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Effects of Forest Types and Environmental Factors on Soil Microbial Biomass in a Coastal Sand Dune of Subtropical China

GAO Wei[1,2,3,4,#], LIN Meimei[5], HUANG Yongrong[3,#], HUANG Shide[3,#], YE Gongfu[3], HUANG Zhiqun[1,2,*]

1. Institute of Geography, Fujian Normal University, Fuzhou 350007, China;
2. Ministry of Education Key Laboratory of Humid Subtropical Eco–Geographical Process, Fuzhou 350007, China;
3. Research Institute of Ecological Environment, Fujian Academy of Forestry, Fuzhou 350012, China;
4. Qingdao Technical College, Qingdao 266520, Shandong, China;
5. Department of Geology and Geography, Georgia Southern University, Savannah, GA 31419, USA

Abstract: Coastal sand dune ecosystems generally have infertile soil with low water-holding capacity and high salinity. However, many plant species have adapted to the harsh sand environment along the southeastern coast of China. Studying the microbial biomass in such an ecosystem can improve our understanding of the roles that microbes play in soil fertility and nutrient cycling. We investigated the differences in soil microbial biomass carbon (MBC) and nitrogen (MBN) contents and their seasonal dynamics in five forest types (a secondary forest and plantations of *Casuarinas*, *Pine*, *Acacia*, and *Eucalyptus*). The results indicated that the seasonal variations of soil MBC and MBN contents in all five forest stands were higher in spring and winter, but lower in summer and autumn. The MBC content was lower in the *Casuarinas* plantation than in the other plantations in the same soil layer. However, no significant differences were observed in MBN contents among the different forest types. The MBC and MBN concentrations were positively correlated with soil moisture, but negatively correlated with soil temperature. The MBC and MBN contents also decreased with increasing soil depth. Across all soil layers, secondary forest had the highest MBC and MBN concentrations. Our study also showed that the MBC and MBN contents were positively affected by total soil carbon (TC), pH, and litter N content, but were negatively impacted by soil bulk density and litter C content. Moreover, the MBN content was positively correlated with root N content. In summary, environmental factors and the differences in litter and fine roots, soil nutrient contents, as well as the soil physical and chemical properties caused by different tree species collectively affected the concentrations of the soil MBC and MBN.

Key words: coastal sand dunes; soil microbial biomass carbon; soil microbial biomass nitrogen; secondary forest; *Pinus elliottii*; *Casuarina equisetifolia*; *Acacia crassicarpa*; *Eucalyptus urophylla* × *E.grandis* plantations

1 Introduction

Soil microorganisms play important roles in soil carbon (C) and nitrogen (N) cycling and mineralization, and they are highly sensitive to changes in soil conditions (Nannipieri et al., 2003; Chodak et al., 2015; Zhu et al., 2017), so they are considered to be important indicators of soil quality and environmental changes (Karlen et al., 1997; Li et al., 2014; Mganga et al., 2015). Soil microbial biomass represents the number of corresponding microorganisms involved in regulating energy and nutrient circulation, and organic matter

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First author: GAO Wei, E-mail: gao01271@163.com; HUANG Yongrong, E-mail: yongrong1224@126.com; HUANG Shide, E-mail: hsd9876@126.com
Contribute equally to this work.

***Corresponding author:** HUANG Zhiqun, E-mail: zhiqunhuang@hotmail.com

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transformation in the soil, so it is an important source of soil active nutrients for plant growth (Xu et al., 2009). Soil microbial biomass carbon (MBC) and nitrogen (MBN) are indispensable active components in C and N cycling in forest ecosystems (Wang et al., 2016a). The study of seasonal fluctuations of soil microbial biomass and their regulating mechanisms can uncover the changing mechanism of soil fertility and its role in C and N cycling in a regional forest (Arancon et al., 2006).

The metabolic processes of soil microorganisms are affected by the comprehensive characteristics of plant community, soil temperature, soil moisture, soil pH, soil foundation fertility, and substrate (Wang et al., 2016a; Camenzind et al., 2018; Liu et al., 2019). Different vegetation covers have different effects on the stability, turnover rates, and availability of soil C and N pools due to the differences in their leaf and root litter inputs (Bréchet et al., 2009), resulting in temporal and spatial variations of soil microorganism responses to vegetation and environmental factors across forest types. For example, previous studies have found significant differences in soil mineral N content between different forest types, which may affect the physiological and metabolic processes of the associated soil microorganisms (Templer and Dawson, 2004; Mueller and Eissenstat, 2012). Wang et al. (2016a) observed a significant correlation between soil total organic C (SOC) and soil microbial biomass, and found that the conversion of tree species changed the quality of the substrate and the nutrient input and output of the ecosystem, thereby affecting the metabolism of the soil microorganisms. In addition, seasonal fluctuations in soil temperature and soil moisture can affect soil N mineralization and cycling (Parker and Schimel, 2011), thus exerting a strong influence on the seasonal variations of soil microbial community composition and biomass (Yang et al., 2009; Zhang et al., 2013; Zhou et al., 2013; Li et al., 2014). This is especially true for soil moisture, due to its important regulating roles in soil substrate diffusion and the water content of microbial cells (Harris, 1980; Manzoni et al., 2012); and its availability is considered to be the primary driving factor in the dynamics of microbial rRNA (Bell et al., 2008; Clark et al., 2009), lipid community structure (Steinberger et al., 1999; Bachar et al., 2010), and microbial function (Bell et al., 2008; Cregger et al., 2012).

Sand dunes are common on the southeastern coast of China, where the infertile soil has low water-holding capacity and high salinity. *Casuarina equisetifolia* L. is an actinorhizal N-fixing species with good wind and salt resistance, and it is often used for the establishment of protection forests in coastal sandy areas. *C. equisetifolia* plantations in China cover approximately 3×10^5 ha and play an important role in local environment improvement and ecological security maintenance efforts (Xiao et al., 2009). However, there are problems with adequate regeneration and productivity declines due to monoculture plantings, which has weakened their ecological benefits. Species from the *Acacia*, *Eucalyptus*, and *Pinus* genera have been introduced to increase species diversity and improve the resistance of coastal protection forests since the 1960s. They are now well established and are important components of many coastal protection forests. A typical secondary forest is dominated by *Litsea glutinosa* (Lour.) C.B. Rob., a native species with a patchy distribution in coastal sandy areas, as a result of long-term protection following various anthropogenic activities (e.g., deforestation or reforestation) or natural disturbances (e.g., typhoons or sand burial).

In coastal sand dunes, the knowledge of environmental controls and variations in their soil microbial biomass across forest types in coastal sandy areas will help to guide afforestation species selection and ecosystem management. Therefore, it is important to understand how the differences in species composition and the seasonal fluctuations of soil temperature and moisture can affect the dynamics of soil microbial biomass, and what roles soil microbial biomass play in soil C and N cycling. The goals of this study were to: 1) Investigate the soil MBC and MBN contents and their seasonal dynamics across five forest types (a secondary forest of *L. glutinosa* and plantations of *Casuarinas*, *Pine*, *Acacia*, and *Eucalyptus*) in the southeastern coast of Fujian province; 2) Identify factors that correlate with soil MBC and MBN contents, including litterfall, litter C and N contents, fine root biomass, and root C and N contents; and 3) Measure the physical and chemical properties of the soils, including soil temperature and soil moisture; and evaluate their effects on the soil C and N cycling across the different forest types.

2 Materials and methods

2.1 Study site

The study was conducted at Chishan Forestry Center of Dongshan County (23°38′N, 117°24′E) in southeastern Fujian Province, China (Fig. 1). The climate of this region is of the subtropical maritime monsoon type with a mean annual temperature ranging from 13.1 ℃ in January to 27.3 ℃ in July. Mean annual precipitation and evapotranspiration are 1104 mm and 2028 mm, respectively. The Rainy season is from May to September when 61% of the rainfall occurs, while the dry season is usually from November to the next February (Fig. 2). The soil is a typical udipsamment with low nutrient content and a thickness of 80−100 cm.

Five forest stands, including a secondary forest and plantations of *Casuarina*, *Pine*, *Acacia*, and *Eucalyptus,* were selected as experimental groups in December 2014. These stands have similar elevations and soil types, each with an average slope of less than 10°. The detailed site characteristics and topsoil properties of the five forest stands are shown in Table 1.

The secondary forest is composed of native vegetation resulting from secondary succession with distinct tree, shrub,

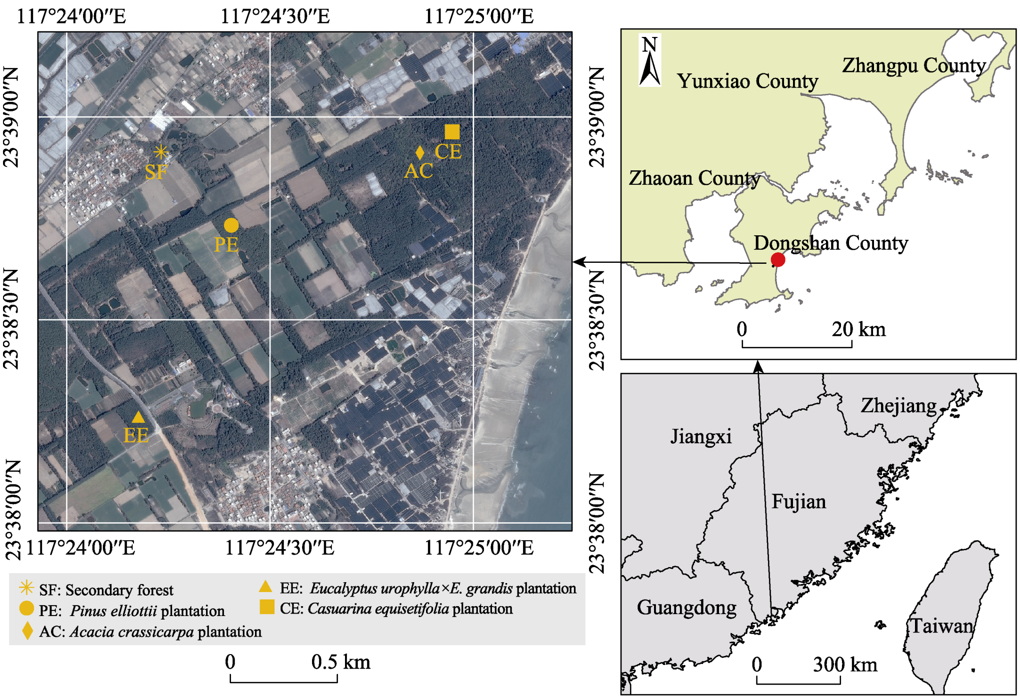

Fig. 1 The location of the study area in Fujian Province, Southern China

Table 1 Detailed site characteristics and topsoil properties of the five forest stands on the southeastern coast of China

Variable	*Eucalyptus*	*Pine*	*Acacia*	*Casuarinas*	Secondary forest
Stand age (yr)	11	21	22	22	＞50
Forest average DBH (cm)	15.60	21.00	21.10	17.90	9.70
Mean tree height (m)	11.40	13.90	12.50	14.90	5.60
Tree density (ind ha^{-1})	1300	1500	950	1600	1400
Litterfall (mg ha^{-1} yr^{-1})	12.32ab	12.99a	10.06b	10.08b	12.67a
Litter C (g kg^{-1})	473.40bc	499.70ab	513.60a	497.70ab	495.80c
Litter N (g kg^{-1})	9.21c	6.58d	15.10b	8.83c	16.41a
Litter C:N ratio	51.55b	77.12a	34.07c	56.43b	28.05c
Litter cellulose (g kg^{-1})	114.80d	217.90b	172.10c	275.20a	157.40c
Litter lignin (g kg^{-1})	179.90e	365.90b	449.30a	227.50d	300.60c
Litter lignin: N ratio	19.60c	56.50a	29.80b	25.80b	18.30c
Root Biomass (mg ha^{-1})	2.16ab	1.05b	1.84ab	3.04a	2.77a
Root C (g kg^{-1})	376.40ab	365.10b	304.80c	412.70a	378.00ab
Root N (g kg^{-1})	5.70c	6.30c	10.50b	19.70a	19.20a
Root C: N ratio	69.90a	63.50a	29.00b	20.90b	19.80b
Bulk density (g cm^{-3})	1.36b	1.23cd	1.28bc	1.45a	1.17d
pH	5.00b	4.65c	4.73c	4.71c	6.57a
Total C (g kg^{-1})	6.65b	4.33b	4.08b	3.17b	12.71a
Total N (g kg^{-1})	0.54b	0.53bc	0.53bc	0.27c	1.26a
Soil C: N ratio	11.97a	8.12b	7.70b	11.58a	9.91ab
Soil NH_4^+-N concentration (μg g^{-1})	3.52c	3.78c	6.27b	4.38c	7.00a
Soil NO_3^--N concentration (μg g^{-1})	0.20b	1.14b	1.47b	0.87b	18.20a
Total inorganic N (μg g^{-1})	2.30b	3.90b	6.50b	3.10b	25.80a
Soil DOC (mg kg^{-1})	56.20b	40.40b	42.20b	53.30b	84.80a
Soil DON (mg kg^{-1})	2.80bc	3.30bc	6.80b	0.60c	22.5a0
Available P (mg kg^{-1})	0.57b	0.61b	1.26b	0.89b	20.49a
Exchangeable Mg (mg kg^{-1})	0.28b	0.33b	0.26b	0.32b	0.71a

Note: Data are the averages of the replicate plots taken from each forest stand; different letters in the same row represent significant differences at the 0.05 level, and the same below.

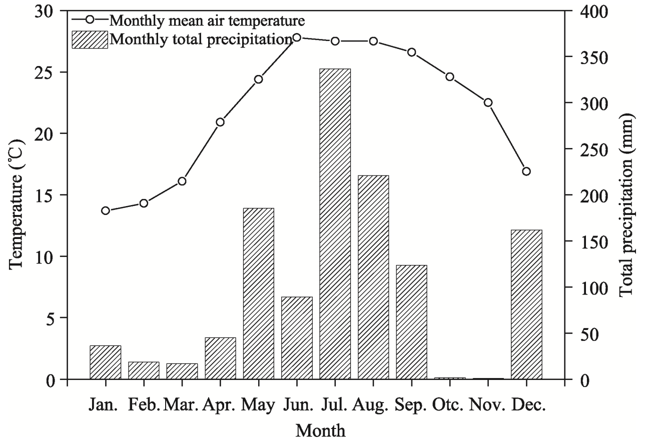

Fig. 2 Monthly cumulative precipitation and monthly mean air temperature in 2015

and herbaceous layers, which regenerates naturally and has been afforded long term protection by local people. The age of the secondary forest is more than 50 years, and the dominant species in the canopy are *L. glutinosa* and *Celtis sinensis* Willd. The shrub layer is predominantly *Glochidion eriocarpum*, *Litsea rotundifolia*, *Bridelia tomentosa,* and *Anodendron affine* (Hook. et Arn.) Druce, and the main herb species are *Ophiopogon bodinieri* and *Arthraxon hispidus* var. hispidus. Both *Casuarinas* and *Acacia* plantations were established in 1992 with main tree species of *C. equisetifolia* and *Acacia crassicarpa,* respectively. The pine plantation was planted with *Pinus elliottii* Engelm. and slash pine in 1993. The *Eucalyptus* plantation was established in 2004 with *Eucalyptus urophylla* × *E.grandis* crosses; the previous species on this site was *P. elliottii*, which was planted in 1976. The canopy densities of the different plantations are greater than 0.7 with few shrubs and grasses in the understory (Gao et al., 2018).

2.2 Experimental design and measurement

In each of the five forest stands, four 20 m × 20 m plots were established with a 10 m buffer between each plot. In July 2015, ten soil cores (1.0 m length × 5 cm diameter) were collected along the diagonal of each plot from the soil surface to a 100-cm depth. Fine roots (< 2 mm diameter) were washed out and the remaining fine-root biomass was estimated following Yang et al. (2004).

Five litter traps (1 m × 1 m) with 1 mm nylon mesh were randomly arranged 0.3 m above the forest floor in each plot for litter collection. From March 2015 to February 2016, litter was collected monthly for determining annual litterfall.

Ten soil pits along the diagonal of each plot were used to collect soil at both 0–10 cm (topsoil) and 10–20 cm (subsoil) depths in April (spring), July (summer), September (autumn), and November (winter) 2015. A 500 g sample was collected from each layer of every plot, and 300 g portions of each were air-dried, ground, and sieved through a 2-mm sieve for microbial biomass analysis. The remaining soil was ground and sieved through a 0.149-mm sieve for total soil carbon (TC) and total N (TN) analysis. Soil bulk density in each layer was calculated using intact soil cores (100 cm^3). Soil temperature was obtained using an instantaneous digital thermometer (AM-11T, Avalon company, USA), and soil moisture was determined using an oven-drying method.

Soil microbial biomass C (MBC) and N (MBN) were analyzed following the chloroform fumigation-extraction method (Brookes et al., 1985). Briefly, soils were fumigated for 24 h with $CHCl_3$, after which the fumigant was removed, the soils were extracted with 0.5 M K_2SO_4, and their C and N concentrations were estimated based on the differences between the chloroform fumigated and unfumigated soil divided by correction factors of 0.45 (Joergensen and Müller, 1996a) and 0.54 (Joergensen and Müller, 1996b), respectively. Specifically, the organic C concentration in the extracted solution was measured using a TOC-VCPH/CPN Analyzer (Shimadzu, Japan) and the organic N content was measured using a continuous flow analyzer (SAN+ +, Skalar Analytical B.V.). Soil TC and TN were determined using an elemental analyzer (Vario EL III, Elementar Analysensysteme GmbH, Hanau, Germany). Soil pH was measured with a pH meter.

2.3 Data analysis

Data from each of the four plots were averaged for further analysis. To test the significances of differences in soil C and N contents, soil pH, soil bulk density, as well as the soil MBC and MBN contents between different forest types, we used one-way analysis of variance (ANOVA) with Duncan's multiple comparison method at a significance level of 0.05. We also used Pearson correlation analysis to determine how annual litterfall, litter C and N content, fine root biomass, root C and N content, soil temperature, and soil moisture correlated with the soil MBC and MBN contents. All statistical analyses were performed using the PASW Statistics 18.0 for Windows.

3 Results

3.1 Environmental variables

The soil pH, soil C and N content, and soil C: N ratio under different forests all decreased with the increase of soil depth (Table 2), whereas the soil bulk density increased with soil depth. In the topsoil, the soil pH values of plantations were significantly lower than that of the secondary forest, and no significant difference was found in soil pH values among *Pine*, *Acacia*, and *Casuarinas*, which were all significantly lower than that of *Eucalyptus*. The soil bulk density of *Casuarinas* was significantly higher than those of the other forests, followed by *Eucalyptus* and *Acacia*. However, the soil bulk density of *Pine* and secondary forest were much lower than those of the other forests. On average, the soil C and N contents of secondary forest were significantly higher than those of the plantations, the soil N content of *Eucalyptus* was significantly higher than that of *Casuarinas*, and the soil C: N ratios of *Eucalyptus* and *Casuarinas* were significantly higher than those of the other forests.

In the subsoil, the soil pH and soil C and N concentrations in the secondary forest were all higher than those of the plantations, whereas the soil bulk density was lower than those of the plantations. No significant differences were found in soil pH, soil C content, or soil bulk density among the different plantations. In terms of soil N content, there was no significant difference among *Eucalyptus*, *Pine*, and *Acacia* plantations, which were each significantly higher than that of *Casuarinas*, and no significant difference was observed in the soil C: N ratio among the different forests.

Table 2 Soil pH, soil bulk density, soil C and N content, and soil C: N ratio for the different forests (*N*=4)

Soil depth (cm)	Forest types	Soil pH	Bulk density (g cm^{-3})	Soil C content (g kg^{-1})	Soil N content (g kg^{-1})	Soil C: N
0–10	*Eucalyptus*	5.00±0.08b	1.36±0.04b	6.65±2.67b	0.54±0.09b	11.97±2.91a
	Pine	4.65±0.13c	1.23±0.06cd	4.33±1.21b	0.53±0.04bc	8.12±1.80b
	Acacia	4.73±0.12c	1.28±0.10bc	4.08±0.35b	0.53±0.05bc	7.7±0.08b
	Casuarinas	4.71±0.08c	1.45±0.04a	3.17±0.69b	0.27±0.05c	11.58±1.08a
	Secondary forest	6.57±0.22a	1.17±0.04d	12.71±4.94a	1.26±0.34a	9.91±1.23ab
10–20	*Eucalyptus*	4.71±0.18b	1.47±0.04a	1.85±0.34b	0.31±0.07b	6.16±0.91a
	Pine	4.72±0.19b	1.43±0.02a	1.96±0.51b	0.31±0.02b	6.32±1.50a
	Acacia	4.76±0.09b	1.39±0.09a	1.68±0.13b	0.31±0.03b	5.46±0.30a
	Casuarinas	4.92±0.05b	1.47±0.04a	1.25±0.22b	0.14±0.02c	9.27±1.26a
	Secondary forest	6.50±0.69a	1.31±0.02b	4.57±0.93a	0.54±0.09a	8.44±1.15a

The temperatures of topsoil and subsoil were both higher in summer and autumn and lower in spring and winter, which is consistent with the general rule (Fig. 3a and 3b). The water contents in both topsoil and subsoil under different forests showed apparent seasonal variations, and were always higher for a given forest type in winter and spring but lower in summer and autumn (Fig. 3c and 3d). In the topsoil, the soil water contents of the five forests in different seasons were all higher in secondary forest and lower in *Casuarinas*. In the subsoil, the soil water content in winter was higher in *Eucalyptus*, but lower in *Pine* and *Casuarinas*, and no significant differences were found in spring, summer

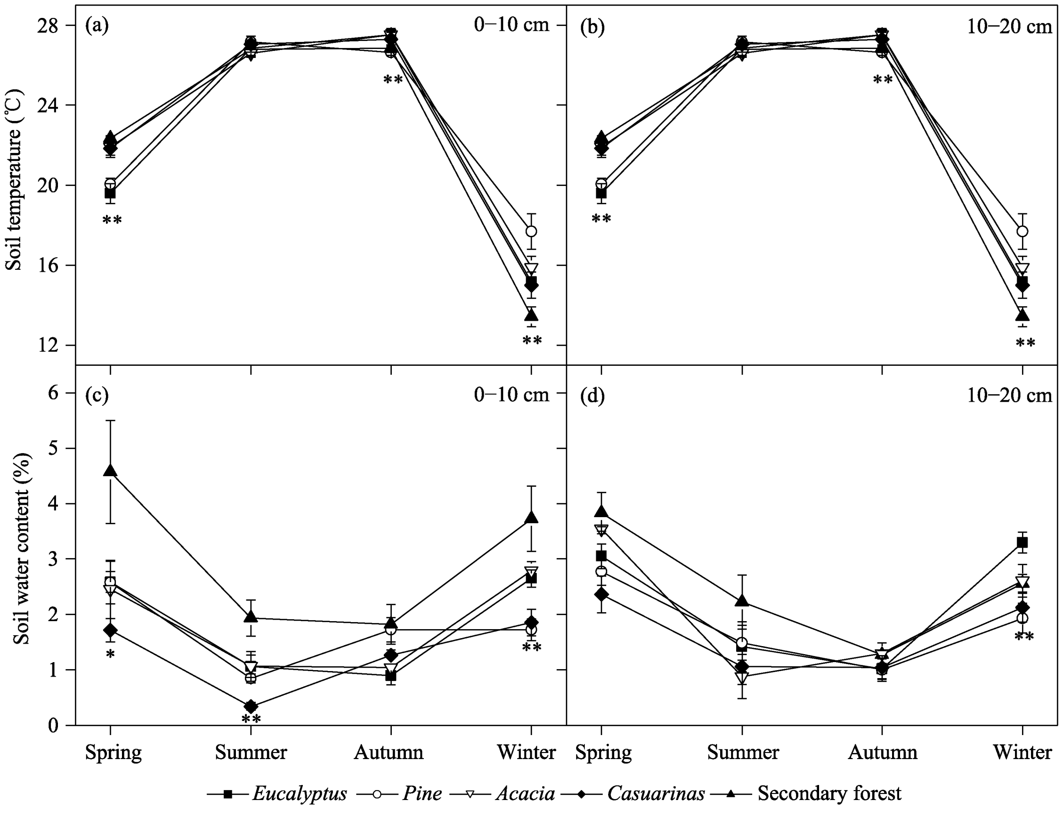

Fig. 3 Seasonal variations of soil temperature and soil water content under different forest types

Note: * significant difference at $P<0.05$; ** significant difference at $P<0.01$.

and autumn among the different forests.

3.2 Seasonal variations of MBC and MBN

No significant difference was found in the seasonal variations of MBC content in the topsoil of *Pine* and *Casuarinas* plantations or in the subsoil of *Acacia* plantation, except that the MBC contents under different forests varied greatly among the different seasons (Fig. 4), being higher in spring or winter and lower in summer or autumn. The peak values of MBC content vary with forest type, which were 189.8, 101.6, 132.6, 58.5, and 536.1 mg kg^{-1} in the topsoil and 128.3, 122.3, 55.4, 34, and 299 mg kg^{-1} in the subsoil of *Eucalyptus*, *Pine*, *Acacia*, *Casuarinas*, and secondary forest, respectively.

The MBN content of different forests showed obvious seasonal variations, except for *Eucalyptus* (Fig. 4), which were higher in spring or winter and lower in summer or autumn. The peak values of MBN content were 12.7, 12.2, 19.9, 15.3, and 60.7 mg kg^{-1} in the topsoil and 17.6, 9.6, 13.9, 11.8, and 60.5 mg kg^{-1} in the subsoil of *Eucalyptus*, *Pine*, *Acacia*, *Casuarinas*, and secondary forest, respectively.

3.3 MBC and MBN under different forests

The annual mean MBC and MBN contents under different forests decreased with the increase of soil depth (Fig. 5). The

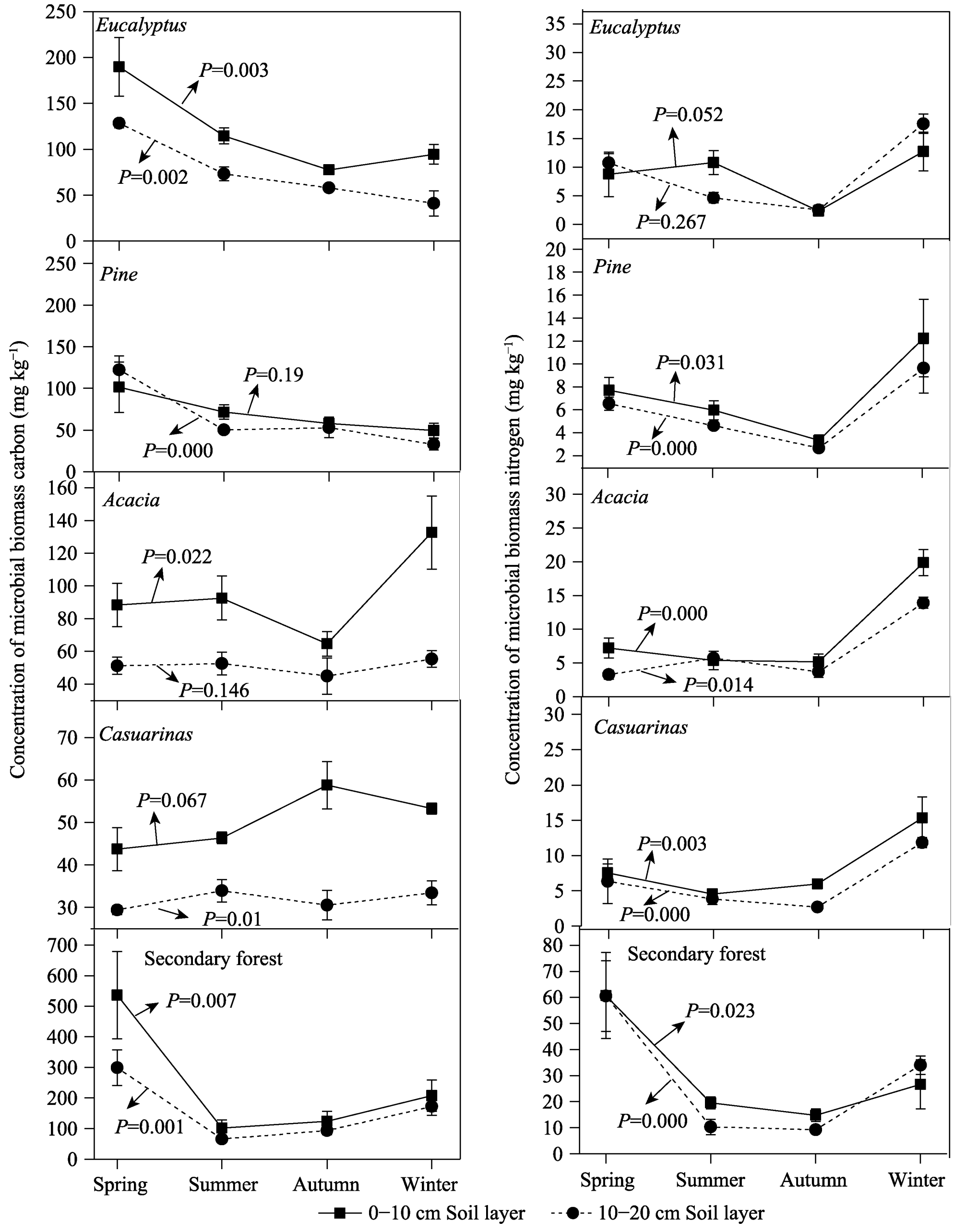

Fig. 4 Seasonal variations of MBC and MBN under different forests

mean MBC contents in *Eucalyptus*, *Acacia*, and *Casuarinas* differed significantly between topsoil and subsoil, but no significant differences were found in *Pine* and secondary forest between the two soil layers. The mean MBC content of secondary forest was significantly higher than those of the plantations in the same soil layer, and the mean MBC contents both in topsoil and subsoil of *Eucalyptus*, and in the subsoil of *Pine* were all significantly higher than the corresponding values of *Casuarinas*. No significant difference was found among the other plantations. The mean MBN contents differed significantly between topsoil and subsoil in *Acacia*, and no significant differences were found between the two soil layers under the other forests. The mean soil MBN content of secondary forest was significantly higher than those of the plantations in the same soil layer, and no significant difference was found in MBN content among the plantations in the same layer.

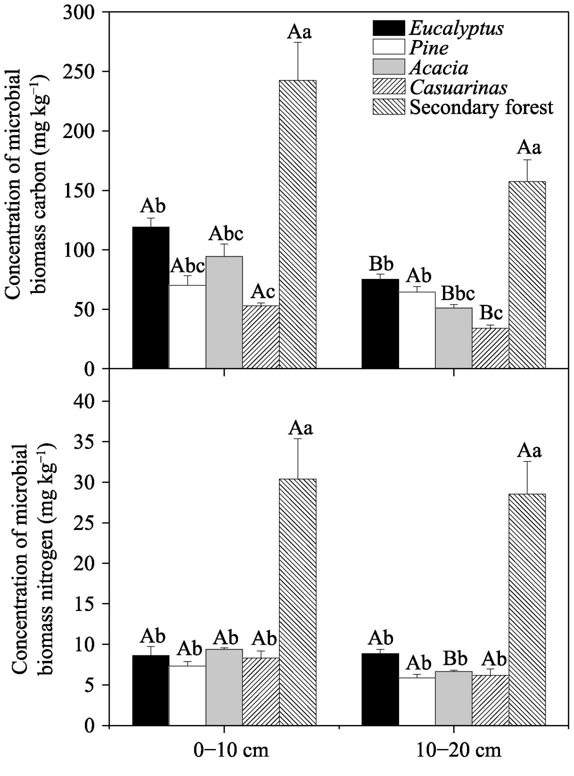

Fig. 5 Annual mean MBC and MBN contents under different forests

Note: Different capital letters indicate significant differences between topsoil and subsoil under the same forest type, and different small letters indicate significant differences among different forests in the same soil layer, the same below.

The soil MBC: MBN ratio in the topsoil of *Eucalyptus* was significantly higher than that of the subsoil. However, no significant difference was observed between topsoil and subsoil in the other forests. In the topsoil, the soil MBC: MBN ratio of *Eucalyptus* was significantly higher than those of the other forests, and no significant difference was observed among other forests. In the subsoil, the corresponding ratio was highest in *Pine*, followed by *Eucalyptus* and *Acacia* plantations, and lowest in secondary forest and *Casuarinas* (Fig. 6).

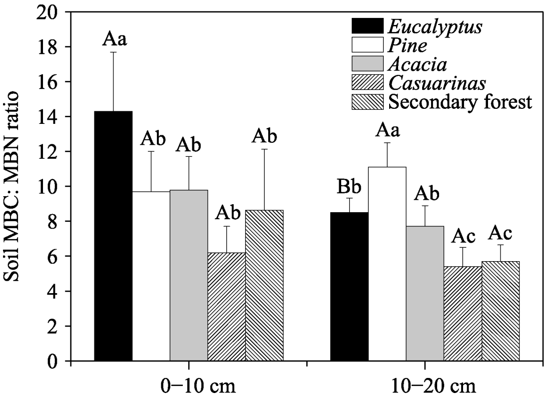

Fig. 6 Soil MBC: MBN ratio under different forests

The percentages of soil MBC and MBN within TC and TN, respectively, in topsoil were all lower than those in subsoil under each of the different forests. The percentages of soil MBC within TC under *Eucalyptus*, *Pine*, *Casuarinas*, and secondary forest differed significantly between topsoil and subsoil. The percentages of soil MBN within TN under *Eucalyptus*, *Acacia* and secondary forest differed significantly between topsoil and subsoil. Specifically, the percentage of soil MBC within TC in the subsoil of *Eucalyptus* was significantly higher than that of *Casuarinas*. In addition, no significant differences were found among different forests either in topsoil and subsoil. The percentage of soil MBN within TN in the topsoil of *Casuarinas* was significantly higher than those of *Eucalyptus*, *Acacia* and *Pine*, and the corresponding value in secondary forest was also higher than that of *Pine*. However, no significant differences were found among different forests either in topsoil and subsoil (Fig. 7).

3.4 Relationship between soil MBC and MBN contents and environmental factors

The effects of soil temperature and water content on the seasonal changes of soil MBC and MBN vary with forest types. However, the seasonal variations of soil MBC and MBN under different forests were all negatively correlated with soil temperature and positively correlated with soil water content (Table 3).

The MBC and MBN contents under different forests were significantly and positively correlated with TC, pH and litter N, and negatively correlated with soil bulk density and litter C. In addition, the MBN content was also significantly and positively correlated with root N both in topsoil and subsoil, and the MBC content in the subsoil was significantly and negatively correlated with root C (Table 4).

Table 3 Pearson correlations between seasonal variations of soil MBC and MBN and soil temperature as well as water content

Forest types	*T*—MBC		*T*—MBN		*W*—MBC		*W*—MBN	
	0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm
Eucalyptus	−0.216	−0.007	−0.421	-0.937^{**}	0.388	0.170	0.346	0.760^{**}
Pine	−0.027	−0.151	-0.629^{**}	-0.709^{**}	0.257	0.576^{*}	0.066	0.522^{*}
Acacia	-0.640^{**}	−0.217	-0.857^{**}	-0.786^{**}	0.537^{*}	0.057	0.553^{*}	0.082
Casuarinas	−0.269	−0.132	-0.785^{**}	-0.773^{**}	0.100	0.352	0.619^{*}	0.592^{*}
Secondary forest	−0.178	−0.346	−0.158	−0.413	0.734^{**}	0.713^{**}	0.618^{*}	0.819^{**}

Note: * significant correlations at $P<0.05$; ** significant correlations at $P<0.01$; the same below.

Table 4 Pearson correlations between soil MBC and MBN and properties of soil, litter and fine roots

Soil depth (cm)	Variable	MBN	TC	TN	Bulk density	pH	Litterfall	Litter C	Litter N	Root biomass	Root C	Root N
0–10	MBC	0.750^{**}	0.697^{**}	−0.030	-0.609^{**}	0.899^{**}	0.202	-0.500^{*}	0.651^{**}	0.301	−0.388	0.326
	MBN	1	0.820^{**}	−0.050	-0.586^{**}	0.915^{**}	0.408	-0.624^{**}	0.671^{**}	0.151	−0.188	0.505^{*}
10–20	MBC	0.855^{**}	0.904^{**}	0.274	-0.585^{**}	0.787^{**}	0.474^{*}	-0.459^{*}	0.447^{*}	0.113	-0.453^{*}	0.178
	MBN	1	0.926^{**}	−0.130	-0.646^{**}	0.952^{**}	0.419	-0.593^{**}	0.643^{**}	0.243	−0.215	0.510^{*}

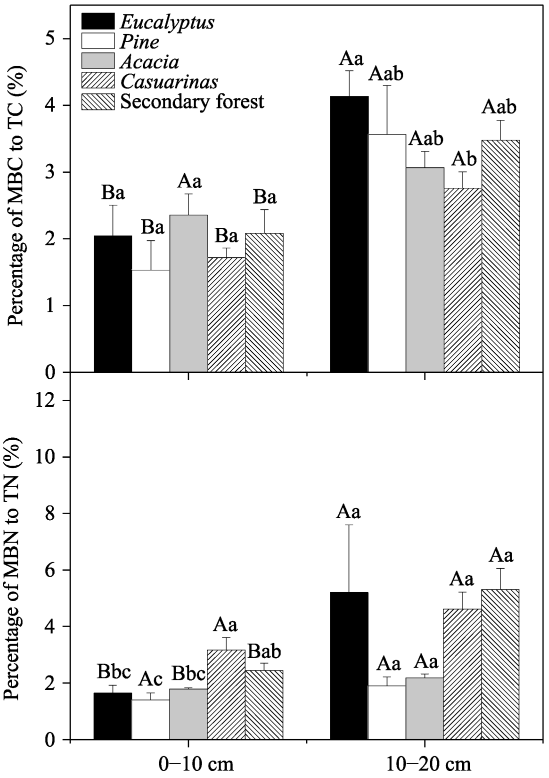

Fig. 7 Percentages of soil MBC and MBN within TC and TN, respectively, under different forests

4 Discussion

4.1 Soil C and N contents under different forests

The qualities and quantities of soil C and soil N can be affected by forest types due to the variations in tree species composition, litter quantity and quality, root turnover rate, as well as root exudates in different forests (Paul et al., 2002; Pérez-Cruzado et al., 2012; Wang et al., 2013; Hoogmoed et al., 2014; Deng and Shangguan, 2017). In our study, the soil C and N contents of the secondary forest were significantly higher than those of plantations, and these differences were mainly attributed to the former having a longer stand age and higher litter quantity and quality. The development time of the secondary forest is longer than the plantations, so it takes longer to incorporate the C and N inputs into the soil through litter and fine roots. In addition, the secondary forest has higher annual litterfall and root biomass, as well as higher C and N contents with a lower C: N ratio (Table 1). Therefore, the secondary forest can input more C and N into the soil because of its more rapid litter decomposition and root turnover rates. No significant difference was found in soil C content between N-fixing trees and non-N-fixing trees in the plantations, the soil N content was lowest under *Casuarinas*, and no noticeable difference was observed in soil N content between *Acacia* and non-N-fixing trees. Generally, the N-fixing trees have higher soil C and N contents than non-N-fixing trees under the same management practices and site conditions (Resh et al., 2002; Ussiri et al., 2006; Wang et al., 2010), because of the higher N contents in their litter and root exudates. Decomposition of these components can increase soil N content (Forrester et al., 2007), which will accelerate the tree growth and increase the C input from roots to soil, and consequently, increase the soil C content (Resh et al., 2002; Jandl et al., 2007). However, some studies have suggested that phosphorus is the main factor that limits the growth and N-fixation of nodular plants (Pearson and Vitousek, 2001). So the lower available phosphorus content in soil may limit the growth of N-fixing bacteria, thus affecting the N-fixation capacity of N-fixing trees (especially non-legume trees), and the N-fixing trees without N-fixing capacity may input less C and N into the soil compared with non-N-fixing trees (Hoogmoed et al., 2014). Therefore, the lower soil N content under N-fixing trees in our study may be related to the lower soil available phosphorus content in coastal sandy dunes (Table 1).

4.2 MBC and MBN contents, and MBC/MBN ratios under different forests

The soil microbial biomass varies greatly among different forests, which is the combined result of tree species and environmental factors (Liu and Wang, 2010; Li et al., 2014). In our study, the MBC and MBN contents under secondary forest were significantly higher than those of plantations in the different soil layers, and the MBC contents under *Casuarinas* were the lowest, in both topsoil and subsoil. No significant difference in MBN content was observed among plantations. First of all, compared with the plantations, the diversity of tree species of secondary forest provided a variety of litter and root exudates with various quality and quantity characteristics, which would provide rich substrates for the soil microorganisms, and accelerate their growth and reproduction (Wardle, 2010). Secondly, the litter C: N ratio and lignin: N ratio of secondary forest were much lower and consistent with easier litter decomposition; however, the higher tannin content and higher C:N ratio in the litter of *Casuarinas* may limit its decomposition rate (Ye et al., 2012). In addition, the withered branches of *Casuarinas* were often harvested for fuel by local residents, which can greatly reduce the carbon input from its litter to soil, and ultimately affect the growth and reproduction of soil microorganisms.

The mean MBC and MBN contents decreased with the increase of soil depth under the different forests, which is consistent with previous findings (Hu et al., 1997; Li et al., 2014; Wang et al., 2016b). The MBC contents differed significantly between topsoil and subsoil under *Eucalyptus* and *Casuarinas*, and the MBN and MBC contents all differed significantly between topsoil and subsoil under *Acacia*. According to the previous studies, most of the soil microorganisms are heterotrophic types. The topsoil has a good water permeability and high pH due to the full contact with air; the quantity of litter input is higher and the root exudates are rich in nutrients in the topsoil, which is conducive to the growth and reproduction of soil microorganisms, and leads to the increased microbial activity (Yang et al., 2009; Luan et al., 2011; Wang et al., 2016b). With the increase of soil depth, however, the litter decomposition and root exudates are gradually reduced, which slows down the synthetic metabolism of microorganisms in the subsoil, and leads to decreases in MBC and MBN contents with the increase of soil depth (Hu et al., 1997; Li et al., 2014).

The MBC: MBN ratio reflects the relative ratio between fungi and bacteria in the soil (Qiu et al., 2010), and the fungi are dominant in a microbial community when the MBC: MBN ratio is between 4 and 15, while the bacteria are dominant when the MBC:MBN ratio is between 3 and 5 (Sarathchandra et al., 1988). In this study, the MBC: MBN ratio under *Eucalyptus* was significantly higher than those under other forests in topsoil, and the MBC: MBN ratio under *Pine* was significantly higher than those of other forests in subsoil, which means the advantages of bacteria in the soils of *Eucalyptus* and *Pine* plantations were higher than those of other forests in topsoil and subsoil, respectively. Studies have shown that under both *Eucalyptus* and *Pine* are eutrophic species of mycorrhizal fungi, and three types of ectomycorrhizal, endogenous mycorrhizal and mixed mycorrhizal are found under *Eucalyptus* (Zhu et al., 2001). The *Pine* is a mainly ectomycorrhizal species (Tam, 1994), while *Acacia* and *Casuarinas* are leguminous and actinomycetes plants, respectively. Therefore, there are large proportions of rhizobium and actinomycetes among the symbiotic bacteria under *Acacia* and *Casuarinas* plantations. As a result, the MBC: MBN ratios under *Acacia* and *Casuarinas* were lower than those of *Eucalyptus* and *Pine*. Furthermore, the MBC: MBN ratio under coniferous forests is generally higher than that of broad-leaved forests (Liu and Wang, 2010), which means that fungi are more dominant in coniferous forests than in broad-leaved forests. This may also be one of the reasons why the MBC: MBN ratio under *Pine* was higher than under the other forests in this study.

The percentages of soil MBC and MBN within TC and TN in topsoil, respectively, were lower than those in subsoil under the same forests, which indicate that the carbon and nitrogen accumulations in the subsoil are higher than in the topsoil, and the soil organic matter is transferred from topsoil to subsoil (Li et al., 2014). These percentages represent the conversion efficiency of soil organic carbon by microorganisms and reflect the effectiveness of the utilization of soil substances (Chang et al., 2011). Previous studies have shown that these percentages in broad-leaved forest were higher than in coniferous forest, which indicates that the ability to maintain soil microbial biomass and the accumulations of soil carbon and nitrogen under broad-leaved forest are higher than under coniferous forest (Li et al., 2014). In our study, the percentage of MBC within TC under *Pine* plantation was the lowest in topsoil (no significant difference), while the percentage of MBN within TN under *Pine* plantation was the lowest in both topsoil and subsoil, which is consistent with the existing results.

4.3 Seasonal variation of MBC and MBN and its influencing factors

In this study, the MBC and MBN contents of different forests showed similar seasonal variations, which were single peak curves with higher values in spring or winter and lower values in summer or autumn. This agrees with the results from the coastal sandy dunes of Taiwan (Chen et al., 2005). Although May to September is the rainy season in the study area (Fig. 2), the soils in this sandy area have high temperatures and lack sufficient water-holding capacity during this period, resulting in the high evaporation dispersion. Therefore, the effective water content of the soil can be extremely diminished, leading to a significantly lower soil water content in summer and autumn than in winter and spring (Fig. 2). The lower soil water content in summer and autumn may limit the effectiveness of soil substrate activity; the soil microorganisms may die because of the lack of "food", leading to the sharp decline in soil microbial biomass. In contrast, the suitable soil temperature and moisture in winter and spring provide a good metabolic environment for soil microorganisms, which promotes their growth and reproduction. In addition, the growth rate of plants tends to be higher in summer, which means a larger demand for soil nutrients. This may also be one of the important reasons for the lower soil microbial biomass in summer, because it would limit the availability of nutrients to soil microorganisms.

The soil pH is considered to be the main factor driving the spatial distribution of a soil microbial community, and pH is closely related to the microbial activity; when the pH value is lower than 7, the soil microbial activity increases gradually with an increase of soil pH (Shen et al., 2013; Feng et al., 2014; Landesman et al., 2014). As an important source of soil C and N, the quantity and quality of root exudates and litter can affect the input of organic carbon to the soil by providing carbon, nitrogen, and energy sources for microbial synthesis and metabolism (Wang et al., 2016b), and consequently, affect the soil microbial biomass. In this study, the differences of MBC and MBN contents under different forest types are closely related to the litter quality and soil physical and chemical properties. The MBC and MBN contents were significantly positively correlated with TC, pH, and litter N, and negatively correlated with soil bulk density and litter C. In addition, the MBN contents are also significantly positively correlated with root N in both topsoil and subsoil, whereas the MBC content in the subsoil is significantly negatively correlated with root C, which is consistent with the existing results (Xu et al., 2009; Li et al., 2014).

5 Conclusions

The differences in soil microbial biomass C and N contents and their seasonal dynamics under five forest types (a secondary forest of *L. glutinosa*, and *Casuarinas*, *Pine*, *Acacia*, and *Eucalyptus* plantations) in the southeastern coast of Fujian province were investigated. The seasonal variations showed MBC and MBN contents which were all higher in spring and winter but lower in summer and autumn, and the seasonal variations of MBC and MBN were negatively correlated with soil temperature and positively correlated with soil water content, which indicated that the amount of microbial biomass in the sand dune forest ecosystem was largely controlled by soil moisture and soil temperature.

The mean MBC and MBN contents decreased with an increase of soil depth across the five forest types. Specifically, the MBC and MBN contents under secondary forest were significantly higher than those of plantations among the different soil layers; the MBC content under *Casuarinas* was the lowest in both topsoil and subsoil. These results imply that the long-term management of *Casuarinas* plantations led to soil decline, and the introduction of native tree species can modify soil parameters and consequently influence the belowground microbial community.

The MBC and MBN contents were significantly positively correlated with TC, pH, and litter N, and negatively correlated with soil bulk density and litter C. In addition, the MBN content was also significantly positively correlated with root N in both topsoil and subsoil, and the MBC content in the subsoil was significantly negatively correlated with root C. We found that several factors—environmental factors and the differences in litter and fine roots, soil nutrient contents, as well as the soil physical and chemical properties caused by different tree species—acted together to affect the concentrations of the soil MBC and MBN.

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林分类型和环境因子对中国南亚热带海岸沙地土壤微生物量的影响

高　伟[1,2,3,4]，林媚媚[5]，黄雍容[3]，黄石德[3]，叶功富[3]，黄志群[1,2]

1. 福建师范大学地理研究所，福州 350007；
2. 湿润亚热带生态—地理过程教育部重点实验室，福州 350007；
3. 福建省林业科学研究院生态环境研究所，福州 350012；
4. 青岛职业技术学院，山东青岛 266520；
5. 南乔治亚大学地质地理系，萨凡纳 GA 31419，美国

摘　要：海岸沙地生态系统通常具有较低的土壤养分、较低的土壤持水能力和较高的含盐量，但很多植物已经适应了中国东南沿海这一恶劣的沙地环境，研究此类生态系统中的土壤微生物生物量可以加深我们对微生物在土壤肥力和养分循环中作用的理解。基于此，我们比较了南亚热带海岸沙地 5 种森林类型（次生林和木麻黄、湿地松、厚荚相思和尾巨桉人工林）土壤微生物生物量碳（MBC）和土壤微生物生物量氮（MBN）含量的差异及其季节动态。结果表明，5 种林分土壤 MBC 和 MBN 含量的季节变化在春、冬两季均较高，夏、秋两季较低。同一土层中木麻黄人工林 MBC 含量低于其它人工林。不同林型间 MBN 含量差异不显著。MBC 和 MBN 浓度与土壤水分呈正相关，与土壤温度呈负相关。MBC 和 MBN 含量也随着土壤深度的增加而降低。在所有土壤层中，次生林的 MBC 和 MBN 浓度最高。研究还表明，土壤全碳（TC）、pH 和凋落物氮含量对 MBC 和 MBN 含量有显著影响，而土壤容重和凋落物碳含量对 MBC 和 MBN 含量有显著影响。MBN 含量与细根氮含量呈正相关。综上所述，环境因子、凋落物和细根的差异、土壤养分含量以及不同树种引起的土壤理化性质共同影响着土壤 MBC 和 MBN 的浓度。

关键词：海岸沙地；土壤微生物生物量碳；土壤微生物生物量氮；次生林；湿地松；木麻黄；厚荚相思；尾巨桉人工林