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Changes in soil heterotrophic respiration, carbon availability, and microbial function in seven forests along a climate gradient

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Abstract Soil microbial communities play an essential role in soil carbon (C) emission and C sequestration in forest ecosystems. However, little information is available regarding the relationship between soil C dynamics and microbial substrate utilization at large scales. Along the North–South Transect of Eastern China (NSTEC), seven forests representative of boreal, temperate and tropical biomes were examined. Soil heterotrophic respiration (R_h), soil dissolved organic C (DOC), microbial biomass C (MBC), and microbial community-level physiological profiles (CLPPs) were investigated using biochemical measurements, static chamber-gas chromatography analysis, and Biolog-Eco microplates, respectively. We found that soil R_h rates were significantly higher in subtropical and boreal forests than in temperate forests. Conversely, the concentrations of soil DOC and MBC, as well as microbial metabolic activity and functional diversity, were consistently higher in temperate forests than in subtropical forests. There were considerably different substrate utilization profiles among the boreal, temperate, and subtropical forests. Soil microorganisms from the temperate and boreal forests mainly metabolized high-energy substrates, while those from the subtropical forests used all substrates equally. In addition, soil R_h rates were significantly and negatively related to soil labile C concentrations, total metabolic activity, and the intensity of individual substrate utilization, indicating that soil microbes assimilated more soil substrates, thereby reducing CO_2 emissions. Overall, our study suggests that climate factors, as well as substrate availability, dominate the activities and functions of soil microbes at large scales.

Keywords Soil heterotrophic respiration · Labile carbon concentration · Microbial substrate utilization · Functional diversity · Forest biomes

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Introduction

Forests play an important role in the global carbon (C) cycle, especially in the sequestration of atmospheric CO_2 derived from fossil fuel combustion (Lal 2005). It is estimated that forest ecosystems cover approximately 4.1 billion hectares globally, and include three principal forest biomes: boreal, temperate, and tropical forests (Dixon and Wisniewski 1995). Forest vegetation and soils contain about 1,240 Pg of C, with soils accounting for two-thirds of this amount (Dixon et al. 1994). Forest soil C stocks are mediated by soil microbial communities and are in dynamic equilibrium with environmental factors (Lal 2005). In general, the soil organic C (SOC) storage of boreal forests (296 Mg C ha^{-1}) is significantly higher than those of temperate and tropical forests (122 Mg C ha^{-1}). As a result, these forests respond differently to climate change and anthropogenic disturbance (Powers and Schlesinger 2002). Thus, understanding the mechanisms and controlling factors of SOC dynamics in each forest biome is important for identifying and enhancing natural C sinks to mitigate climate change.

Forest soil microbial communities and their functions can be affected by an array of factors, such as climate (Dell et al. 2012), vegetation (Mitchell et al. 2012), soil types (Li et al. 2004), quantity and quality of organic matter (Tu et al. 2006), nutrient availability (Kunito et al. 2009), and management practices (Wang et al. 2011). For example, weather conditions strongly affect soil microbiological parameters, and air temperature and vapor pressure deficit (VPD) can explain 86 % of the seasonal variation in the rate of soil respiration in a

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Norway spruce forest (Ekblad et al. 2005). Elevated temperatures tend to reduce the total microbial biomass and the relative abundance of Gram-negative bacteria and fungi (Schindlbacher et al. 2011). Soil water availability impacts osmotic potential, the transport of nutrients and energy, cellular metabolism, and competitive interactions of microbes (Li et al. 2004). Broadleaved tree species are considered highly favorable for microbial activity relative to coniferous species because root exudates and litter from broadleaved forests typically have higher contents of water-soluble sugars, organic acids, and amino acids (Priha and Smolander 1997; Priha et al. 2001). Therefore, soil C input rates and properties can significantly impact soil microbial biomass, composition, and activities (Fontaine et al. 2004; Brant et al. 2006; Tu et al. 2006), and shifts in soil microbial community structure may, in turn, alter soil C processes (Dell et al. 2012). However, most of the studies conducted thus far have been confined to a single forest biome or have been focused on one or two controlling factors (Ultra et al. 2013), and few have dealt with the integrated effects of climate, vegetation, and soil substrate availability on soil microbial communities and the soil C cycle in the three principal forest biomes.

The terrestrial transect approach has previously been used to study the effects of changes in climate, land use, and atmospheric composition on the biogeochemistry and vegetation dynamics of terrestrial ecosystems (Canadell et al. 2002). The North–South Transect of Eastern China (NSTEC) is the fifteenth standard transect established, in 2005, by the International Geosphere-Biosphere Program (IGBP). It consists of many types of vegetation, from boreal forest to tropical rain forest, and the behaviors of its ecosystems are mainly driven by temperature, followed by precipitation (Fang et al. 2010). From north to south, mean annual temperatures vary from −7 °C in the cold, temperate, continental monsoon climatic zone to over 26 °C in the equatorial monsoon climatic zone; mean annual precipitation increases from less than 230 mm in the semiarid grassland zone to about 2,200 mm in the tropical rain forest zone (Fang et al. 2010). These sites provide an ideal experimental system to explore the patterns of the soil C cycle and microbial substrate utilization at large scales. Along the NSTEC, Fang et al. (2010) documented that the annual mean soil CO_2 fluxes in the boreal and temperate forests were significantly lower than those of the subtropical and tropical forests. Zheng et al. (2009) also reported that the spatial variations in the temperature sensitivity (Q_{10}) of soil CO_2 flux were primarily determined by soil temperature, SOC content, and ecosystem type. To date, few studies have focused on the environmental control of soil CO_2 flux, and considerably less is known about the relationship between the soil C cycle and microbial function at large scales (Dell et al. 2012).

In this study, we examined the spatial patterns of soil labile C content, the soil heterotrophic respiration (R_h) rate, and the metabolic activity and functional diversity of microbial communities in the boreal, temperate, and tropical forest biomes along the NSTEC. We also clarified the functional linkage between the soil R_h rate and microbial substrate utilization. We expected that the soil R_h rate would change along a latitudinal gradient and would be constrained by native climatic regimes and forest types; specifically, we expected that subtropical forests would have greater soil R_h rates than boreal and temperate forests. Furthermore, we predicted that temperate forests would have higher microbial metabolic activities and more closed C cycles than subtropical and boreal forests due to environmental stresses.

Methods

Site description and soil sampling

Along the NSTEC, field measurements and soil sampling were conducted in three forest sites: Great Xin'an Mountain in Northeast China; Dongling Mountain in North China, and Dinghu Mountain in South China. These sites differ substantially in their climate, vegetation, and soil properties (Table 1). At each climatic zone, we examined all the representative forest types. The Great Xin'an Mountain site has a cold-temperate humid climate, and its vegetation type is boreal forest, with dominant species being *Larix gmelinii* and *Betula platyphylla* (hereafter referred to as GX-Boreal forest). The Dongling Mountain site is characterized by a warm-temperate, semi-humid climate. A pine plantation (*Pinus tabuliformis*), secondary oak forest (*Quercus wutaishanica*), and secondary birch forest (*Betula platyphylla*) were chosen along an altitude gradient (hereafter referred to as DL-Pine, DL-Oak, and DL-Birch forests, respectively). Dinghu Mountain is characterized by a typical subtropical monsoon climate, and a disturbed pine plantation (*Pinus massoniana*), rehabilitated conifer and broadleaf mixed forest (*Pinus massoniana, Schima superba*), and old-growth evergreen broadleaved forest (*Castanopsis chinensis, Cryptocarya chinensis, Cryptocarya concinna, Erythrophleum fordii, and Cyathea podophylla*) were selected along a successional stage (hereafter referred to as DH-Pine, DH-Mixed, and DH-Broadleaf forests, respectively). For each forest type, three 10 m × 20 m plots were randomly selected. Although air temperate, precipitation, and nitrogen (N) deposition decrease from south to north along the NSTEC, SOC storage in the Dongling Mountain site is significantly lower than those of the Great Xin'an Mountain and Dinghu Mountain sites (Table 1).

All soil samples were taken in August 2011 to reduce the interference caused by differences in sampling times. At each plot, the litter layer was removed and mineral soil at depths of 0–15 cm was collected using a core sampler (2.5 cm in diameter). Five soil samples were taken from each plot and combined into one sample. The 21 soil samples were transported to the lab in chilled polystyrene boxes and stored at 4 °C for analysis.

Table 1 The stand characteristics and surface soil (0–20 cm) properties of seven forests in the three forest biomes along the North–South Transect of Eastern China (NSTEC)

Areas	Great Xin'an mountain[a]		Dongling mountain[a]		Dinghu mountain[a]		
Latitude (°)	50.83	39.96	39.96	39.96	23.17	23.17	23.17
Longitude (°)	121.50	115.42	115.42	115.43	112.57	112.57	112.57
Altitude (m)	810	1350	1150	1050	75	150	300
Climate zone	Boreal	Temperate	Temperate	Temperate	Subtropical	Subtropical	Subtropical
MAT (°C)	−5.4	3.7	4.8	4.3	20.9	20.9	20.9
MAP (mm)	500	761.0	611.9	565.6	1564	1564	1564
MAE (mm)	800	1164.0	1077.3	1025.7	1115	1115	1115
Aridity index	1.6	1.53	1.76	1.81	0.71	0.71	0.71
N deposition (kg N ha^{-1} $year^{-1}$)	8.50	23.3	23.3	23.3	28.4	28.4	28.4
Forest type	Mature boreal forest	Secondary birch forest	Secondary oak forest	Pine plantation	Pine plantation	Needle-broadleaf mixed forest	Evergreen broadleaved forest
Forest age	200	100	80	30	30	75	400
Tree height (m)	14.1	8.4	6.2	9.4	6.9	7.7	10.0
DBH (cm)	16.0	9.5	9.7	13.5	17.5	14.2	18.5
Sand (2–0.05 mm, %)	23.71	46.60	47.95	45.30	39.2	36.80	24.80
Silt (0.05–0.002 mm, %)	53.76	19.30	24.05	24.20	26.5	29.40	34.70
Clay (< 0.002 mm, %)	22.53	34.10	28.00	30.50	34.3	33.80	40.50
Litterfall (Mg C ha^{-1} $year^{-1}$)	2.50	1.63	1.87	2.34	1.80	4.30	4.20
SOC (kg m^{-2})	14.62	13.05	6.58	4.78	10.52	11.13	16.41
Total N (g kg^{-1})	1.83	2.68	2.29	1.71	0.90	1.00	1.90
C/N	7.99	4.87	2.87	2.79	11.69	11.13	8.64
Soil pH	5.31	6.74	7.25	6.69	3.86	3.88	3.73

MAT mean annual temperature, *MAP* mean annual precipitation, *MAE* mean annual evaporation, *DBH* diameter at breast height
[a]Data sources: database of Chinese Ecosystem Research Network (CERN) and Fang et al. (2010)

Soil R_h measurement

Soil R_h was measured using the trenching method. Two trench subplots (each 70 cm × 70 cm) were established at each plot. The subplots were prepared by making vertical cuts along the boundaries extending to 40 cm below the ground surface (approximately the bottom of the root zone) with a steel knife, severing all roots. The broken roots in the subplots were not removed to avoid further disturbances. Pieces of 0.5-cm thick polyethylene board were inserted into the vertical cuts to inhibit root regrowth. A square chamber and collar (0.125 m^3) was designated to measure soil CO_2 flux using the static opaque chamber and gas chromatography method (Fang et al. 2010). The collar was inserted to a soil depth of 10 cm. The soil CO_2 flux was measured between 9:00 and 11:00 AM by fitting the chambers to the collars for 30 min. Four gas samples were taken using 100 ml plastic syringes at intervals of 0, 10, 20, and 30 min after closing the chambers. All gas samples were then injected into the gas chromatograph (Agilent GC-7890A, Santa Clara, California, USA) to determine the CO_2 concentration. The soil R_h rate was calculated based on the slope of the linear regression between the CO_2 concentration and time (Wang and Wang 2003). The soil R_h rate was measured at least three times per month during the growing season.

Dissolved organic carbon (DOC) and microbial biomass C (MBC) determination

The DOC of the soil samples was extracted with deionized water (solid to water ratio of 1:2.5 w/v) by shaking fresh soil samples for 1 h on a horizontal shaker at room temperature. The soil solution was filtered using 0.45-μm polytetrafluoroethylene filters, and the extracts were immediately analyzed for DOC concentration using a TOC analyzer (Liqui TOCII, Elementar, Hanau, Germany). Soil MBC was measured using the fumigation–extraction method, as described in Vance et al. (1987). Concentrations of K_2SO_4-extracted C in $CHCl_3$-fumigated and non-fumigated soils were determined using a TOC analyzer (Liqui TOCII, Elementar). MBC was equal to the quotient of the difference between extracted organic C from fumigated and non-fumigated soils and an exchange coefficient (k_{EC} = 0.38).

Microbial substrate utilization

Microbial community level physiological profiles (CLPPs) were determined using a Biolog EcoPlate™ (Biolog Inc., Hayward, California, USA) (Garland and Mills 1991). Briefly, 10 g of fresh soil was added to 100 ml of a 0.85 % NaCl solution and shaken on an orbital shaker for 30 min at 190 rpm. A 150-μl aliquot of supernatant from 1:1,000 dilutions of each soil sample was added to each well. The plates were incubated at 25 °C, and color development in each well was recorded as the optical density (OD) at 590 nm using a microplate reader (GENios ProTM, Tecan Trading AG, Männedorf, Switzerland) over a 7-day period (0, 24, 48, 72, 96, 120, 144, and 168 h). The average well color development (AWCD), Shannon richness index (H'), Shannon evenness index (E), and Simpson dominance index (D) were calculated based on the absorption values after EcoPlate™ incubation for 144 h (Gomez et al. 2006). Additionally, the 31 C sources were divided into six

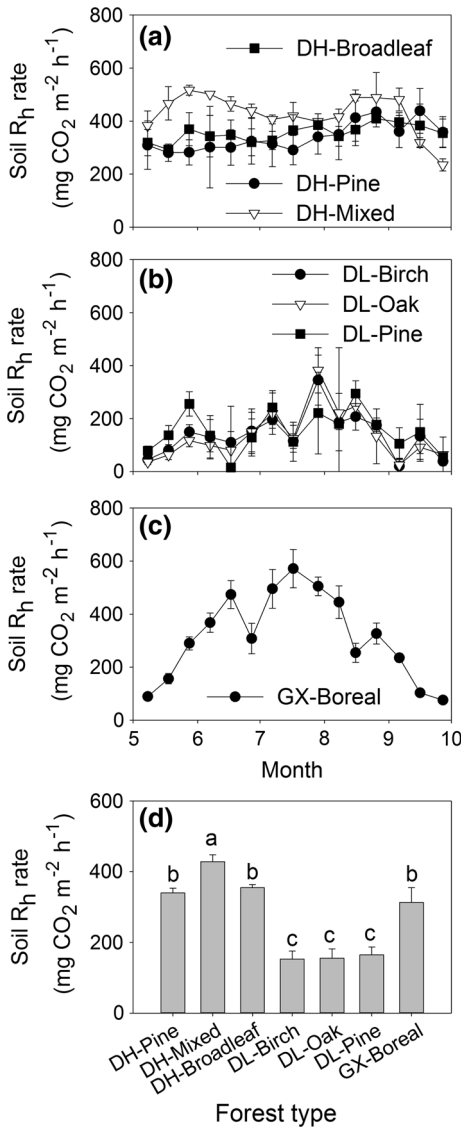

Fig. 1 Seasonal variations in soil heterotrophic respiration (R_h) rates in the seven forests distributed in the three forest biomes. DH-Broadleaf, DH-Pine, and DH-Mixed in **a** represent the evergreen broadleaved, pine, and mixed forests in Dinghu Mountain, respectively. DL-Birch, DL-Oak, and DL-Pine in **b** represent the birch, oak, and pine forests in Dongling Mountain, respectively. GX-boreal in **c** represents the boreal forest in the Great Xin'an Mountain. **d** Shows the mean soil R_h rates in the seven forests during the entire observation period. The data are the means and standard errors of three replicates. *Different lowercase letters* indicate significant differences among forests

groups, carbohydrates, carboxylic acids, amines, amino acids, polymers, and miscellaneous, as suggested by Zak et al. (1994). The average absorbance of all C sources within each group was computed as the intensity of single substrate utilization.

Statistical analysis

We used a one-way analysis of variance (ANOVA) with a Tukey's Honestly Significant Difference (HSD) test to evaluate the effects of forest type on the soil R_h rate, labile C concentration, AWCD value, and functional diversity indices. Principal component analysis (PCA) of the primary Biolog data was used to analyze site similarity and to identify substrate redundancy. Simple linear regression was used to analyze the relationships between the soil R_h rate and the soil labile C concentration, as well as between the soil R_h rate and microbial substrate utilization.

Results

Soil R_h rate

Soil R_h rates in the subtropical forests remained relatively constant throughout the growing season (Fig. 1a), whereas those of the temperate and boreal forests exhibited a single peak at the end of July (Fig. 1b, c). Furthermore, the seasonal difference in soil R_h rates was more pronounced in the boreal and temperate forests than in the subtropical forests (Fig. 1). The average soil R_h rates in the subtropical and boreal forests ranged from 312.91 to 428.43 mg CO_2 m^{-2} h^{-1}, which was significantly higher than those of the temperate forests, which ranged from 152.70 to 164.64 mg CO_2 m^{-2} h^{-1} (Fig. 1d). Within the subtropical climatic zone, the soil R_h rate in the mixed forest was higher than those of the pine plantation and evergreen broadleaved forests (Fig. 1d). However, in the warm-temperate climatic zone, the difference in soil R_h rates along the latitude gradient among the birch, oak, and pine forests was not significant (Fig. 1d).

Soil DOC and MBC concentrations

Soil DOC is a labile component of soil organic matter and is susceptible to degradation by heterotrophic microbes. The average DOC concentration in the subtropical forest soils ranged from 93.54 to 93.75 mg kg^{-1}, which was significantly lower than those of the temperate and boreal forest soils, which ranged from 142.92 to

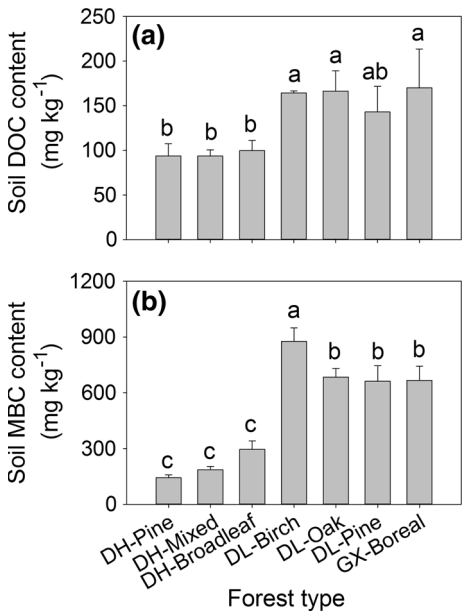

Fig. 2 Concentrations of soil dissolved organic C (DOC) and microbial biomass C (MBC) in the seven forests. On the x-axis, DH-Pine, DH-Mixed, and DH-Broadleaf represent the pine, mixed, and evergreen broadleaved forests in Dinghu Mountain, respectively. DL-Birch, DL-Oak, and DL-Pine represent the birch, oak, and pine forests in Dongling Mountain, respectively. GX-boreal represents the boreal forest in the Great Xin'an Mountain. *Different lowercase letters* indicate significant differences among forests

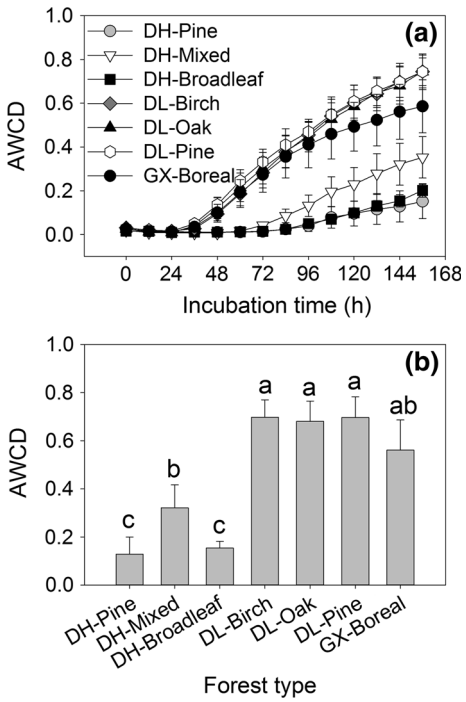

Fig. 3 Variation of microbial substrate utilization during a 168-h incubation and the average well color development (AWCD) values for the seven forests. On the x-axis, DH-Pine, DH-Mixed, and DH-Broadleaf represent the pine, mixed, and evergreen broadleaved forests in Dinghu Mountain, respectively. DL-Birch, DL-Oak, and DL-Pine represent the birch, oak, and pine forests in Dongling Mountain, respectively. GX-boreal represents the boreal forest in the Great Xin'an Mountain. *Different lowercase letters* indicate significant differences among forests

Table 2 Functional diversity indices for carbon utilization by soil microbial communities

Forests types[a]	Shannon H'[b]	Shannon E[b]	Simpson D[b]
GX-Boreal	2.84 ± 0.170ab	1.11 ± 0.024b	0.93 ± 0.012ab
DL-Birch	3.10 ± 0.067a	1.21 ± 0.056a	0.95 ± 0.005a
DL-Oak	3.04 ± 0.089a	1.15 ± 0.059ab	0.95 ± 0.005a
DL-Pine	3.08 ± 0.055a	1.13 ± 0.006ab	0.95 ± 0.003a
DH-Pine	2.59 ± 0.095b	1.13 ± 0.041ab	0.90 ± 0.007b
DH-Mixed	2.95 ± 0.087a	1.14 ± 0.027ab	0.94 ± 0.007ab
DH-Broadleaf	2.78 ± 0.180ab	1.14 ± 0.011ab	0.92 ± 0.023b

[a]GX-boreal represents the boreal forest in Great Xin'an Mountain. DL-Birch, DL-Oak, and DL-Pine represent the birch forest, oak forest, and pine forest in Dongling Mountain, respectively. DH-Pine, DH-Mixed, and DH-Broadleaf represent the pine forest, mixed forest, and evergreen broadleaved forest in Dinghu Mountain, respectively

[b]Indices were calculated based on the optical density values after 144 h of incubation. Data are expressed as means ± standard errors. Different lowercase letters indicate significant differences among forests

169.93 mg kg^{-1} (Fig. 2a). Similarly, the soil MBC concentration averaged 667.05 mg kg^{-1} in the boreal forest, and ranged from 661.48 to 875.89 mg kg^{-1} in the three temperate forests. Overall, soil MBC concentrations in the boreal and temperate forests were three times as high as those of the subtropical forests (Fig. 2b). However, there were no significant differences in soil DOC and MBC concentrations between the boreal and temperate forests, nor between forests in the same climatic zones (Fig. 2). These results showed that the temperate and boreal forest soils had higher C availability and total microbial biomass than the subtropical forest soils.

Patterns of microbial substrate utilization

The curves for color development during the incubation period were sigmoidal, and the overall AWCD values of the temperate and boreal forests increased more rapidly than the subtropical forests after 24 h (Fig. 3a). Color development was significantly higher for the temperate forest soils than for the subtropical forest soils, while that of the boreal forest soil was intermediate (Fig. 3b). Among the subtropical forests, the mixed forest exhibited a higher soil AWCD value than the pine and evergreen broadleaved forests (Fig. 3b). In addition, significant differences in the mean values of H', E, and D were detected among the seven forest soils, and soil microbial functional diversity tended to decrease from the temperate forests to the boreal and subtropical forests (Table 2). In the subtropical climatic zone, the value of H' for the mixed forest soils was significantly higher than that of the pine forest soils (Table 2).

The intensity of individual substrate utilization by microbial communities was generally consistent with the total AWCD (Gomez et al. 2006). Across the seven forests, soil microorganisms utilized the six substrates in the same order, with carboxylic acids being the most utilized substrate, followed by amino acids and carbohydrates, polymers, amines, and miscellaneous substrates (Fig. 4). The intensity of substrate utilization followed the order temperate > boreal > subtropical forests (Fig. 4), with the exception of miscellaneous substrates. In the subtropical climatic zone, the intensity of microbial substrate utilization in the mixed forest tended to be higher than those of the pine and broadleaved forests (Fig. 4). Principal component analysis of the CLPP data revealed that the first two principal components (PC1 and PC2) accounted for 70.1 and 6.8 % of the variance, respectively (Fig. 5). Moreover, microorganisms from the temperate forests metabolized mainly sugars, amino acids, and carboxylic acids, while those from the subtropical forests utilized substrates in equal proportions.

Relationships between soil R_h, labile C, and microbial substrate utilization

In large scales, soil R_h rates were significantly and negatively related to soil MBC and DOC concentrations (Fig. 6a, b). Except for miscellaneous substrates, soil R_h rates were significantly and negatively related to microbial metabolic activities (AWCD) and the intensity of individual substrate utilization (Fig. 6c–i). Moreover, the correlation coefficients were higher between soil R_h rates and the utilization intensities of carbohydrates and polymers than between soil R_h rates and the utilization intensity of other substrates (Fig. 6d–i).

Discussion

Effects of forest biomes on soil R_h and labile C

Soil R_h reflects the soil microbial physiological status, and a high value indicates a high turnover in the belowground C pool in forest ecosystems (Ananyeva et al. 2008). The rates of soil R_h along the NSTEC were in the order subtropical > boreal > temperate forests, which was consistent with the variation patterns of the aridity index and SOC stocks (Table 1). These results indicated that soil R_h rates at large scales were driven by the combination of precipitation and temperature, as

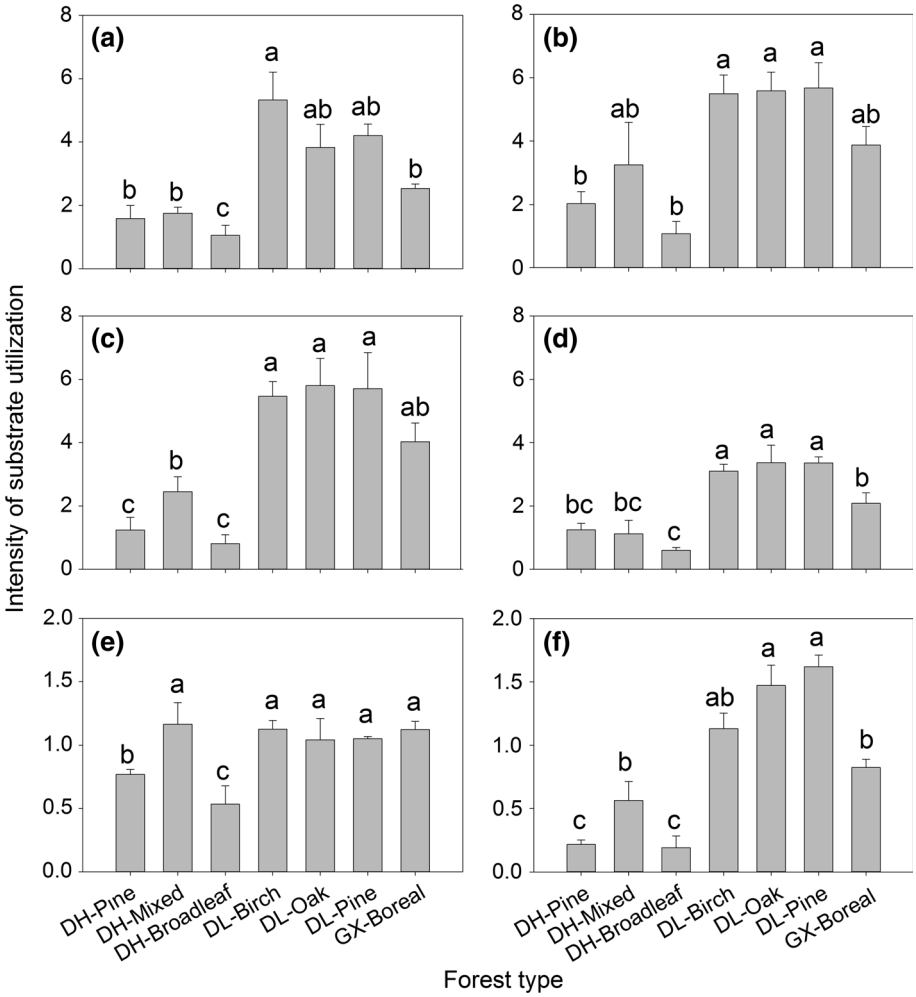

Fig. 4 Characteristics of microbial utilization of carbohydrates (**a**), carboxylic acids (**b**), amino acids (**c**), polymers (**d**), miscellaneous (**e**), and amines (**f**) in the seven forests. On the x-axis, DH-Pine, DH-Mixed, and DH-Broadleaf represent the pine, mixed, and evergreen broadleaved forests in Dinghu Mountain, respectively. DL-Birch, DL-Oak, and DL-Pine represent the birch, oak, and pine forests in Dongling Mountain, respectively. GX-boreal represents the boreal forest in the Great Xin'an Mountain. *Different lowercase letters* indicate significant differences among forests

well as by substrate amounts. Similarly, Zheng et al. (2009) and Yu et al. (2010) documented that forest ecosystems in southern China had the largest soil CO_2 emissions because of their higher temperatures, and the annual soil respiration rates in the boreal forests in Northeast China were higher than those in central China because of their high SOC stocks. Insam (1990) also found that an increase in the precipitation/evaporation ratio led to an increase in substrate-induced respiration per soil C unit. Among the three subtropical forests, we observed higher R_h rates in mixed forest soils than in pine and evergreen broadleaved forest soils, which was consistent with the pattern of soil microbial metabolic activities (Fig. 3). The above results suggested that the soil R_h rate at the local scale was largely dominated by substrate availability and soil microbial metabolism (Lõhmus et al. 2006).

Soil DOC is an easily accessible source of energy and C resources for soil microbes, and, correspondingly, its production and consumption are dominated by soil microbial communities (Jones et al. 2008; Hagedorn et al. 2012). Soil MBC reflects the degree of C immo-

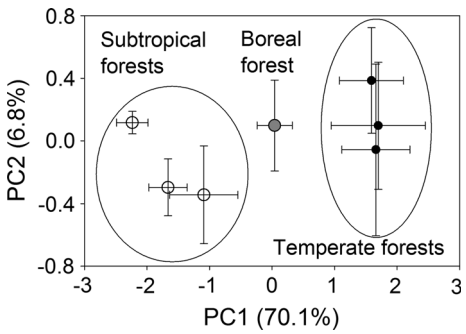

Fig. 5 Principal component analysis of soil microbial utilization of C sources of different forest types. All values were based on a 144-h incubation. Data in parentheses indicate the percentage of total variation accounted for by each principal component

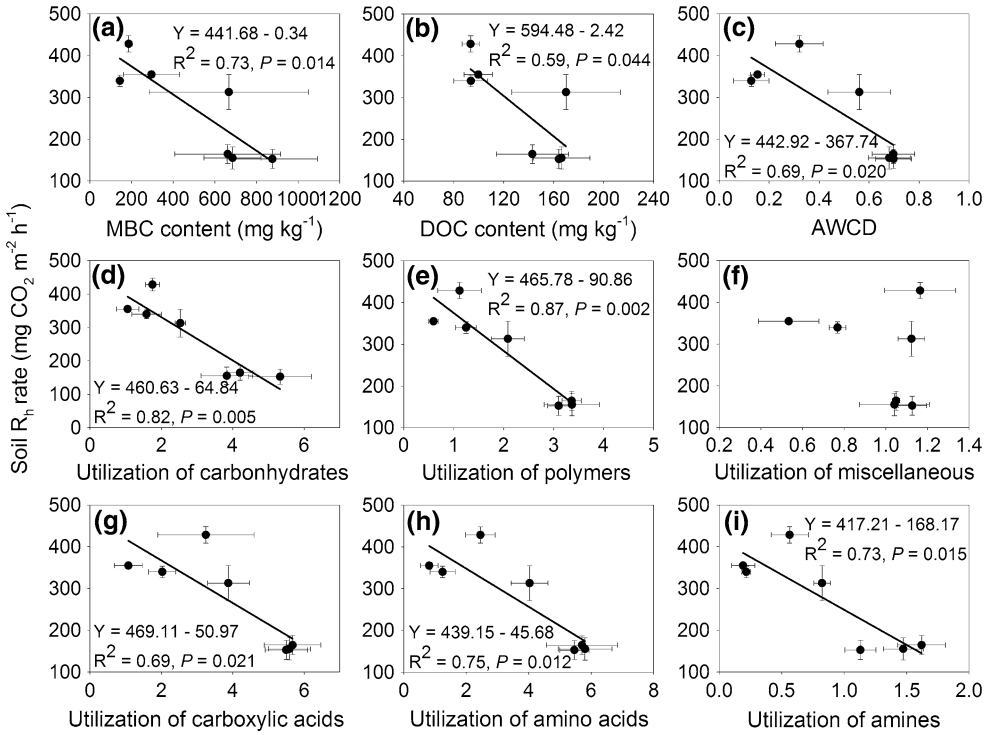

Fig. 6 Relationships between soil heterotrophic respiration (R_h) rates and soil dissolved organic C (DOC), microbial biomass C (MBC), average well color development (AWCD), and utilization of individual substrates

bilization, and higher concentrations indicate that more C is assimilated into microbial biomass, which reduces the losses of C through chemical and physical processes (Liu et al. 2010). The concentrations of soil DOC and MBC in the temperate and boreal forests were higher than those of subtropical forests (Figs. 2, 3), indicating a higher production/consumption ratio of soil DOC and higher microbial C immobilization in the high-latitude forests. In general, subtropical forests, which probably contain litter with a larger percentage of recalcitrant compounds (e.g., lignin), may have a higher fungi/bacteria ratio compared with temperate forests (Liu et al. 2012; Zhang et al. 2013). Furthermore, soil bacteria are the primary decomposers of simple carbohydrates, organic acids, and amino acids, whereas soil fungi are the primary decomposers of recalcitrant compounds (Myers et al. 2001). Therefore, the difference in microbial community composition (e.g., fungi/bacteria) and chemical properties (e.g., C/N) of litter and SOM under different forest types and climatic zones can be responsible for the spatial variation of soil DOC and MBC concentrations (Paul 2006; Waldrop and Zak 2006; Hagedorn et al. 2008).

The inverse relationships between soil R_h rates and labile C contents, as well as between soil R_h rates and the utilization of individual C resources across three forest zones (Fig. 6a, b), indicated a shift of soil C turnover from open to closed with increasing soil labile C contents. In other words, more soil substrates were assimilated by soil microbes and, therefore, less CO_2 was emitted. Furthermore, these inverse relationships could imply different resource utilization strategies in boreal and temperate forests ('*k* strategist') compared with subtropical forests ('*r* strategist') (Nogueira and Melo 2006; Fierer et al. 2007). Existing evidence shows that physiological stresses, such as seasonal drought, low temperature, and low N availability, decrease the amount of C substrates used for respiration and increase their conversion into microbial biomass in temperate and boreal forests (Zhong et al. 2009; Hu et al. 2010; Liu et al. 2010; Wei et al. 2011).

Effects of forest biomes on microbial metabolic activity and functional diversity

The AWCD reflects the sole C source utilization ability of the soil microbial community (Garland and Mills 1991). The higher AWCD values in the temperate soils, in comparison with those of the boreal and subtropical forest soils, indicated that the C-poor temperate forests utilized C substrates more effectively than the C-rich boreal and subtropical forests. Among the six groups of substrates, microbial communities in the temperate forest soils mainly used carbohydrates, carboxylic acids, and amino acids (Fig. 4), suggesting that microorganisms probably use easily degradable and high-energy substrates (Kunito et al. 2009). The spatial pattern of microbial metabolic activity could be related to soil water availability (Marschner and Kalbitz 2003), nutrient availability (Wang et al. 2011), and soil pH (Saleh-Lakha et al. 2005), etc. For example, soil microbial

activity is limited more by water than C or N in forests (Li et al. 2004; Chaer et al. 2009), and the higher soil microbial activity in the temperate forests relative to those of the boreal and subtropical forests might be associated with microbes that are resistant to drought stress (Papatheodorou et al. 2004). Additionally, N availability strongly regulates soil microbial activities and processes in the forests of the East Asian monsoon climate region (Liu et al. 2011; Wang et al. 2011). In N-poor temperate and boreal forest soils, more photoassimilates are allocated below ground to support microbial processes. Furthermore, soil acidity in subtropical forests has also been linked to a decrease in the availability of C to microbial communities (Grayston et al. 2004), and to slower litter decomposition and microbial growth rates (White et al. 2005; Ultra et al. 2013).

The Shannon-Wiener index (H') is a measure of the richness and distribution of the microbial population, the Shannon evenness index (E) reflects the comparability of substrate utilization between all utilized substrates, while the Simpson dominance index (D) reflects the dominance and concentration of the utilized C substrates (Gomez et al. 2006). The temperate forests had a higher catabolic diversity relative to the boreal and subtropical forests, which was consistent with the patterns of the aridity index and labile C contents (Table 1; Fig. 2). These results suggest that soil microbial functional diversity is dominated by climatic factors, followed by C-oxidation pathways (Zak et al. 1994; Carney and Matson 2005). We believe that the semi-humid, temperate forests possibly maintain their high functional diversity by enhancing the turnover of plant biomass and enhancing root exudation under seasonal drought stress (Zak et al. 2003). Additionally, in the subtropical forests, the Shannon H' index in the mixed forest was higher than that of the pine forest, which was mainly attributed to a difference in soil pH (Table 1). Numerous studies have shown that soil acidification has a significant negative effect on the diversity of soil microbial communities (Fierer and Jackson 2006; Lauber et al. 2009).

Conclusions

This study characterized the patterns in the soil R_h rate, labile C concentration, microbial substrate utilization, and functional diversity in three forest biomes along the NSTEC. The soil R_h rates in the subtropical forests were significantly higher than those of the temperate and boreal forests, whereas their soil labile C contents and microbial metabolic activities were lower. Soil microbial communities in the temperate forest soils tended to use easily metabolized, high-energy substrates, while those in the subtropical forests used all substrates equally. Although our study has provided some insights into the pattern of soil C turnover and microbial metabolism in the three forest biomes, there remain serious gaps in our understanding of the linkage between microbial community dynamics and soil functions. Therefore, subsequent research should focus on the composition, structure, and genetic diversity of soil microbial communities along the NSTEC.

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