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REGULAR ARTICLE

Differential magnitude of rhizosphere effects on soil aggregation at three stages of subtropical secondary forest successions

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Abstract
Background and aims Roots and their rhizosphere considerably influence soil structure by regulating soil aggregate formation and stabilization. This study aimed to examine the rhizosphere effects on soil aggregation and explore potential mechanisms along secondary forest successions.
Methods Effects of roots and their rhizosphere on soil aggregation in two subtropical secondary forest successions were examined by separating soils into rhizosphere and bulk soils. Soil aggregate mean weight diameter (MWD), soil organic carbon (SOC), soil nutrients, and fine-root traits were simultaneously measured.
Results Soil aggregate MWD increased significantly in the bulk soils along secondary forest successions, but did not differ in the rhizosphere soils. Rhizosphere effects on soil aggregate MWD (i.e., root-induced differences between the rhizosphere and bulk soils) were thus significantly higher at the early-successional stage of subtropical forest with low soil fertility than those at the late stages with high fertility. Rhizosphere significantly increased SOC and soil total nitrogen (TN) throughout the entire secondary forest successions, which was nonlinearly correlated with soil aggregate MWD. Principal components regression analysis showed that SOC was the primary abiotic factor and

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positively correlated with soil aggregate MWD. As for biotic factors, fine-root length density and N concentration were two important root traits having significant effects on soil aggregate stability. An improved conceptual framework was developed to advance our understanding of soil aggregation and rhizosphere effects, highlighting the roles of soil fertility (i.e., SOC and available nutrients), root traits, and forest age in driving soil aggregation.

Conclusions Impacts of root-derived organic compounds inputs to rhizosphere on soil aggregation were stronger at the early-successional stage of subtropical forest than those at the late stages. This succession-specific pattern in rhizosphere effects largely resulted from the nonlinear relationships between soil aggregate MWD and SOC concentration with a plateau at high SOC. Incorporating the SOC-dependent rhizosphere effects on biogeochemical cycle into Earth system models might improve the prediction of forest soil C dynamics.

Keywords Forest chronosequence · Forest age · Fine-root traits · Soil aggregate stability · Soil organic carbon

Introduction

Soil aggregation is a natural occurring process, which holds particles firmly in the soil and shapes soil matrix with pore spaces (Yu et al. 2012; Rillig et al. 2015). In terrestrial ecosystems, a wide range of ecosystem functions are affected by soil aggregation, including plant growth, soil C sequestration, and soil fertility improvement (Wilson et al. 2009; An et al. 2013; He et al. 2018). Improvement of soil aggregation by land development (e.g., forest restoration and grassland recovery) will protect soil organic carbon (SOC) from microbial decomposition and decrease soil erosion (Amézketa 1999; DíAz-Zorita et al. 2002; Fang et al. 2016). Formation and stabilization of soil aggregates are regulated by a range of abiotic (e.g., soil properties, Chenu et al. 2000; Almajmaie et al. 2017) and biotic factors (e.g., plant and soil microbial interactions, Rillig et al. 2015). However, effects of root traits and related rhizosphere processes on soil aggregation remain poorly understood, although some studies indicated their importance in driving soil aggregation (Six et al. 2004; Rillig and Mummey 2006; Leifheit et al. 2014).

Plants affect soil aggregation largely through rooting systems and their rhizosphere (Rillig and Mummey 2006; Leifheit et al. 2014). Plant roots and associated fungi usually enhance soil aggregation by enmeshing soil particles to develop soil macro-aggregates and exuding a range of high energy small molecular weight compounds into their surrounding soils (rhizosphere, Wilson et al. 2009; Erktan et al. 2016). Consequently, some of most complex biological and ecological processes occur in the rhizosphere (Philippot et al. 2013; Finzi et al. 2015). For example, the chemical compounds and microbes in the rhizosphere have stronger cementing effects on soil particles, resulting in greater soil aggregate stability in the rhizosphere than those in non-rhizosphere soil (Caravaca et al. 2002; Six et al. 2004). Meanwhile, rhizosphere soils have higher SOC, nutrient concentration, and microbial population abundance, leading to increased SOC decomposition and nutrient mineralization relative to bulk soils (Phillips and Fahey 2008; Berg and Smalla 2009). Although positive effects of plant rhizosphere on soil aggregation have been widely accepted, what the main driving factors (e.g., roots, SOC, nutrients) are in regulating the rhizosphere effects remains largely unknown (Bronick and Lal 2005; Cheng et al. 2014).

A prevailing ecological hypothesis suggests that rhizosphere C inputs is one of the main factors in mediating the magnitude of rhizosphere effects, which are indirectly influenced by tree species, developmental stage, and soil fertility (e.g., nitrogen and phosphorus, Phillips and Fahey 2008). This hypothesis has been widely confirmed in soil microbial activity, C and nutrient cycling (Phillips et al. 2011; Cheng et al. 2014; Zhu et al. 2014). For example, a nitrogen (N) fertilization experiment demonstrated that high levels of soil fertility might limit the rhizosphere effects on microbial biomass and activity, C and N mineralization by reducing root C inputs (Phillips and Fahey 2006). However, whether the effects of rhizosphere on soil aggregation are regulated by root C inputs and soil properties remain highly elusive as well as the indirect effect of forest development. If this knowledge gap is not fully bridged, it will impede us to incorporate these potential effects into regional and global models for global C prediction.

Although a few studies have investigated effects of plant roots and their rhizosphere on soil aggregate stability in agricultural and grassland ecosystems (Sparling and Cheshire 1985; Caravaca et al. 2002; Wu et al. 2014), little information is available in forest ecosystems

(Demenois et al. 2017), especially subtropical forests. Evergreen broad-leaved forest (EBLF) is the typical subtropical vegetation, covering 4% of forest area in China (8.3×10^6 ha, Chinese Ministry of Forestry 2014), with important roles in ecosystem functions and services. Due to long-term human disturbances, EBLF is shifting to more degraded vegetation such as shrubs and croplands with great soil degradation and erosion (Wang et al. 2005). Secondary forest succession could rapidly improve soil fertility partly by enhancing soil aggregation (Aweto 1981; Yang et al. 2011). Better mechanistic understanding of how rhizosphere effects and soil properties drive soil aggregation can help us to reveal the process of SOC accumulation and nutrient cycling in forest ecosystems.

Along the forest succession, many studies have linked the changes in soil aggregation to biotic (e.g., plant community composition, root traits and root exudate production) and abiotic factors (e.g., SOC and nutrient availability, Mardhiah et al. 2014; Demenois et al. 2018a). In this study, we selected two secondary successional forests in subtropical China to (i) examine to what extent rhizosphere effects on soil aggregation changes along secondary forest successions; and (ii) probe main factors in regulating the magnitude of rhizosphere effects on soil aggregation. We hypothesized that (i) rhizosphere effects on soil aggregation would be stronger at the late-successional stage of subtropical forest relative to the early one; and (ii) inputs of root-derived organic compounds to rhizosphere would be an important factor in regulating the magnitude of rhizosphere effects.

Materials and methods

Experimental sites and forest successional stages

The study site is located in Tiantong National Station for Forest Ecosystem Research (29°48′N, 121°47′E), Zhejiang province, in China. The region has a typical monsoon climate with a hot, humid summer and a dry cold winter. Mean annual temperature is 16.2 °C and mean annual precipitation is 1374.7 mm (Yan et al. 2009; Zhou et al. 2017). The soil is hilly red and yellow earths (Acrisols and Cambisols in the FAO soil classification, respectively) with a pH range from 4.4 to 5.1. The parental material is Mesozoic sediments and acidic intrusive rocks, including quartzite and granite (Yan et al. 2006). Soil texture is mainly medium to heavy loam (18.8 ~ 33.1% sand, 37.5 ~ 43.7% silt, and 34 ~ 38.4% clay, Zhang et al. 1997).

In this study, we chose two sub-tropical secondary forest successions, which were composed of the three representative successional stages based on both forest age and species composition (early stage: secondary shrubs at 20 ~ 25 years old; middle stage: *Schima superba* forest at 50 ~ 55 years old, and late stage: climax evergreen broad-leaf forests (EBLFs) at 105 ~ 120 years old). One of secondary forest successions was located in the west of Tiantong temple (Fig. 1), consisting of three plots in the secondary shrubs (25 years, early stage), the *Schima superba* forest (55 years, middle stage), and the climax *Castanopsis fargesii* forest (120 years, late stage). Another secondary forest succession was located in the east of Tiantong temple (Fig. 1), including one plot in the secondary shrubs (20 years, early stage, the other two plots had been destroyed by human disturbance), three plots in the *Schima superba* forest (50 years, middle stage), and three plots in the climax *Castanopsis carlesii* forest (105 years, late stage). As the climax communities of old-aged EBLFs, we found that *Castanopsis fargesii* and *Castanopsis carlesii* forests shared similar root traits and soil properties at our experimental sites (data shown in the result section). In this study, we thus combined these two communities as replicates to examine rhizosphere effect at late-successional stage despite of their difference in plant community. Each plot has an area of 20 m × 20 m, with at least 50 m buffering zones between the plots for a given type of forest. The plots were located on similar slope position and elevation with at least 100 m apart from the forest edge. The soils in each successional stage were developed from the same quartzitic parent material (Yan et al. 2009). Tree height, basal area (the area of a breast-high cross section of all the trees per hectare), and stem density (number of individuals) were measured in August, 2015. Tree height was measured by a portable laser range finder. Details of community characteristics were shown in Table S1.

Soil sample collection and analyses

Soils were sampled randomly at five points per plot on October 3, 2015. Organic soil layer was shallow across the entire forest successions. Upper (0–15 cm) and deeper (15–30 cm) mineral soil layers were sampled

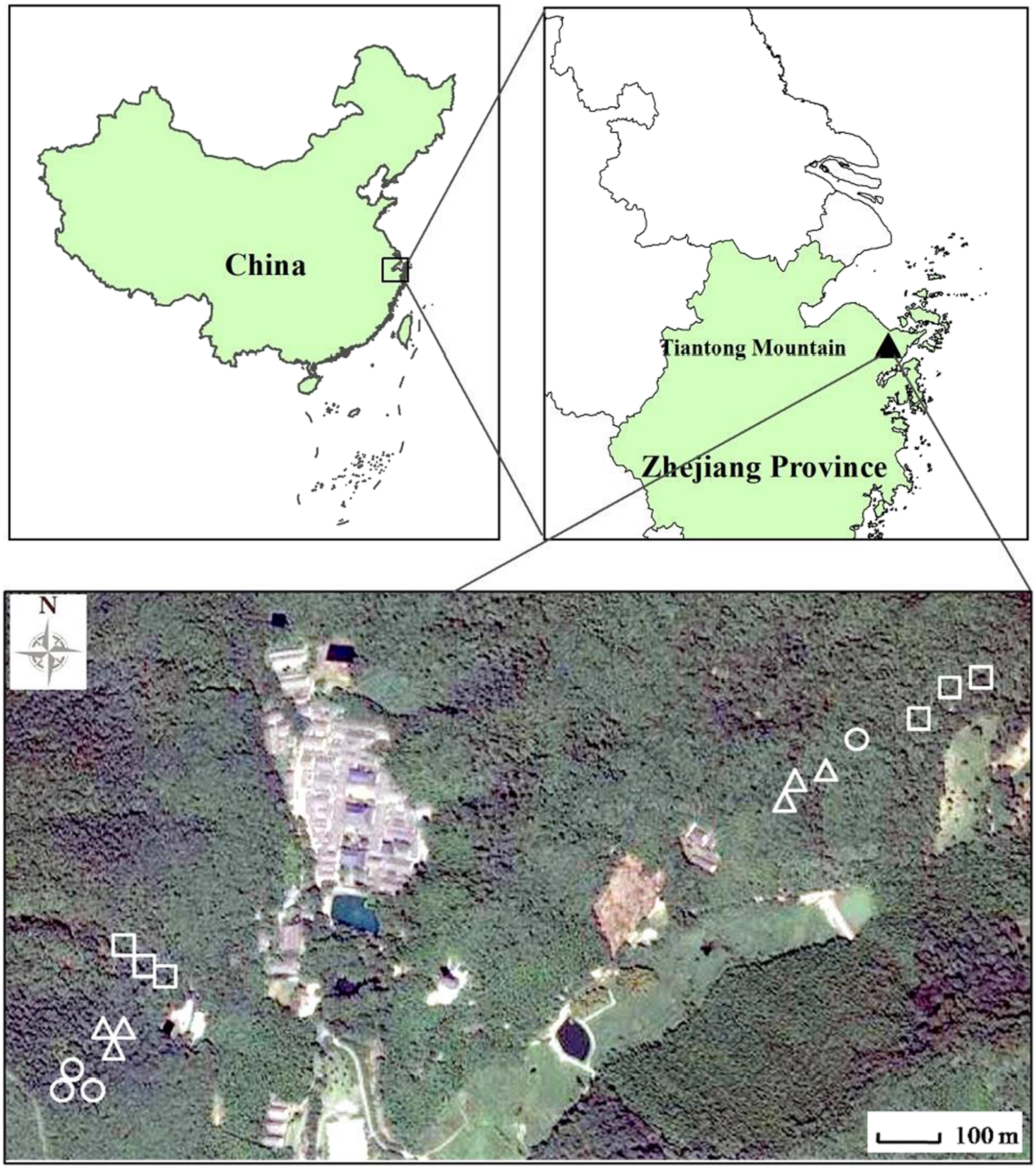

Fig. 1 Location of the sampling sites in Tiantong mountain, Ningbo city, southeast China. The circle, triangle and square sites indicate 20–25, 50–55, and 105–120 yr., respectively, photograph provided by Google Earth Online

with a cylindrical core (diameter: 10 cm, length: 15 cm) to preserve soil structure. Upper soil samples (0–15 cm soil layer) were separated into three parts: upper rhizosphere soils (soil surrounding the roots), upper bulk soils (root-free soils), and upper mixed soils (including rhizosphere and bulk soils). A quarter of soils at each core were separated from the upper undisturbed soils (Fig. S1) as upper mixed soils. In the remaining three quarters of upper soil samples, fine roots (diameter < 2 mm) and adhering rhizosphere soils were carefully collected with forceps and gently shaken to remove loose soils. The soils remaining attached to the fine roots after shaking were considered as upper rhizosphere soils, while those root-free soils were upper bulk soils (Phillips and Fahey 2008; Ai et al. 2012). This shaking-remaining method is currently an only feasible way to collect a sufficient mass of rhizosphere soils for process-based assays, and widely used to investigate the rhizosphere effects (Finzi et al. 2015; Massaccesi et al. 2015). The subsoil (15–30 cm layer) was also collected as deeper mixed soils and was not divided into the above three parts, since rhizosphere soils were rare in subsoil layer duo to low fine-root distribution (Finzi et al. 2015). Five soil sub-samples per plot were gently sieved through a 5-mm sieve, and then mixed to obtain one composite soil sample. Composite soil samples were air-dried at room temperature for five days.

Soil sub-samples (50 g) were taken from composite soil samples, and re-sieved through a 0.149 mm sieve. Soil organic carbon (SOC) and total nitrogen (STN) concentrations were measured using an elemental analyser (Vario EL LII, Elementar, Germany). Soil inorganic N (SIN) was extracted from field samples by shaking with 2 *M* KCl at a soil solution ratio of 1:10, followed by centrifuging at 2000 rpm for 20 min. Soil total phosphorus (TP) was extracted by using heating digestion method and analysed by atomic absorption spectrophotometry using molybdenum antimony blue colorimetry (Murphy and Riley 1962). Soil cation exchange capacity (CEC) was determined by leaching the soil with ammonium acetate. Soil pH was measured at a 1:2.5 soil/water (*w*/w) ratio with a glass electrode.

Soil aggregate measurements

Soil aggregate stability was measured as the abundance of water stable aggregates (WSA) by immersing a stack of sieves (from top to bottom: 2-mm, 1-mm, 0.5-mm, 0.25-mm, 0.106-mm) in a bucket of water (Kemper et al. 1986). Another air-dried soil sub-sample (50 g) was rewetted by capillary action and was then carefully placed on the top sieve of the stack. All sieves were kept immersed while being moved up and down (approximately 3 cm) for 10 min. The materials remaining on each sieve were then crushed and passed through the sieve to separate the materials into soil (passing through the sieve) and coarse (remaining on the sieve) fractions. Soil fractions from each sieve size (2–5 mm, 1–2 mm, 0.5–1 mm, 0.25–0.5 mm, 0.106–0.25 mm, and 0–0.106 mm) were collected, dried at 65 °C for 48 h to the constant weight, and then weighed separately. Total coarse materials and primarily sand were also weighed. Mean weight diameter (MWD) was calculated as the sum of the proportion of aggregates in each size class, proportionally weighted by the mean diameter of aggregates in that size class (approached as mean size of upper and lower limit of sieve size used: 3.5 mm, 1.5 mm, 0.75 mm, 0.375 mm, 0.178 mm, and 0.053 mm, respectively). Mean weight diameter (MWD, mm) of soil aggregates was calculated as follows:

$$MWD = \frac{\sum_{i=1}^{i=6} Mi \times Di}{\sum_{i=1}^{i=6} Mi}$$

where each of the six classes of diameter ($i = 1$–6), Di [mm] is the central diameter of each size class. The extreme classes (D1 and D6) are 3.5 and 0.053 mm, respectively. Mi [g] is the mass of stable soil aggregates isolated within a diameter size class. After wet-sieving, SOC concentrations in different soil aggregate fractions were measured using an elemental analyser (Vario EL LII, Elementar, Germany).

Root characteristic measurements

Fine roots (diameter < 2 mm) were carefully removed from the soil by tweezers and placed in water to remove the attached soil and organic matter particles. Representative sub-samples of roots (2 g fresh mass) were selected for root morphological measurements. Fresh roots were kept intact, and scanned at a resolution of 400 dpi on a desktop scanner (Epson Expression 10000XL scanner). Background impurities (e.g., shadows and spots) at each image were removed manually by an operator using Adobe Photoshop version 8.0 LE (Adobe Systems) prior to further analysis. The remaining root samples were oven-dried for 48 h at 60 °C and weighed. Total fine-root length and the length of fine roots in 10 diameter classes (0.2 mm width from 0 to 2 mm), and mean fine-root diameter were measured by analysing scanned images with WinRHIZO Arabidopsis version 2012b (Regents Instruments Inc., Quebec Canada). The percentage of very fine roots to total fine roots was defined as the ratio of length in the concerned root classes (diameter < 0.2 mm) to total fine-root length. Total root dry mass was calculated as the sum of the dry mass of roots for morphological analysis and those of the remaining roots. Root length density (RLD), including fine-root (diameter < 2 mm) and very fine root (diameter < 0.2 mm) length density, was defined by the total root length per unit of soil volume. Specific root length (SRL) was calculated as the ratio between total root length and root dry mass. Dried root samples were ground in a Wiley mill to pass a 40-mesh screen; fine-root N concentration was determined by using a Vario MAX elemental analyser (Elementar, Germany).

Statistical analyses

Rhizosphere effects on soil aggregation were calculated as the root-induced difference (% difference) in soil aggregate MWD between paired rhizosphere and bulk soil samples (Phillips and Fahey 2008). The magnitude of rhizosphere effects were also analysed for their statistical difference from zero (i.e., positive, negative, or neutral rhizosphere effects). Responses of rhizosphere effects to secondary forest succession were tested by one-way ANOVA approach. Interactive effects of forest succession with rhizosphere (difference between upper rhizosphere and upper bulk soils) and soil depth (upper mixed and deeper mixed soils) on soil properties were determined by two-way ANOVA (Tables S5 and S6). One-way ANOVA were performed when interactive effects were significant. Impacts of secondary forest succession, soil aggregate fraction, and rhizosphere/soil depth on aggregate-associated SOC concentration were analysed by three-way ANOVA (Tables S2 and S3). Two-way ANOVA was performed when three-way interactive effects were significant (Table S4).

Factors regulating rhizosphere effects were determined by Pearson correlation analysis. Meanwhile, the relationships between soil aggregate MWD and other soil properties or root characteristics were examined to explore the potential governing mechanism. Relative contributions of these variables to soil aggregate stability were explored via a principal component analysis (PCA) and general linear models (GLMs). Prior to PCA, non-linear correlations between variables were examined and data transformation was applied to linearize the interrelationships between these variables. Specifically, SOC, TN, TP, CEC, fine root length (FRL) and very fine root length (VFRL) density were log-transformed, because they were non-linearly correlated with soil aggregate MWD. These variables were considered non independent for $\rho \geq 0.7$ and $P < 0.001$ with a Spearman correlation test (Fig. S2, Demenois et al. 2018b). Ln TN, ln TP, ln C/N ratio, ln CEC, ln VRL and SRL were consequently not included in the PCA (Fig. S2).

Following PCA, GLMs were used to quantify the best model to predict soil aggregate stability. The first and second principal components (PCA 1 and 2) were used as new variables to test the different general linear models because other components were not correlated with soil aggregate stability. This method allowed us to deal with the limited number of observation (32 MWD observations (mixed soils, 16 plots × two soil layers) for 5 independent explanatory variables, Grueber et al. 2011; Demenois et al. 2018b). The best model was quantified as the combination of variables that produced the lowest corrected Akaike Information Criterion (AICc). ANOVA test was undertook by SPSS software (SPSS, Inc., Chicago, IL, USA), and GLMs and AICc analyses were performed by *R* software (*R* Core Team). The site distribution was plotted using ArcGIS 10.0 software (ESRI, Redlands, CA, USA). Figures were drawn in SigmaPlot and *R* software 197 (Systat Software Inc., CA, USA).

Results

Soil aggregate mean weight diameter

Along secondary forest successions, soil aggregate MWD increased significantly in the upper bulk soils, upper and deeper mixed soils, but did not differ in the upper rhizosphere soils (Fig. 2a; $P > 0.05$). Rhizosphere effects (i.e., root-induced differences between rhizosphere soils and bulk soils) on soil aggregate MWD were the greatest at the early-successional stage. In this stage, roots and their rhizosphere increased soil aggregate MWD by 92.9% compared to that in upper bulk soils (Fig. 2b). However, root-induced differences (i.e., percentage differences) were significantly smaller at the late stage of secondary forest successions compared with those at the early stages (Fig. 2b, c; $P < 0.05$). Soil aggregate MWD was also influenced by soil depth (two-way ANOVA, $P = 0.022$). Throughout the forest successions, soil aggregate MWD was greater in the upper mixed soils than the deeper mixed soils (Fig. 2a; T test, $P < 0.05$).

Aggregate-associated SOC along secondary forest successions

Aggregate-associated SOC at the late-successional stage was higher relative to those at the early and middle stages (Tables S3 and S4). Higher SOC were also observed in 5–2 mm, 1–2 mm, 0.5–1 mm and 0.25–0.5 mm fractions than those in 0.106–0.25 mm and 0–0.106 mm fractions. However, there were no significant differences of aggregate-associated SOC among the three stages of secondary forest successions in the upper rhizosphere soils (Fig. S3, Table S4).

Soil chemistry and their effects on soil aggregate MWD

SOC, soil total nitrogen (TN), soil total phosphorus (TP), and cation exchange capacity (CEC) significantly increased along secondary forest successions (two-way ANOVA, Table S5 and S6), but did not change soil carbon: nitrogen ratio (C/N) and pH ($P > 0.1$). Rhizosphere significantly increased SOC, soil TN, soil C/N, CEC, and decreased soil pH (Table S5, $P < 0.05$), but did not affect soil TP ($P > 0.05$). At the early-successional stage, rhizosphere improved SOC by 94.7%, soil TN by 77.3%, and CEC by 34.9% (relative to upper bulk soils, Fig. 3). The amplitude of those root-induced chemical accumulations tended to increase along the secondary forest succession, although the effects were not statistically significant (Table S7, $P > 0.1$). Soil depth significantly reduced SOC and soil TN ($P < 0.05$), but did not change soil TP, CEC, C/N and pH (Table S6, $P > 0.05$).

Soil aggregate MWD was logarithmically correlated with SOC, TN, TP, and soil CEC with a plateau under the highest values (Fig. 4a, b, c, d, e and f, $P < 0.05$). The magnitude of rhizosphere effects on soil aggregate MWD was linearly correlated with SOC, TN, TP and CEC in upper rhizosphere soils and upper bulk soils, but had no correlation with root-induced differences in these soil chemical parameters (Fig. 4a, b, c, d, e and f; $P > 0.05$).

Fine-root traits and their effects on soil aggregate MWD

Fine-root biomass reached 3.5 g m^{-2} in the upper soil layers at the early-successional stage of forest, which was significantly higher than those at the late stage (1.9 g dry root m^{-2}, Fig. 5a). Specific root length (SRL) in the upper soil layers was higher at the late-successional stage relative to the middle and early ones (Fig. 5d). Fine-root diameter in the upper soil layers was marginally higher at the early-successional stage relative to the late one ($P = 0.081$, Fig. d). Fine-root length density and very fine root (diameter < 0.2 mm) length proportion in both upper and deeper soil layers, and fine-root biomass, SRL and root diameter in the deeper soil layer did not significantly change along the secondary forest succession (Fig. 5, $P > 0.1$). N concentration of fine roots significantly increased in both upper and deeper soil layers along the secondary forest succession (Fig. 5f, $P < 0.05$). The greatest fine-root N concentrations were found at the late-successional stage (10.6 mg g^{-1} dry root in the upper soil layers and 7.9 mg g^{-1} dry root in the deeper soil layers), followed by mid-successional stage (7.9 and 5.3 mg g^{-1} in two soil layers respectively), and early-successional stage (6.8 and 4.8 mg g^{-1} in two soil layers respectively).

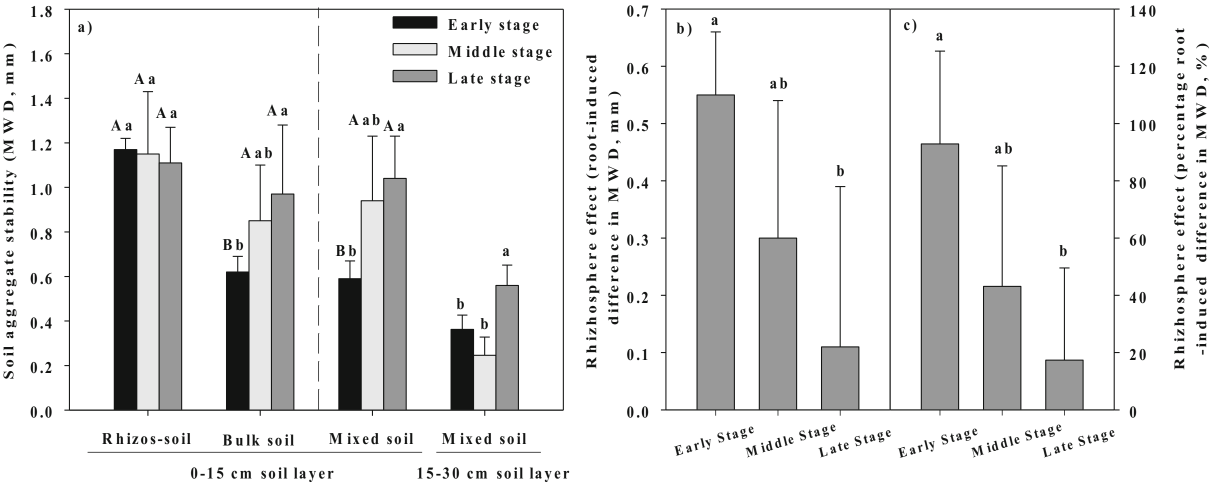

Fig. 2 Soil aggregate mean weight diameter (MWD, refer to soil aggregate stability) in forest secondary succession series. Root-induced difference in soil aggregate MWD = $MWD_{(rhizos\text{-}soil)}$ - $MWD_{(bulk\ soil)}$), and percentage root-induced difference in soil aggregate MWD = ($MWD_{(rhizos\text{-}soil)}$ - $MWD_{(bulk\ soil)}$) / $MWD_{(bulk\ soil)}$. Different lowercase letters above bars show significant effects of secondary forest succession, diverse capital letters indicate significant difference among different fractions of soils. Vertical bars represent the standard error

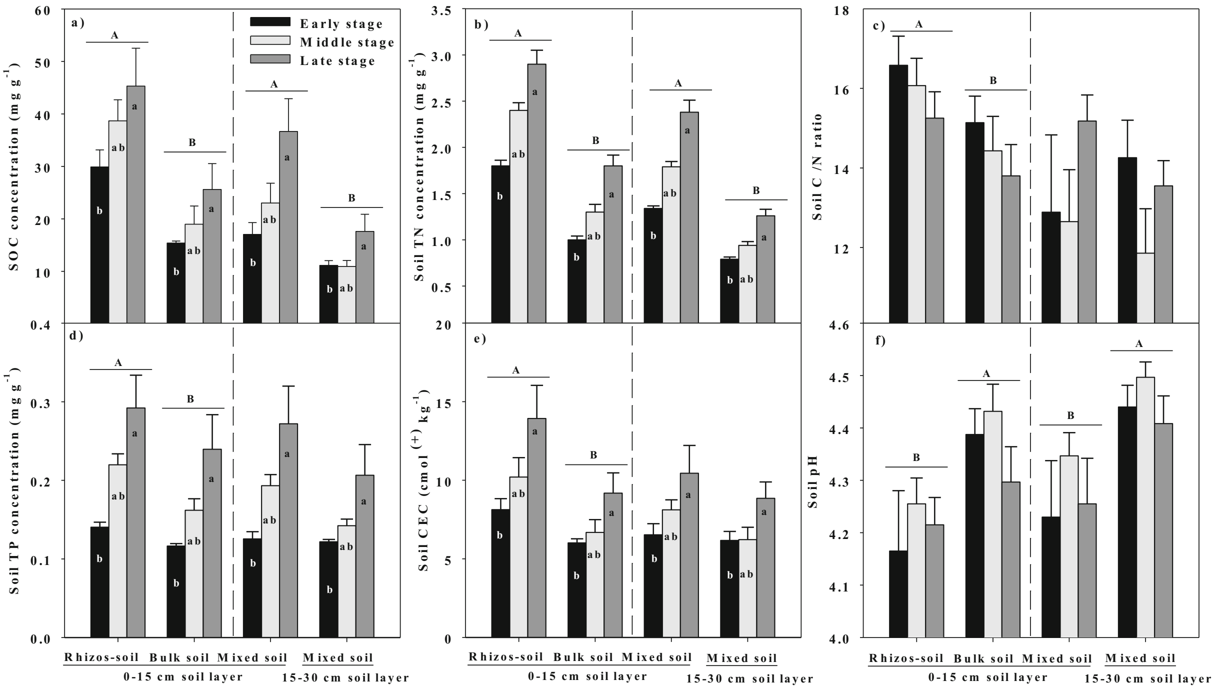

Fig. 3 Soil chemistry in forest secondary succession series. Effects of secondary forest succession and rhizosphere as well as soil depth on soil chemistry were analysed by two-way ANOVA test approach. Different lowercase letters show significant effects of secondary forest succession, diverse capital letters indicate significant difference among different fractions of soils. Vertical bars represent the standard error

Correlation analysis showed that soil aggregate MWD in mixed soils (including upper and deeper mixed soil layers) was logarithmically correlated with fine-root length density and very fine root length density (Fig. 6b; $P < 0.01$), and linearly correlated with fine-root SRL and N concentration (Fig. 6a; $P < 0.01$). Soil aggregate MWD in upper bulk soils was linearly correlated with fine-root length density, very fine root length density (Fig. 6b; $P < 0.05$), and fine-root SRL (Fig. 6a; $P < 0.01$). No correlations between fine-root traits and soil aggregate MWD were detected in upper rhizosphere soils (Fig. 6a; $P > 0.05$).

Relative contribution of soil properties and root traits to the variation in soil aggregate MWD

Principal component analysis (PCA) showed that the first and second principal components (PCA 1 and 2) explained 54% and 21% of the total variance, respectively (Fig. S4). PCA 1 was positively correlated with SOC, fine-root length density, inorganic N, and fine-root N, and negatively correlated with soil pH. PCA 2 was positively correlated with fine-root N and soil pH, and negatively correlated with fine-root length density (Table 1). Results from the general linear models (GLMs) showed that PCA 1, 2, and their combination had significant impacts on soil aggregate MWD (Table 2). The best model (AICc = −19.8, Fig. 7) included the two principal components (PCA 1 and 2) on soil aggregate MWD but with the highly significant effect of PCA 1. Based on the distinct contributions of different variables from PCA 1 and 2 (Table 1), SOC was the primary abiotic factor and positively correlated with soil aggregate MWD relative to soil inorganic N and soil pH. As for biotic factors, fine-root length density and N concentration was two important root traits having significant effects on soil aggregate stability.

Discussion

Effects of forest succession on soil aggregation

Forest development improves soil aggregate stability through affecting biotic (e.g., plant community and microbial population) and abiotic (e.g., soil chemistry) characteristics (Mardhiah et al. 2014; Erktan et al. 2016). In our study, soil aggregate stability significantly

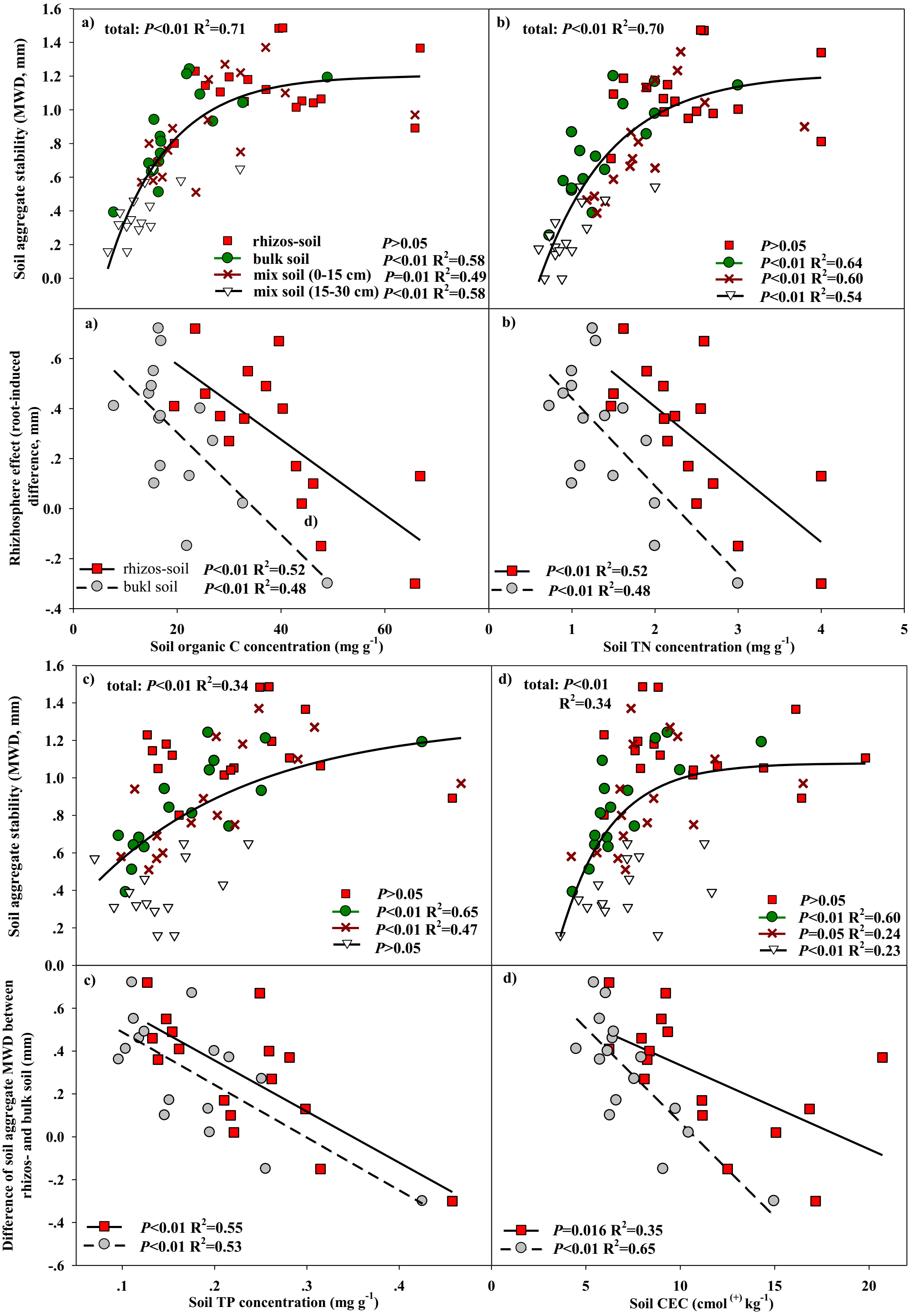

Fig. 4 Relationships between soil aggregate MWD and soil chemistry among different fractions of soils

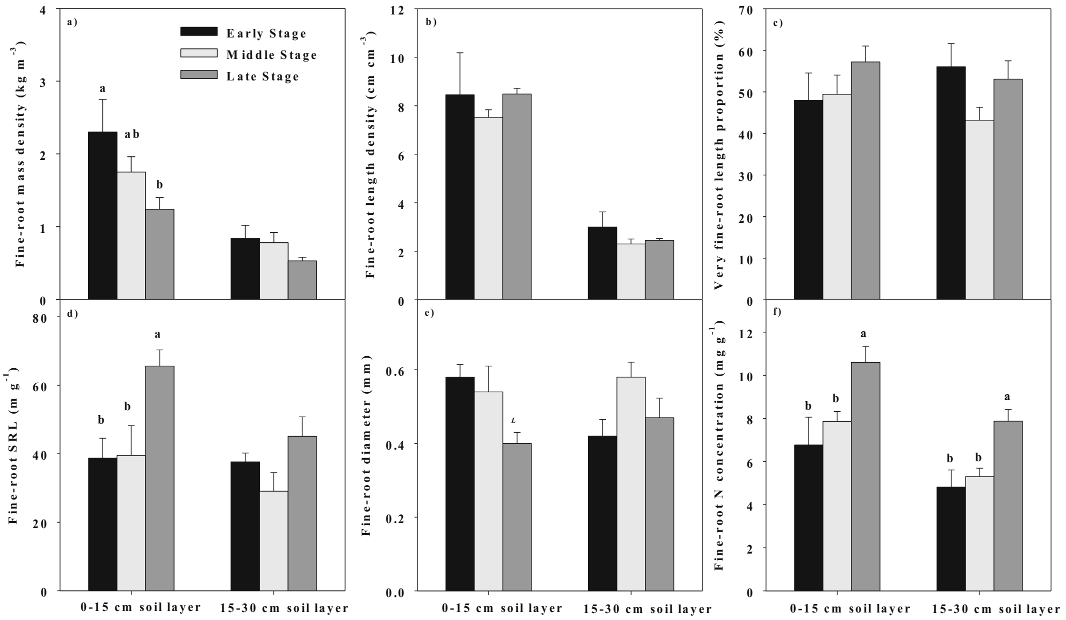

Fig. 5 Changes of fine-traits along forest secondary succession. Different lowercase letters above bars show significant effects of secondary forest succession. *L* represent marginally significant difference $0.05 < P < 0.1$. Vertical bars represent the standard error

increased along the secondary forest successions (Fig. 2), which was consistent with other studies in the long-term forest chronosequences (Zhou et al. 2012; Qiu et al. 2015). At the early-successional stage, soil aggregate

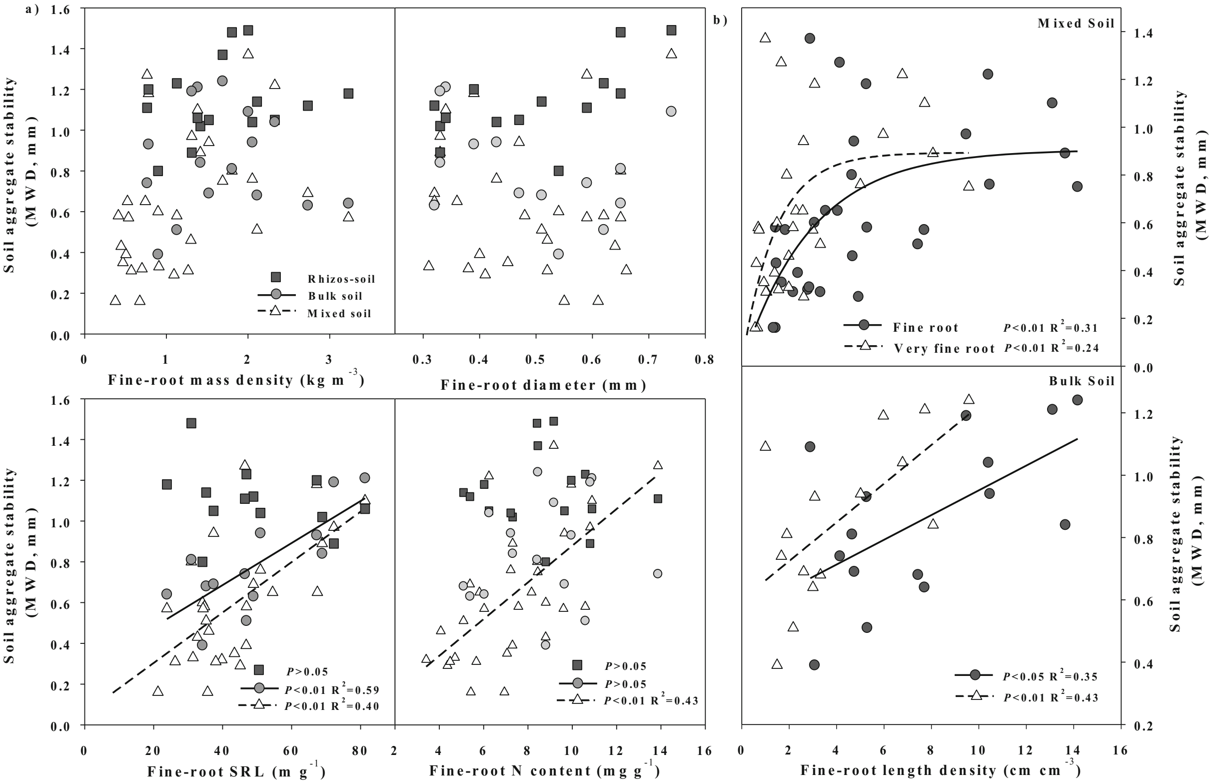

Fig. 6 Relationships between fine-root functional traits and soil aggregate MWD. Mixed soils refer to combined 0–15 cm and 15–30 cm mixed soils

Table 1 Contributions of soil and root characteristics to PCA 1 and 2 of the principal component analysis

PCA 1	Variables	Position on the axis	Contribution (%)	Cumulative contribution (%)	Cos^2
	ln SOC	+	29.257	29.26	0.792
	ln FRL	+	24.233	53.49	0.656
	IN	+	17.584	71.07	0.476
	pH	–	16.919	87.99	0.458
	Root N	+	12.006	100	0.325
PCA 2	Variables	Position on the axis	Contribution (%)	Cumulative contribution (%)	Cos^2
	Root N	+	48.000	48.00	0.504
	pH	+	29.904	77.90	0.314
	ln FRL	–	15.238	93.14	0.160
	ln SOC	+	3.809	96.95	0.040
	IN	+	3.047	100	0.032

SOC soil organic carbon; *FRL* fine-root length density; *IN* inorganic nitrogen

mean weight diameter (MWD, 0.59 and 0.36 mm in soil layers of 0–15 and 15–30 cm, respectively, Fig. 2a) was relatively low due to soil degradation and erosion induced by anthropogenic cutting of mature forests (Zuazo 2008; Bouwman 2010). Soil aggregate MWD in topsoils (the 0–15 cm soil layer) increased by 1.6 times from the early to mid-successional stages (0.014 mm year^{-1}, Fig. 2a). The increased rate in soil aggregate MWD was approximately close to a 40-year chronosequence of fluvial islands with an increase rate of 0.02 mm year^{-1} (Mardhiah et al. 2014). Such strong increases suggested that secondary forest succession was an efficient strategy to improve stabilization of soil structure for the human-disturbed forests. Soil aggregate MWD in topsoils increased slightly from the mid- to late-successional stages in the present study (Fig. 2), which might be attributed to the high value of soil aggregate MWD at the mid-successional stage. Similarly, previous studies demonstrated that soil aggregate MWD increased strongly with time at diverse sites with the low initial soil aggregate MWD, but changed slightly at sites with the high initial soil aggregate MWD (Zhou et al. 2012; Erktan et al. 2016).

The main mechanism driving soil structure development is soil organic carbon (SOC) accumulation. The present study showed that SOC concentration had the highest explanatory power for the variations of soil aggregate MWD (Table 1, Figs. 4a and 7). The positive role of SOC in soil aggregation has been previously reported (Chenu et al. 2000; Six et al. 2004; An et al. 2013). However, other researchers argued that the positive effects of SOC on soil aggregate stability depended on SOC concentrations (Le Bissonnais and Arrouays 2010; Erktan et al. 2016), due to the fact that a positive relationship between SOC and soil aggregate stability is not always found (Lado et al. 2004; Zhu et al. 2017). In our study, a non-linear relationship between SOC and soil aggregate MWD further demonstrated that the effect of SOC on soil aggregate stability was dependent on SOC concentration (Fig. 4a). The impacts of accumulating SOC on soil aggregate stability was stronger at low SOC concentration (SOC < 27 mg g^{-1} dry soil) compared

Table 2 General linear models predicting soil aggregate stability

Model rank	AICc	Intercept	Parameter (±SD)	
			PCA 1	PCA 2
1	−19.80	0.642^{**}	$0.272 \pm 0.030^{**}$	$0.110 \pm 0.029^{**}$
2	−9.33	0.639^{**}	$0.276 \pm 0.036^{**}$	
3	20.76	0.653^{**}		$0.117 \pm 0.057^{*}$

Levels of significance are *: $P = 0.05$; **: $P < 0.01$. AICc: second-order Akaike Information Criterion

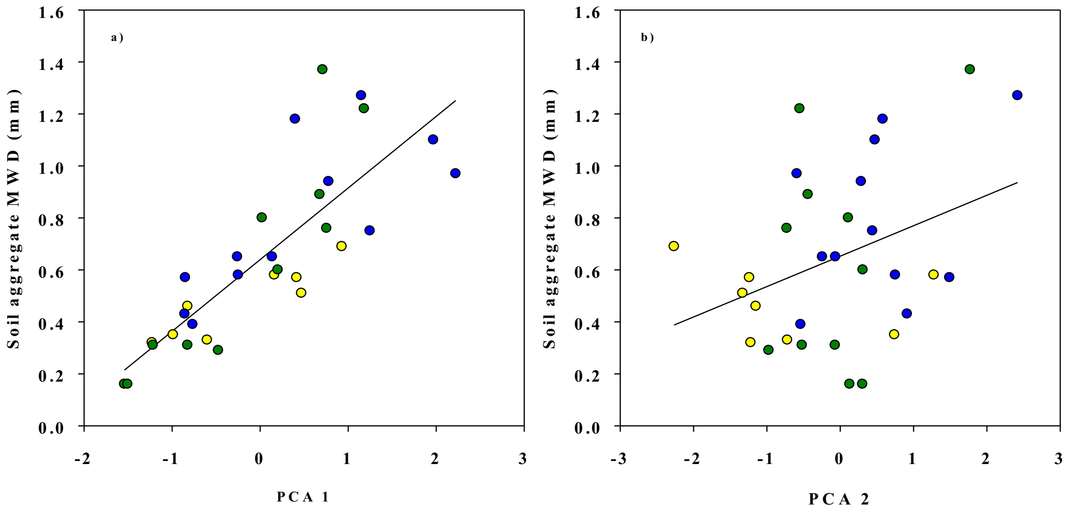

Fig. 7 Best general linear model for predicting soil aggregate stability. AICc of the model = −19.8, levels of significance: intercept<0.001; PCA 1 < 0.001; PCA 2 < 0.001. Colored dots correspond to each plot. Plant communities are indicated by different colours: yellow is the early-successional community; dark green is the mid-successional community; blue is the late-successional community

with that of high SOC concentration (SOC > 27 mg g^{-1} dry soil, Fig. 8b). Linear correlations between SOC and soil aggregate stability have been mostly found in agriculture land and grassland where SOC is below or close to 27 mg g^{-1} dry soil (Six et al. 2004; An et al. 2013; Podwojewski et al. 2014). However, in our study, we had a wider range of SOC concentration (from 13.1 to 66.8 mg g^{-1} dry soil) compared to grasslands and agricultural lands, which may explain non-linear relationship between SOC and soil aggregate MWD.

Soil nutrient availability is another important factor to affect soil aggregation. We found strong correlations of soil aggregate MWD with soil total nitrogen (TN), total phosphorus (TP), cation exchange capacity (CEC; Fig. 4a, b, c and d), and soil inorganic N concentrations (Table 2; Fig. 7). However, the relative contributions of soil TN, TP and CEC to the variations in soil aggregate MWD could not be quantified because they were non independent variables, which were tightly correlated with SOC (Fig. S2, $P < 0.001$). There appears evident that soil nutrient availability regulates soil aggregation through indirect mechanisms concerning SOC inputs and stabilization (Bronick and Lal 2005). The effects of soil N and P concentrations on soil aggregation could be explained by changes in shoot and root growth (Wan 2008; Nielsen et al. 2015), plant production (Lu et al. 2011; He et al. 2015), and root colonization of arbuscular mycorrhizal fungi (Facelli and Facelli 2002; Wilson et al. 2009). Soil CEC could increase soil aggregation through forming bridges between clay and SOM particles, which were resistant to slaking (Bronick and Lal 2005). Dissolved organic compounds (DOC) can be coupled with soil metal cation at low pH, leading to decreased microbial access to SOC and reduced mineralization, which further promotes soil aggregate stability (Six et al. 2004). Thus, the accumulations of soil TN, TP, CEC and inorganic N along the secondary forest succession may have indirectly contributed to the increase in soil aggregate MWD.

Soil pH may regulate soil aggregation through influencing plant growth, metal ion solubility, microbial activity, and clay dispersion (Haynes and Naidu 1998; Tahmasbian et al. 2017). Consistently, our analyses reported that changes of soil pH were tightly related to variations of soil aggregate MWD (Table 2; Fig. 7). Although no significant changes of soil pH were observed along the secondary forest successions (Fig. 3f), rhizosphere decreased soil pH throughout the forest succession. The observed decrease in soil pH may result from the inputs of root exudation and organic acids (Russel 1960). In addition, soil iron and aluminum may also be generally important in governing soil aggregation stability (Amézketa 1999; Demenois et al. 2018b). However, our study did not find significant differences among the three successional stages of subtropical forests and rhizosphere effects on soil total iron and aluminum, and exchangeable iron and aluminum. Therefore, soil iron and aluminum may not be the

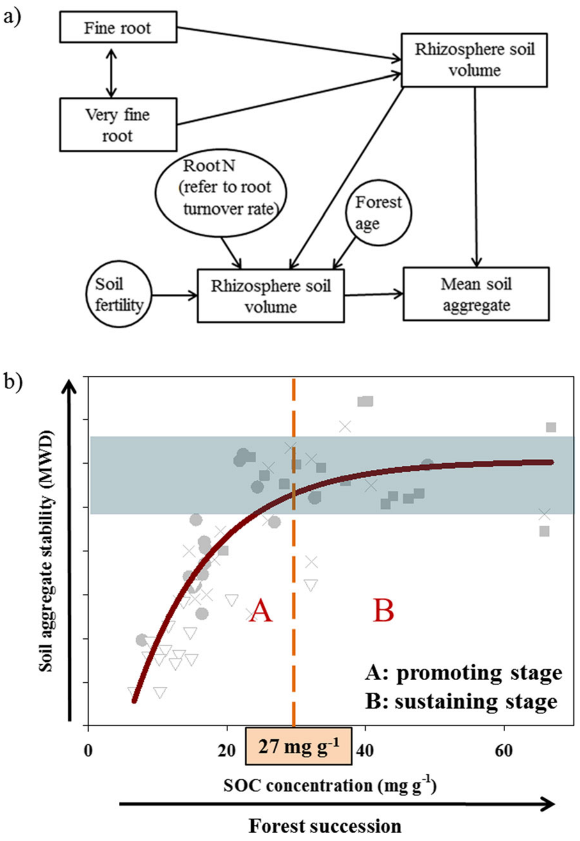

Fig. 8 Improved conceptual framework to explain rhizosphere effects on soil aggregation. Single-headed arrows indicate direct causal relationships and double-headed arrows indicate unanalysed correlations in Fig. a. Inflection point (27 mg C g^{-1} dry soil) in Fig. b was determined by piece-wise linear function in *R* software. Blue stripe refers to the main scope of rhizosphere soil aggregate WMD (Mean ± SD)

driving factors for soil aggregation in our experimental sites (Data not shown).

Effects of root and their rhizosphere on soil aggregation

Roots and their rhizosphere usually promote soil aggregate stability, but the extent in which rhizosphere affects soil aggregate stability varies in different terrestrial ecosystems (Bronick and Lal 2005; Cheng et al. 2014). Our results showed that rhizosphere effect on soil aggregation was mainly regulated by soil fertility (i.e., SOC and available nutrients), with a stronger effect in the early-successional forest with low soil fertility and weaker effect in the late-successional forest with high fertility. Rhizosphere effects on soil microbial activity and nutrient cycling regulated by soil fertility has been widely examined (Phillips and Fahey 2006; Cheng et al. 2014). According to plant C allocation theory, plants would decrease C inputs to rhizosphere in fertile soils (Phillips and Fahey 2008), leading to stronger rhizosphere effects at low than high fertility (Phillips and Fahey 2006). However, in our study, no difference in rhizosphere C input (root-induced difference between rhizosphere and bulk soils, Table S7) was observed. Therefore, our study suggested that rhizosphere effects on soil aggregation regulated by soil fertility may have been largely resulted from the SOC-dependent impacts of accumulating SOC rather than the quantity of rhizosphere C inputs.

Throughout the secondary forest successions, the C inputs from roots significantly increased SOC in the rhizosphere soils compared with that of bulk soils. Increased SOC in the rhizosphere soils were also observed along secondary forest successions, where soil aggregate MWD did not change (Figs. 2a and 3a). This further suggested that the effect of SOC accumulation on soil aggregation was weak at high soil fertility. The lack of relationship between soil aggregate MWD and SOC accumulation in the rhizosphere was inconsistent with previous studies, which have reported a strong correlation of SOC accumulation with soil aggregate MWD and macro-aggregate (Six et al. 2004; Erktan et al. 2016). Our present study showed that plant C inputs to the rhizosphere were largely allocated to the micro-aggregates (fractions of 0–0.25 mm, Fig. S3). This may explain the absence of response in soil aggregate MWD to varying SOC in the rhizosphere with respect to forest succession.

Fine-root traits are important biotic factors to regulate soil aggregation (Mardhiah et al. 2014; Erktan et al. 2016). Fine-root length density is one of the critical root traits related to rhizosphere soil volume and root N is generally used as an indicator of root turnover rate (Valverde-Barrantes et al. 2007; McCormack et al. 2012). Our study showed that both fine-root length density and N concentration were able to better explain the variations of soil aggregate MWD than other root traits (Table 2; Fig. 7). Roots influence soil aggregation largely through rhizo-deposition, root mass, root density, root turnover, and associated fungi (Amézketa 1999). Consistently, our study observed that rhizosphere increased a range of soil chemistry (i.e., SOC, inorganic N and CEC, Fig. 3) and thus promoted soil aggregate MWD. Fine-root mass density in the upper soil layer decreased along the secondary forest succession, while numerous studies reported higher fine-root mass density at the late-successional stage (Erktan et al. 2016; Demenois et al. 2018b). This successional-specific pattern in fine-root mass density in our study probably resulted from higher stem density at the early-successional stage relative to the middle and late stages (Table S1). However, fine-root length density in the upper soil layer did not significantly differ among different successional stages, largely resulting from higher SRL at the late-successional stage (Fig. 5a). Generally, plants reduce C allocation to pioneer/transport roots and allocate relatively more C to absorptive/fibrous roots in response to high nutrient availability (Wang et al. 2013; Wurzburger and Wright 2015), probably resulting in thinner root diameter and higher proportion of fibrous roots (Data not shown) at the late-successional stages.

Conceptual framework for soil aggregation

A better mechanistic understanding of soil aggregation is quite important to reveal the process of SOC and nutrient cycling. Based on the linear relationship of soil aggregate MWD and SOC in previous studies, several conceptual frameworks had been assumed to explain effects of plant and soil properties on soil aggregation, suggesting that rhizosphere effects on soil aggregation were affected by rhizosphere C inputs (Miller and Jastrow 1990; Jastrow et al. 1998). However, we found the nonlinear relationship between soil aggregate MWD and soil properties with a plateau under high SOC content, indicating that impacts of rhizosphere (inputs of SOC and nutrients) on soil aggregation were stronger at low than high soil fertility. Thus, rhizosphere effects on soil aggregation were more strongly determined by soil fertility, rhizosphere soil volume (represented by fine-root length and very fine root length), and root turnover rate (represented by root N concentration) combined than rhizosphere C inputs (Fig. 8a).

Based on the non-linear correlation of soil aggregate MWD with soil properties, we developed an improved conceptual framework to explain rhizosphere effects on soil aggregation in forest succession, highlighting the roles of soil fertility, root traits (root length density and root N concentration), and forest age in driving soil aggregation. This improved framework separated the forest development into two stages: promoting stage and sustaining stage (Fig. 8b). At the promoting stage when SOC is below the threshold value (approximately 27 mg C g^{-1} dry soil), the promotion of soil aggregation would be driven by rhizosphere effects and SOC accumulation has a stronger effect on soil aggregation in soils with lower SOC. At the sustaining stage when initial SOC exceeds the threshold value, the SOC accumulation through inputs of rhizosphere SOC would not further promote soil aggregation, but the input of high level of rhizosphere SOC would persistently sustain soil aggregate stability.

Conclusions

Roots and their rhizosphere play crucial roles in driving soil aggregation, which affects a wide range of ecosystem functions. In our study, rhizosphere effects on soil aggregation were significantly higher at the early-successional stage of subtropical forest with low soil fertility than those at the late stages. Soil aggregate MWD was non-linearly and positively correlated with soil properties along the secondary forest succession, indicating that impacts of rhizosphere on soil aggregation were stronger at low than high soil fertility. An improved conceptual framework was developed to explain the rhizosphere effects on soil aggregation, highlighting the roles of soil fertility (i.e., SOC and available nutrients), root traits, and forest age in driving soil aggregation. The improved conceptual framework provides new insight into effects of rhizosphere and soil properties in driving soil aggregation, which can help us to reveal the process of SOC accumulation and nutrient cycling in forest ecosystems.

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