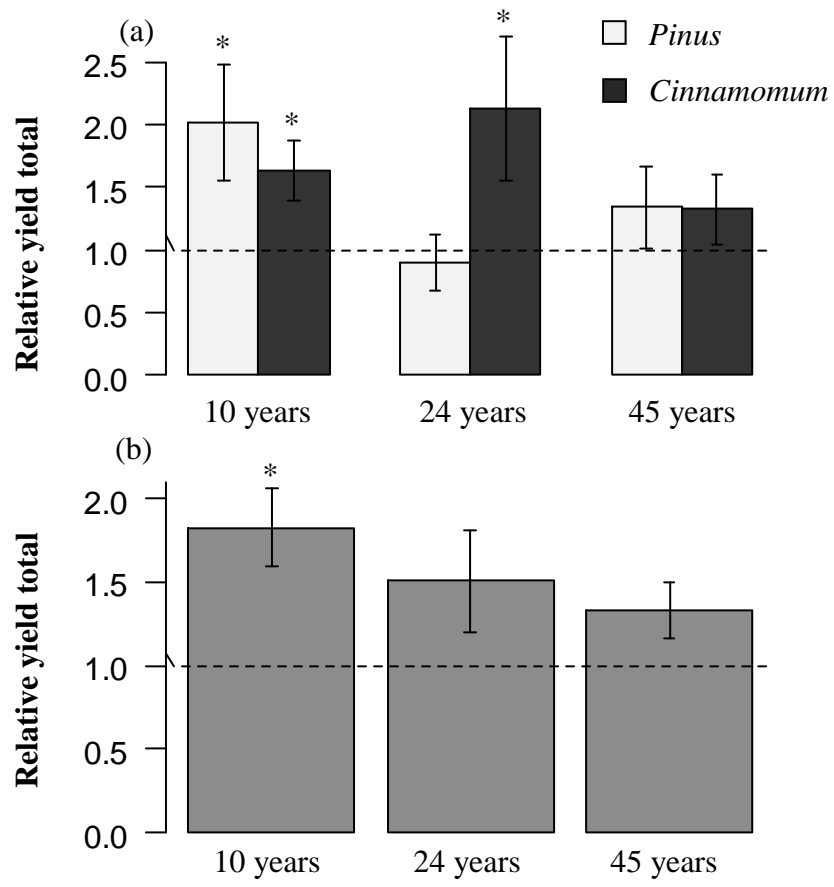


Fig. 2



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Fig.3

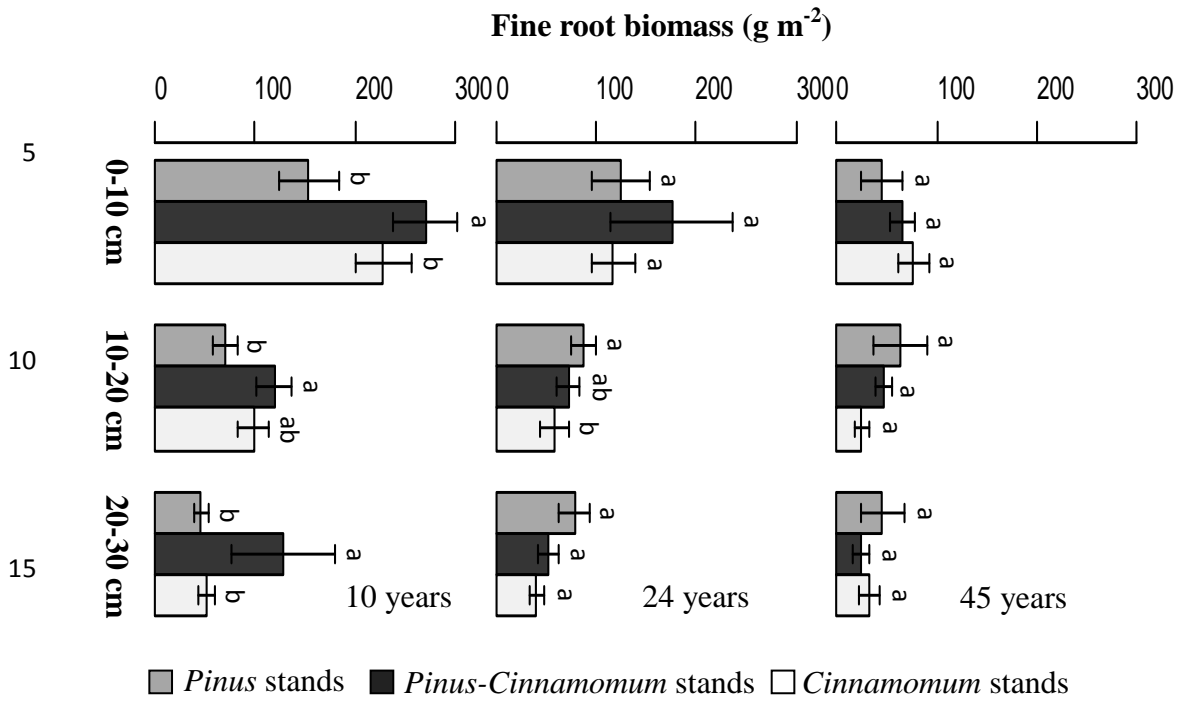
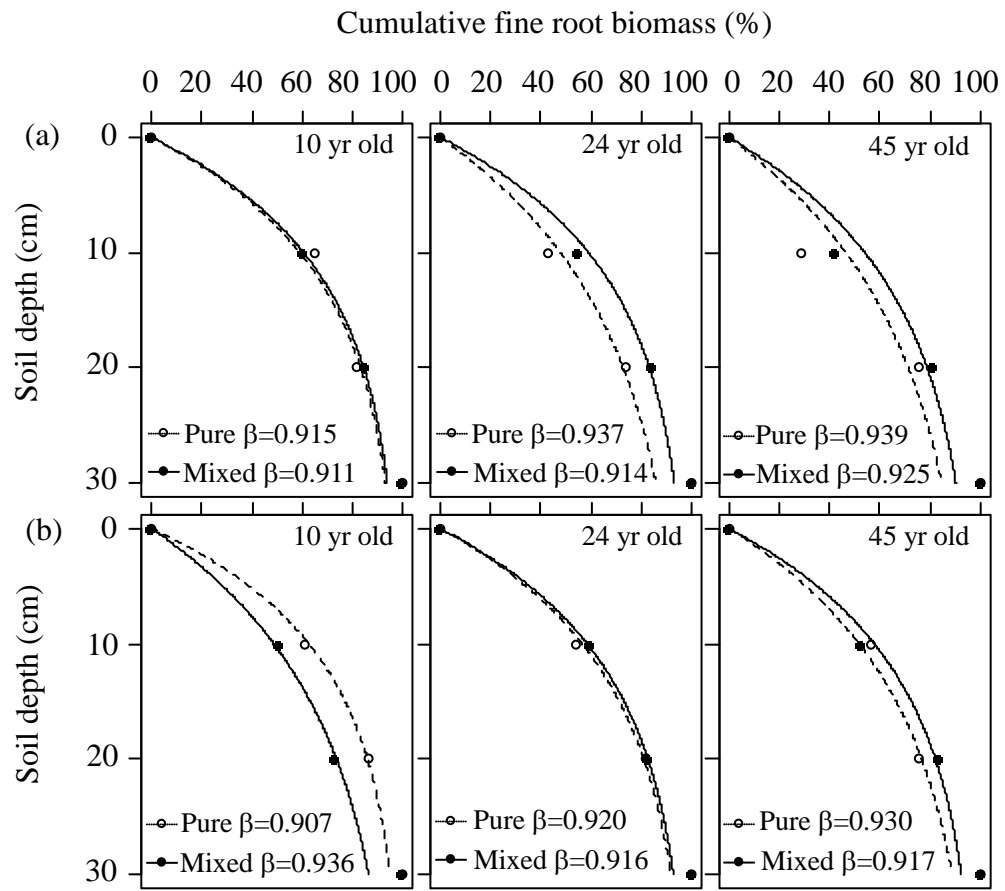
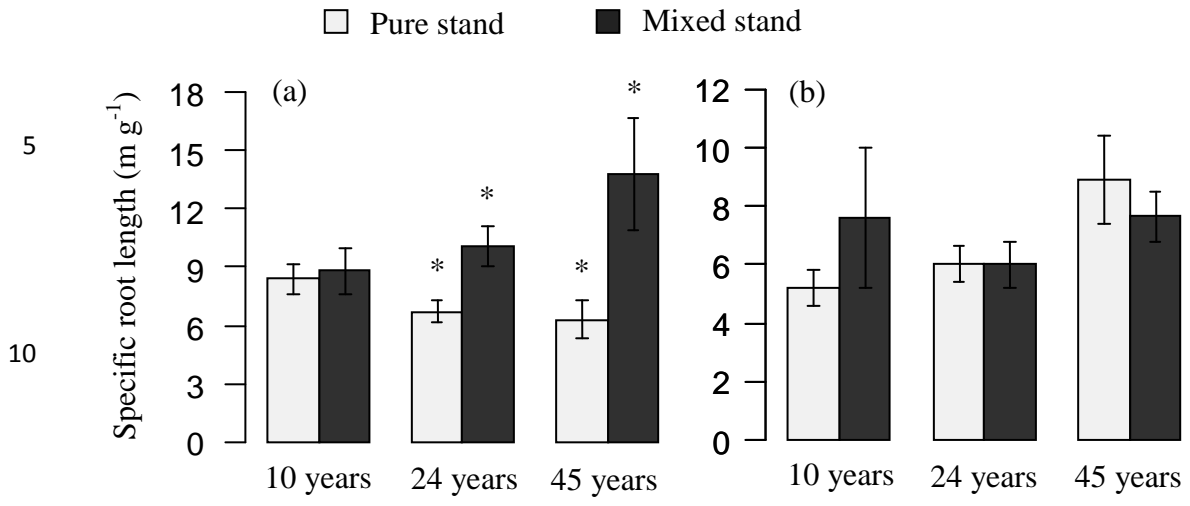


Fig.4



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Fig. 5



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