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Effects of tea planting age on soil microbial biomass C:N:P stoichiometry and microbial quotient

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Abstract: This study aimed to determine the effect of tea planting age on stoichiometric ratios of microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) and soil microbial quotient (SMQ, expressed as *q*MBC, *q*MBN, and *q*MBP, respectively). A chronological sequence of tea plantations (3, 8, 17, 25, and 34 years) was selected in a small watershed in the Three Gorges Reservoir Area, and a slope farmland was selected as control. The results showed that with the increase of tea plantation age, soil and microbial biomass C, N, P contents, soil C:N and C:P elevated significantly, while soil N:P overall declined; the MBC:P and MBN:P increased first and then decreased, but MBC:N varied insignificantly. The tea plantation age affected SMQ notably. *q*MBC first decreased and then increased following the tea planting age, while *q*MBN and *q*MBP went up in a fluctuating pattern. In this study, *q*MBC positively correlated with soil N:P and microbial biomass C:N:P, but negatively correlated with soil C:N and C:P; on the contrary, *q*MBN and *q*MBP negatively correlated with soil N:P and microbial biomass C:N:P, but positively correlated with soil C:N and C:P. Generally, the variations of soil microbial biomass and SMQ could reflect the soil quality of tea plantations.

Keywords: stoichiometric characteristics; microbes; chronosequence; *Camellia sinensis* L.

As an important component of nutrients turnover and the food chain, soil microbes play vital roles in driving and regulating terrestrial ecosystem processes and key elements cycling like carbon (C), nitrogen (N), and phosphorus (P) (Cui et al. 2018, Zhang et al. 2021, Wang et al. 2022). Microbial biomass carbon (MBC), nitrogen (MBN) and phosphorus (MBP) are crucial constituents of the soil microbial biomass (SMB), and their proportions in corresponding soil elements, namely soil microbial quotient (SMQ, expressed as *q*MBC, *q*MBN, and *q*MBP for microbial quotient C, N, and P, respectively), are the key indicators of soil quality and represent how efficiently soil nutrients being used by microbes (Chen et al. 2021, Yan et al. 2022). SMQ can be considered as an integrative measure of edaphic properties, soil biodiversity, substrate quality and quantity that reflects soil microbe stress adaptability and biomass productivity (Sinsabaugh et al. 2016, Malik et al. 2018). SMQ thus can serve as an early alert warning for microbial status during ecosystem succession induced by environmental stresses or human disturbance (Yan

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et al. 2022). Moreover, due to the vital functions of soil microbes in plant-soil-microbe systems and SMB as a major reservoir of soil available C, N and P, the stoichiometric-coordinated relationship between soil and microbes would be conducive to a thorough comprehension of the nutrient limitation status and revealing the dynamic mechanism of nutrient balance (Zhang et al. 2019, Wang et al. 2022).

Soil microbes are very sensitive to environmental changes, and their biomass C:N:P stoichiometry could variate with climate, biome, soil ecological stoichiometry, land use, vegetation succession, etc. (Zhou and Wang 2016, 2017). It was reported that the climate variables of mean annual temperature and mean annual precipitation substantially regulated SMB (Xu et al. 2013). Soil C:N:P stoichiometry also profoundly impacted the community composition, structure, and biomass of soil microbes (Graham et al. 2021). Land-use types could affect the microbial community composition and abundance by changing the biotic and abiotic factors (Zhang et al. 2020). Changes in site conditions of the soil arising from vegetation succession directly led to variations of the microbial community structure and function (Shao et al. 2019, Zhong et al. 2020), thereby driving different characteristics of microbial biomass C:N:P stoichiometry with the restoration age (Zhang et al. 2018). Zhou and Wang (2016) found that SMB and SMQ increased prominently with the advance of ecosystem succession.

Tea (*Camellia sinensis* L.) is one of the crucial cash crops in numerous developing countries such as India, China, and Kenya. China covered approximately 3.05 million ha of tea cultivation in 2017, accounting for 45.9% of the tea planting area worldwide (Yan et al. 2020). In China, tea plantations are widely distributed in 19 provinces, principally in tropical and subtropical areas with favourable conditions like water, light and heat (Yan et al. 2020). The Three Gorges Reservoir Area (TGRA) is located upstream of the Yangtze River in China. The inherent ecosystem vulnerability and strong anthropogenic disturbances have triggered serious soil erosion in this region, exacerbating the ecological environment and degrading land productivity (Zhang et al. 2020). To reverse this situation, the Chinese government has implemented a series of ecological projects in the last several decades, e.g., the Soil and Water Conservation Project in the Upper Reaches of the Yangtze River, the "Grain for Green" project, and the Ecological Shelter Project of the TGRA (Xu et al. 2020). These projects have generated favourable impacts on vegetation recovery and soil conservation. Due to the implementation of these conservation projects, the small watershed dominated by farmlands has been converted into a mosaic pattern of multiple modes with tea plantations, orchards, forestlands and farmlands (Wang et al. 2016). A key practice in the TGRA was converting wastelands or farmlands to tea plantations or citrus orchards (Xu et al. 2020). In the tea plantation ecosystem, soil physicochemical properties, soil and microbial C:N:P stoichiometry will change considerably with tea planting age due to fertilisation management, tea tree pruning and litter returning to soil as well as the accumulation of root exudates (Wang et al. 2019, 2020). As corroborated in many previous types of research, tea planting age rendered remarkable impacts on soil physicochemical properties, fertility level, relevant microbial biomass and activities (Wang et al. 2018, 2019, 2020). However, up to date, studies concerning soil chemical elements cycling and their stoichiometric changes in tea plantations are quite scarce. The dynamics of soil microbial C:N:P stoichiometry and microbial quotient with tea planting ages, as well as their coordinated relationship, are still unclear. Therefore, we chose a small representative watershed in TGRA as our study area to investigate the quantitative effect of tea plantation age on SMB and SMQ and to further identify the interactive relations between SMQ and soil-microbial C:N:P stoichiometry. Our findings could serve as a valuable reference for soil conservation and ecological function maintenance in tea plantation ecosystems and also help to insight into the evolution mechanism of soil quality in tea plantations.

MATERIAL AND METHODS

Study area and site selection. This work was conducted in Zhangjiachong small watershed (110°56'30''–110°57'45''E, 30°46'50''–30°47'40''N) of Zigui Soil and Water Conservation Station, Zigui County, Hubei Province (Figure 1). It locates in the head area of the TGRA and covers an area of 1.62 km^2 with an altitude ranging from 148 to 530 m a.s.l. Subtropical monsoon climate is prevailing with a mean annual temperature of 16.8 °C. The annual mean precipitation is 1 221 mm, with 70% of which occurring from May to September. The soil developed from granite parent material and had a quartz sandy texture. The vegetation is mainly subtropi-

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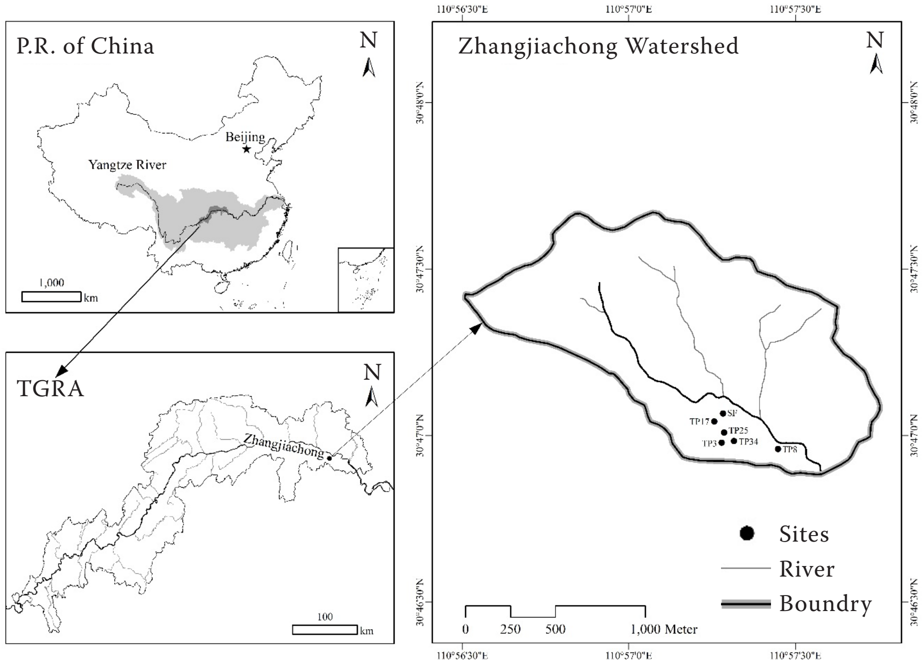

Figure 1. Location of the study area and sampling sites. SF – slope farmland; TP – tea plantation, suffixal number – age since tea was cultivated; TGRA – Three Gorges Reservoir Area

cal evergreen or deciduous broad-leaf and mixed broadleaf-conifer forest, with tea, citrus and chestnut principally distributed in low mountain valleys and semi-alpine areas. "Yihong tea" is the region's main cultivar, and the cultivation ages of these tea plantations are different. The basal and top-dressing fertiliser is applied yearly to all tea plantations with almost unanimous inputs.

This study adopted a space-for-time substitution method to investigate the variations in soil and microbial biomass C, N, and P during tea cultivation. To avoid the potential spatiotemporal mixing effects between the spatial variation of soil properties and the tea planting time, a chronological series of tea plantations (3, 8, 17, 25, and 34 years) cultivated with the identical cultivar (Yihong tea) were selected as the test sites. These tea plantations are distributed in close geomorphic units with similar soil parent material, slope gradient and direction, and fertiliser application. Additionally, a slope farmland of maize was selected as the reference, representing newly cultivated land without planting age.

Soil sampling and analysis. Soil sampling was carried out in August 2020. We randomly demarcated three blocks (15 m × 15 m) within every selected site, each being at least 30 m from the tea plantation edge. Soil cores were collected from the 0–10 cm layer at five locations in an "S"-shaped pattern and were then mixed homogeneously to form a composite sample for each block. We used soil samples from three blocks as replicates to determine the characteristic soil indicators for each selected site. After the stones and roots were manually removed, all samples were sieved through a 2-mm mesh. The sieved samples were then separated into two parts. One part was air-dried under ambient temperature and then sieved through a 0.25-mm mesh to determine soil organic C (SOC), total N (TN) and total P (TP) contents. Another part was stored at 4 °C for measuring microbial biomass C, N, and P (MBC, MBN, and MBP).

SOC was determined with the dichromate oxidation method, TN was measured using the Kjeldahl method, and TP was determined by the molybdenum-antimony resistance colourimetric method after digestion with H_2SO_4 and $HClO_4$ (Zhang et al. 2022). SMB was measured by chloroform fumigation-extraction method (Brookes et al. 1985, Vance et al. 1987, Joergensen 1996), and MBC was determined using an automatic organic carbon analyser (Vario TOC, Elementar, Hanau, Germany), MBN was determined by ultraviolet spectrophotometric colourimetry, MBP was measured by molybdenum-antimony colourimetry with $Na(HCO_3)_2$ extracts. The experimentally-

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derived conversion factors (extractable part of SMB) were 0.45, 0.54, and 0.40 for MBC, MBN and MBP, respectively (Joergensen 1996). In this study, soil C:N was SOC:TN, soil C:P was SOC:TP, and soil N:P was TN:TP.

Statistical analyses. Data were presented as mean ± standard deviation. All statistical analyses were processed with SPSS 24.0 program (SPSS Inc., Chicago, USA). One-way analysis of variance (ANOVA), followed by post hoc multiple comparisons with Fisher's *LSD* (least significant difference) test (α = 0.05), was performed to identify significant differences among treatments. Independent samples *t*-test (α = 0.05) was performed to compare the mean differences between tea plantations and slope farmland. Redundancy analysis (RDA) with CANOCO 5.0 programme (Šmilauer and Lepš 2014) was performed to assess the correlations between SMQ and soil-microbial biomass C:N:P stoichiometry.

RESULTS AND DISCUSSION

Effects of tea planting age on soil SOC, TN and TP contents and stoichiometric ratios. As shown in Figure 2, SOC, TN, and TP contents and their stoichiometric ratios varied among the treatments. SOC content was lowest at SF (CK) and increased significantly with tea planting age (Figure 2A). TN

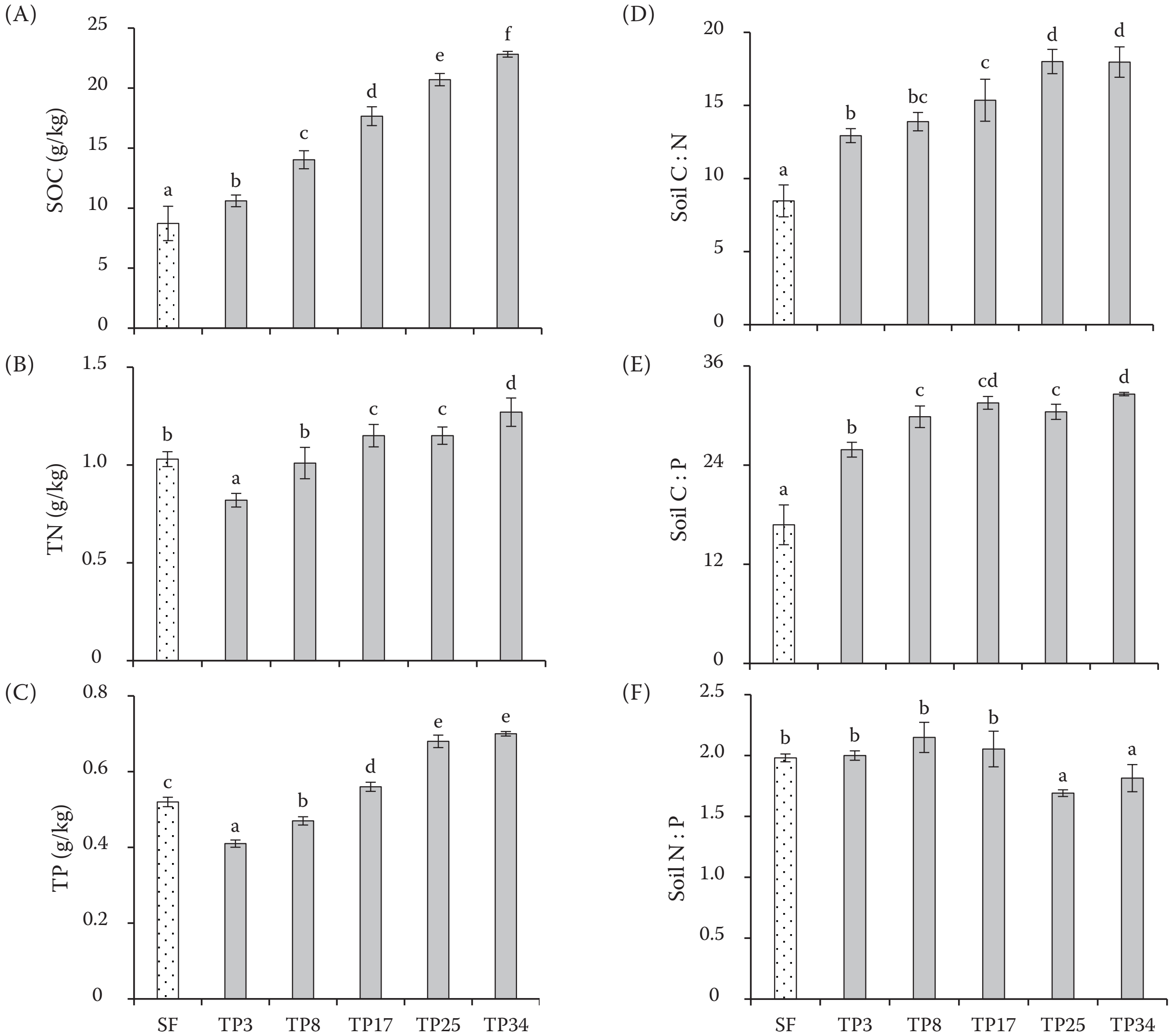

Figure 2. Soil carbon (C), nitrogen (N), phosphorus (P) contents and stoichiometric ratios in tea plantations with different ages (SF – slope farmland; TP – tea plantation; number – age since tea cultivated). Data are means ± standard deviation (n = 3), different letters indicated significant differences among different tea planting ages at 0.05 level. SOC – soil organic carbon; TN – total nitrogen; TP – total phosphorus

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and TP contents displayed similar variation patterns with tea planting age. TN content was lowest at TP3 and highest at TP34 but did not differ significantly between TP8 and SF, as well as between TP17 and TP25 (Figure 2B). TP content was markedly higher in SF than TP3 and TP8 but did not differ notably between TP25 and TP34 (Figure 2C). Tea plantation is a secondary ecosystem greatly disturbed by human activities, and the dynamic variation of soil nutrients following the tea planting age has become the research focus of the tea plantation ecosystem (Zhao et al. 2017). The tea trees are pruned every 1 to 4 years, and their trimmers and litters return to the field and accumulate in the topsoil layer, potentially causing differences in soil physical, chemical and biological properties between the tea plantation and the conventional farmland and the soil properties of different cultivation ages may also be different (Han et al. 2007). In our study, the independent samples *t*-test showed that the mean SOC content for the five chronological tea plantations was 17.16 g/kg, which was prominently greater than that of the slope farmland (8.72 g/kg) and was also higher than the national average level (11.12 g/kg); mean TN and TP contents for the five chronological tea plantations were 1.08 and 0.56 g/kg, respectively, which did not differ significantly from the slope farmland (1.03 and 0.52 g/kg) and also approached the national average level (1.06 and 0.65 g/kg) (He et al. 2020).

The soil C:N and C:P are commonly used to evaluate the availability of soil N and P. Generally, the higher the soil C:N and C:P are, the lower the soil available N and P (Shu et al. 2018). In this study, mean soil C:N and C:P in tea plantations were 15.68 and 30.09, respectively, both higher than the slope farmland and the national average level (Hu et al. 2014). Besides, soil C:N and C:P increased dramatically following the tea planting age (Figure 2D, E), indicating that the accumulation rates of soil available N and P in tea plantations were lower than SOC during the cultivation process, and the tea growth may be limited by N and P. Soil N:P is a predictor of nutrient limitation type. It is generally considered that plant growth is limited by N when soil N:P < 14, limited by P when soil N:P > 16, and co-limited by N and P when 14 < soil N:P < 16 (He et al. 2020). Soil N:P in this study ranged from 1.69 to 2.15, lower than the national average soil N:P (5.2) (Guo et al. 2019), implying that tea growth was predominately limited by N. Furthermore, soil N:P generally declined with the tea planting age's progress, but neither markedly between TP3, TP8 and TP17 nor TP25 and TP34 (Figure 2F). Independent samples *t*-test identified no significant difference in soil N:P between tea plantations and slope farmland.

Effects of tea planting age on soil microbial biomass C, N and P and stoichiometric ratios. In this study, soil MBC ranged from 461 to 760 mg/kg, MBN 41 to 88 mg/kg, and MBP 3 to 10 mg/kg (Table 1). Tea planting age significantly affected soil MBC, MBN, and MBP. Overall, soil MBC, MBN, and MBP in tea plantations increased in the cultivation process and TP34 held a prominent high value. However, MBC did not differ observably before 34 years of cultivation, MBN was not significantly different between TP8 and TP17, and MBP was not significantly different

Table 1. Soil microbial biomass carbon (C), nitrogen (N), phosphorus (P) contents and their stoichiometric ratios (mean ± standard deviation)

Sampling site	Soi microbial biomass C, N, P (mg/kg)			Microbial biomass stoichiometry		
	MBC	MBN	MBP	MBC:N	MBC:P	MBN:P
SF	547.00 ± 43.76^{a}	51.15 ± 2.71^{b}	3.06 ± 0.09^{a}	10.74 ± 1.34^{a}	179.15 ± 18.01^{a}	16.74 ± 1.11^{c}
TP3	461.91 ± 42.11^{a}	41.82 ± 6.63^{a}	3.55 ± 0.54^{a}	11.19 ± 1.62^{a}	133.58 ± 34.48^{ab}	12.12 ± 3.46^{ab}
TP8	534.85 ± 57.90^{a}	53.87 ± 2.06^{b}	3.60 ± 0.49^{a}	9.94 ± 1.16^{a}	152.70 ± 41.75^{a}	15.19 ± 2.33^{bc}
TP17	569.79 ± 60.30^{a}	53.67 ± 4.44^{b}	6.00 ± 0.90^{b}	10.64 ± 1.09^{a}	96.00 ± 14.62^{bc}	9.00 ± 0.60^{a}
TP25	516.61 ± 105.27^{a}	62.22 ± 4.71^{c}	5.64 ± 0.32^{b}	8.25 ± 1.06^{a}	92.24 ± 22.70^{bc}	11.07 ± 1.25^{a}
TP34	759.72 ± 104.39^{b}	87.85 ± 4.49^{d}	9.91 ± 0.43^{c}	8.68 ± 1.40^{a}	76.60 ± 9.12^{c}	8.87 ± 0.40^{a}

SF – slope farmland; TP – tea plantation; number – tea planting age in years. Different lowercase letters in the same column indicated a significant difference between tea planting ages at 0.05. MBC – microbial biomass carbon; MBN – microbial biomass nitrogen; MBP – microbial biomass phosphorus

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between TP17 and TP25. Additionally, the independent samples *t*-test did not detect a significant difference in mean SMB between tea plantations and the slope farmland.

The stoichiometric ratio of SMB is an important index to evaluate the change in microbial community structure (Li et al. 2019). In this study, tea planting age had significant effects on MBC:P and MBN:P but no significant effects on MBC:N; MBC:P and MBN:P increased first and then decreased with tea planting ages (Table 1). Previous studies manifested that the microbial community was dominated by bacteria when MBC:N between 3 and 6 while by fungi between 7 and 12 (Jia et al. 2005); the response of the bacterial community to the tea planting age is more sensitive than that of fungal community, and soil microbial community of tea plantation tended to convert from "bacterial type" to "fungal type" with the increase of cultivation age (Yao et al. 2020). The MBC:N varied from 8.25 to 11.19 in this study (Table 1) with a mean of 9.74, indicating that soil microbes in the tea plantation of this study area were mainly fungi and were limited by N to a certain extent, which was consistent with the abovementioned analysis. The MBC:P was highest for SF and an evident decline was induced by tea cultivation, in particular after 17 years. In tea plantations, MBC:P tended first to increase and then decrease, was highest for TP8 but did not differ significantly from TP3 and lowest for TP34 but did not differ significantly between TP17, TP25 and TP34. The MBN:P was also remarkably higher for SF than those in tea plantations and fluctuated down as the tea cultivation age increased with the peak point at TP8 and valley point at TP34 but did not differ significantly after 17 years of cultivation. Independent samples *t*-test showed that soil MBC:P and MBN:P in tea plantations were significantly lower than in slope farmland, decreasing by 38.5% and 32.8%, respectively. Although this study analysed the characteristics of soil microbial biomass C:N:P in different aged tea plantations, it is still necessary to deeply explore the coupling relationship between soil microbial biomass C:N:P and its community structure to clarify the driving mechanism of variations in soil microbial stoichiometry.

Soil microbial quotient and its relationship with soil-microbe C:N:P stoichiometry. Figure 3 illustrates the variations of soil microbial quotient (SMQ), including *q*MBC (MBC:SOC), *q*MBN (MBN:TN), and *q*MBP (MBP:TP), with the tea plantation age. *q*MBC varied from 2.5% to 4.4% (mean 3.4%) for different tea plantations, which was significantly lower than the slope farmland (6.4%) but higher than the national average level (1.9%) (Xu et al. 2014). *q*MBN varied from 4.6% to 7.0% (mean 5.5%), with TP34 significantly higher than the other tea plantations.

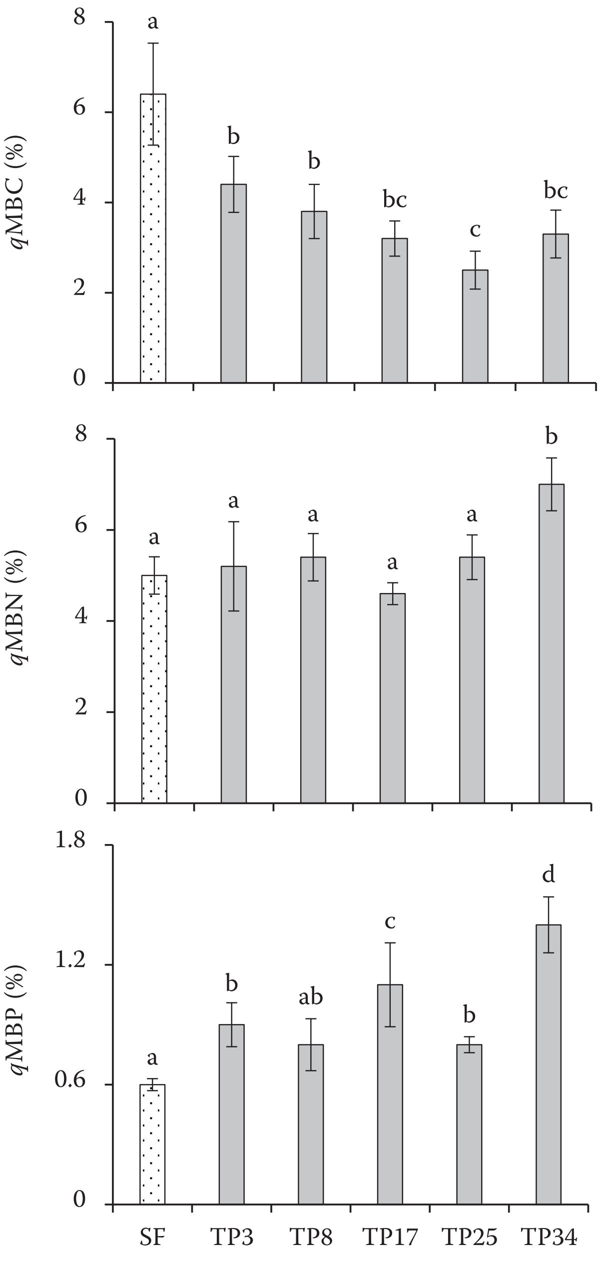

Figure 3. Effects of tea planting age on soil microbial quotient. *q*MBC – quotients of microbial biomass carbon; *q*MBN – quotients of microbial biomass nitrogen; *q*MBP– quotients of microbial biomass phosphorus; SF – slope farmland; TP – tea plantation; number – tea planting age in years. Data are means ± standard deviation (n = 3), different letters indicate significant differences across the tea planting ages ($P < 0.05$)

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Moreover, *q*MBN did not differ significantly from the slope farmland but was higher than the national average level (3.4%) (Xu et al. 2014), indicating that soil microbial activity for N-cycling in the tea plantation of the study area was much higher, while the stability of soil N pool was poor with a relatively lower N content. *q*MBP was 0.8~1.4% (mean 1.0%), significantly higher than the slope farmland. *q*MBC dramatically decreased with the tea plantation age, especially after 17 years of tea cultivation. Nonetheless, fluctuated upward trends during tea cultivation were observed by both *q*MBN and *q*MBP.

Previous research exhibited that the variation degree and direction of SMQ were principally affected by the availability of soil nutrients and the composition and structure of the heterotrophic microbial community (Zhou and Wang 2016). Xu et al. (2014) detected a significantly negative relationship between *q*MBC and soil C:N. Zhou and Wang (2015) also reported that *q*MBC was negatively correlated with soil C:N:P, primarily because soil microbes' growth and metabolism required the coordinated supply of soil C, N, and P. In this study, the redundancy analysis (RDA) with soil and microbial biomass C:N:P as explanatory variables and SMQ as response variable was conducted, and results showed that the first and second axis explained 75.9% and 22.9% of the variability of SMQ, respectively (Figure 4). *q*MBC positively correlated with soil N:P and microbial biomass C:N:P, whereas it negatively correlated with soil C:N and C:P; on the contrary, *q*MBN and *q*MBP negatively correlated with soil N:P and microbial biomass C:N:P, but positively correlated with soil C:N and C:P (Figure 4). The results agreed with Zhou and Wang (2015), who found that the equilibrium between soil-microbial C:N:P and microbial element utilisation had certain impacts on the ecosystem's C, N, and P cycles. Under high soil C:N and C:P conditions, microbial growth would be limited by N or P, leading to a decline in *q*MBC. Therefore, the decrease in SMQ in this study may be associated with the N limitation in this area. Hence, adding N or N-P compound elements may improve the soil quality and the growth of the tea grove. In general, the variation of soil microbial biomass and microbial quotient could directly or indirectly reflect the soil quality of tea plantations. Future study focus could further explore the seasonal dynamics of nutrient elements stoichiometry in tea plantation ecosystems and the influencing mechanism.

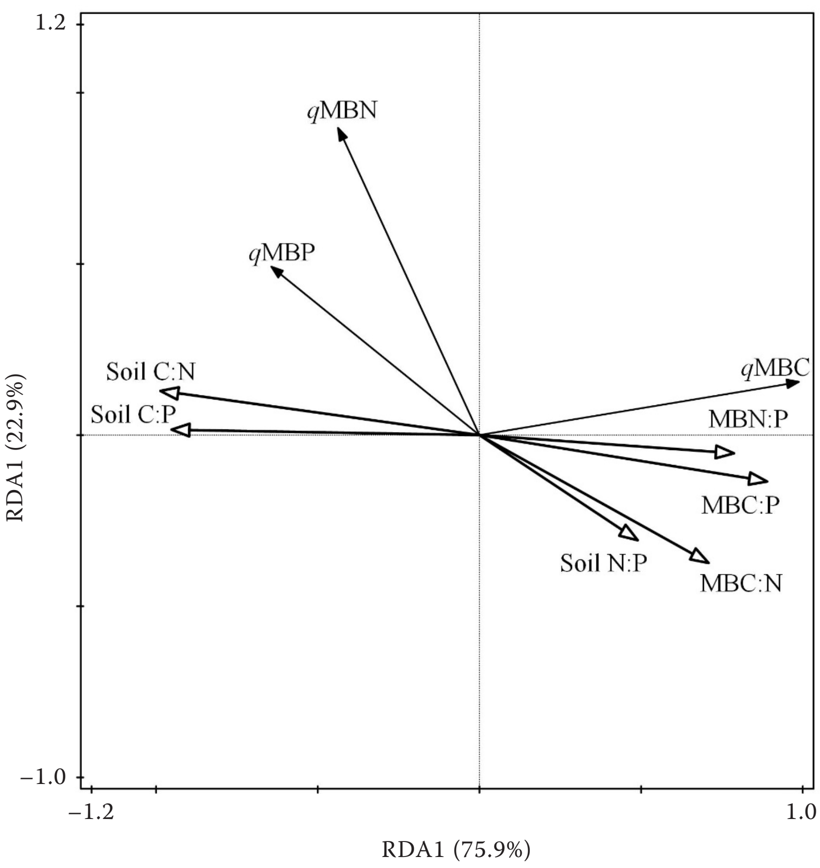

Figure 4. Ordination bi-plot by redundancy analysis (RDA) of soil microbial quotient (SMQ) and soil-microbial C:N:P stoichiometry. The first axis explains 75.9%, and both axes together explain 98.8% of the variation of SMQ. The length and direction of the vectors indicate the strength of the vector effect and the correlation between the vectors, respectively. A long vector for a particular variable indicates that it greatly affects the analysis results, while the opposite is true for a short vector. An angle of < 90° between the vectors indicates a positive correlation. An angle of > 90° between two vectors indicates a negative correlation; MBC – microbial biomass carbon; MBN – microbial biomass nitrogen; MBP – microbial biomass phosphorus; qMBC – quotients of microbial biomass carbon; qMBN – quotients of microbial biomass nitrogen; qMBP– quotients of microbial biomass phosphorus

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