B-1.7.2 Quantitative Analysis of Carbon Flow through Soil Microorganisms in the Boreal Forest Ecosystem

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Abstract In order to clarify the role of microorganisms in the carbon cycle of the boreal forest ecosystem, vertical distributions of soil carbon, soil microbial biomass and microbial activity were studied in a black spruce forest near Candle Lake, Saskatchewan, Canada. Soil microbial biomass was largest in the FH horizon. Soil respiration rate measured using a portable infrared gas analyzer was highest in the FH horizon exceeding 50% of the total CO_2 emission from soil surface. Low but significant CO_2 emission was detected in deeper soil horizons (E and B). Root respiration represented about 54% of the total soil respiration. The amount of carbon evolved through microbial respiration was estimated as 283 gC m^{-2} yr^{-1}. To study the effect of climatic conditions on litter decomposition, the relationship between temperature condition and mass loss rate of moss litter was also examined.

Key Words Boreal Forest, Carbon, Microorganism, Soil

1. Introduction

Recently, the importance of boreal forest ecosystems in the global carbon cycle has received considerable attention. Net primary productivity in boreal forests are generally lower than those in temperate and tropical forests[1], but huge amonunt of organic carbon is stored in soil of boreal forest ecosystems[2]. The global warming is thought to reduce soil carbon storage by stimulating soil microbial activity. However, quantitative data on soil microbial biomass and microbial activity in these ecosystems are rare.

We aimed to clarify the role of microorganisms in the soil carbon flow of the boreal forest ecosystem. For this objective, we examined vertical distributions of soil carbon, microbial biomass and microbial activity in a boreal forest in Canada. To study the effects of temperature condition on the decomposition rate, we also examined the difference in annual mass loss of moss litter along the altitudinal and latitudinal temperature gradients.

2. The role of microorganisms in the soil cabon flow

(1) Site and Methods

Study site

The study site was set in a boreal forest near Candle Lake in Saskatchewan, Canada (53° 50'N, 105° 30'W; about 500m alt.). The site was dominated by black spruce (*Picea mariana* (Mill.) B. S. P.) with a few individuals of aspen (*Populus spp.*). The tree hight ranged from 10m to 16m with some individuals being over 80 years old. A thick moss layer mainly of Hylocomium splendens (Hedw.) B. S. G. had developed on the ground. Mean annual air temperature for 30 years (1961-1990), recorded at Prince Albert about 70km south-west of the study site, was 0.6℃. From November 26, 1994 to May 22, 1995, the soil temperature at 15cm beneath the soil surface was lower than 0℃.

Distribution of carbon and microbial biomass

Three pits deeper than 50cm were dug in the study site. After measuring the thickness of soil horizons, soil samples were taken with a steel cylinder ($100cm^3$). These samples were used for measureing the bulk density and the water holding capacity. The concentrations of carbon and nitrogen in the soils were measured with a CN-corder (Yanaco MT-500, Yanagimoto Co., Ltd., Kyoto). For the measurement of soil microbial biomass, fresh soil samples were kept in a cooling box at 5℃ and brought to Japan. The soil's moisture content was adjusted to 55% (mineral soil) or 100% (organic soil) of the water holding capacity. After the pre-incubation at 5℃ for 10 days, microbial biomass of the sample was determined by the chloroform fumigation-extraction method[3].

Soil respiration

Three pits were dug in the same manner described above. The soil respiration chamber (6000-09, LI-COR, USA) was placed on the surface of each soil horizon. The CO_2 emitted from the surface was measured with a portable infrared gas analyzer (LI-6200, LI-COR, USA).

To study the temperature dependence of soil respiration, we collected soil samples of L and FH horizons in March 1995. They were brought to Japan in a frozen state and kept in a freezer at -20℃ until the measurement of soil respiration. The sample was allowed to thaw at the room temperature prior to the measurement. They were put in a 200-ml Erlenmeyer flask which was connected with a open circuit gas exchange system with an infrared gas analyzer (VIA-300, Horiba Co., Ltd., Kyoto). The flask with soil sample was put in a temperature-controlled growth box. The soil respiration rate was measured at 5, 10 and 15℃, and the Q_{10} was obtained.

Root respiration

In order to know the proportion of root respiration to total soil respiration, root respiration rate was estimated as follows.

To determine the root biomass in each soil horizon, three pits, 0.5m × 0.5m, were dug in the study site. Roots contained in each soil horizon were collected and divided into fine ($\phi < 1mm$), medium ($1 \leqq \phi < 5mm$) and thick ($5mm \leqq \phi$) roots. They are oven dried at 80℃ to obtain their dry weight.

Because it was impossible to measure the respitation rate of intact roots, we measured the respiration rate using cut roots. The root samples collected from the FH horizon were put on a dish 8cm in diameter. The soil respiration chamber was placed on the dish and sealed to prevent gas leakage.

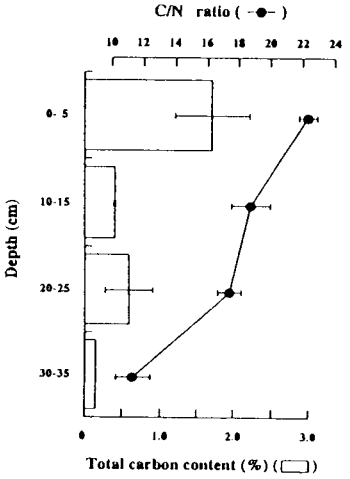

Fig. 1. Vertical changes in carbon content and C/N ratio. Mean values are plotted with one standard error (n = 2~3).

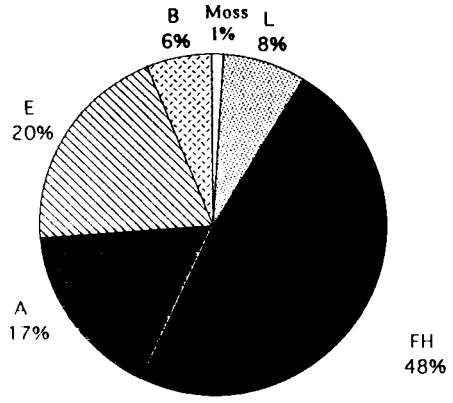

Fig. 2. Distribution of carbon contained in moss, organic and mineral soils (~50cm).

After the measurement of respiration rate, the sample was kept in a box at 15℃ until the next measurement. These samples were repeatedly used for the measurement from 0 to 11 days after the collection. Then, they were brought to Japan and used for the measurement again on 22 days after the collection.

We also examined the effect of root excision on the root respiration rate. Twelve points were selected for the measuement of soil respiration in the study site. For the half of them, part of the ground, 15cm × 15cm in surface area, was cut vertically to 20cm below the ground surface with a knife. Soil respiration rates of these plots as well as the control plots were measured from 0 to 11 days after the root excision.

(2) Results

Distribution of soil carbon

The ground surface was totally covered with thick moss layer. The lower part of the moss layer was composed of brown, dead moss shoots mixed with undecomposed litter of black spruce. This layer will be reffered as L horizon in the following text. Under the L horizon, there was a thick (about 13cm) FH horizon composed mainly of well-decomposed moss shoots and humus. In the mineral soil layer, thin A horizon (0～5cm), thick E horizon (～26cm) and redish brown B horizon were recognized. Ground water table was not observed at least to the depth of 70cm beneath the ground surface.

Vertical changes in carbon concentration and C/N ratio are shown in Fig. 1. Carbon concentration was much higher in the A horizon than in the deeper horizons (E and B). The C/N ratio tended to decrease with increasing soil depth. The ratio of the B horizon was significantly lower than those of the E horizon.

Total amount of carbon contained in moss, litter and soil (to the depth of 50cm from the mineral soil surface) was 6.4kg m^{-2}, about 48% of which was in the FH horizon (Fig. 2). The green moss layer contained only a small proportion of carbon (about 1%). However, moss litter contributed about 20 % of the dry weight of the L horizon. About 9% of carbon was distributed in the moss + L horizon. The A horizon contained about 17% of carbon. Despite the low carbon concentration, the E horizon contributed 20% of carbon. This is largely due to the large bulk density of this horizon.

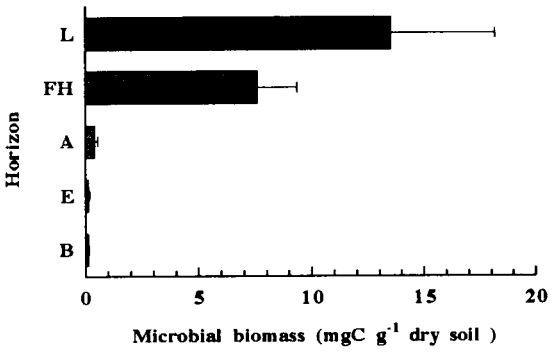

Fig. 3. Soil microbial biomass per gram soil. Mean values are plotted with one standard error (n = 3～6).

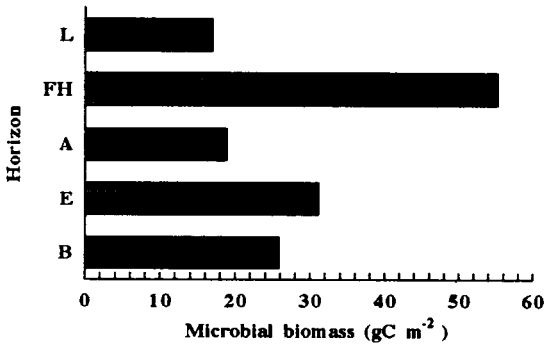

Fig. 4. Soil microbial biomass per square meter.

Microbial biomass

Microbial biomass per dry weight soil was largest in the L horizon (Fig. 3). The biomass in the E and B horizons were extremely low. On the other hand, microbial biomass per ground area was largest in the FH horizon (Fig. 4). The value in the L horizon was smaller than those in the E and B horizons. This is largely due to the low bulk density of the L horizon. The percentage of microbial biomass carbon to the total soil carbon in the L, FH, A, E and B (~50cm) horizons were 3.3, 1.8, 1.7, 2.5 and 6.3%, respectively.

Soil respiration

The CO_2 emission rates at the surface of the L horizon, measured on 3 and 4 August 1994, were within the range from 3.2 to 7.7 μmol m^{-2} s^{-1} (Fig. 5). Air temperature during the measurement fluctuated within the range from 15 to 21℃, but soil temperature (15cm) was much lower (8~12℃) than the air temperature. More than one half of the CO_2 emission was evolved from the FH horizon. The CO_2 emission rates at the surface of the E horizon was about 10% of the total CO_2 emission. However, higher emission rate was sometimes detected at the surface of the B horizon.

The Q_{10} value of respiration rate in the tempeature range from 5 to 15℃ was about 2.3. No significant difference in this value was observed between the L horizon and the FH horizon.

Root respiration

About 92% of the root biomass was in the FH horizon, while roots in the L horizon represented a minor fraction (about 1%) of the root biomass. Root biomass in the A and E horizons comprised 6.9 and 0.1% of the total root biomass, respectively.

Figure 6 shows the time course of the respiration rate of cut roots. The rate was highest just after the sample collection. Then it decreased rapidly and tended to be stable after 5 days following the sample collection. Specific rate of root respiration was larger in the thin roots than in the thicker roots.

Figure 7 shows the effect of root excision on the soil respiration rate. A significant increase of soil respiration rate was observed just after the root excision. Then the rate decreased rapidly and became smaller than those in the control plots. After 5 days following the root excision, the difference in the respiration rate between the excised plot and the control plot was almost constant, about 0.9 μmol m^{-2} s^{-1}. This result suggests that root excision results in a drop of root respiration rate but the cut roots survive and maintain their activity for some time after excision.

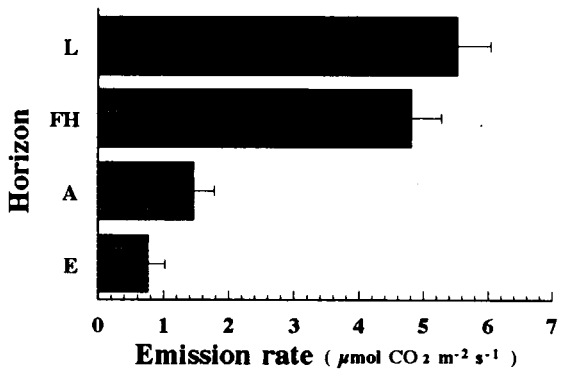

Fig. 5. CO_2 emission rate at the surface of the soil horizons (3~4 August 1994). Mean values are plotted with one standard error (n = 3).

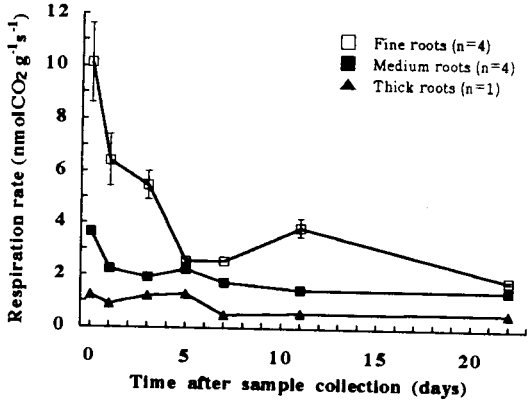

Fig. 6. Changes in the respiration rate of cut roots of *Picea mariana* at 15℃. Vertical bars represent standard errors.

(3) Discussion

There was a well-developed organic layer in this study site, which comprised 56% of the total soil carbon. However, despite of low carbon concentration, the E and B horizons represented a significant fraction (about 26%) of total soil carbon. It seems that these deep soil layers are also important as reservoir of soil carbon in the boreal forest ecosystem.

The significant decline of the C/N ratio in the E and B horizons suggests that soil carbon was lost from these deep soil layers. This assumption was supported by the fact that a significant CO_2 emission rate was detected at the surface of these horizons.

The FH horizon represented the largest fraction of the total CO_2 emission. However, since this layer contained a large amount of root, the contribution of root respiration to the total soil respiration was expected to be large. In order to know the proportion of root respiration to total soil respiration, root respiration rate of each soil horizon was estimated from the root biomass and the respiration rate of cut root. In this calculation, we used the average rate of the root respiration form 5 to 11 days following the sample collection. The decline of the respiration rate caused by the root excision (cf. Fig. 7) was also taken into consideration. It was assumed that respiration of microbe is obtained by subtracting the root respiration from the total respiration.

It was estimated that root respiration represented about 80% of the total respiration in the FH horizon (Fig. 8). On the other hand, the contribution of root respiration to the total respiration was very small in the L and E horizons. Total root respiration represented about 54% of the total soil respiration. This value was similar to the value that had been reported for a *Pinus densiflora* forest in Japan[4].

Microbial respiration in the FH horizon seemed to be small as compared with the large microbial biomass. This may suggest that the activity of microbe in the FH horizon is relatively low. The respiration rate per microbial biomass was higher in the A horizon than in the FH horizon.

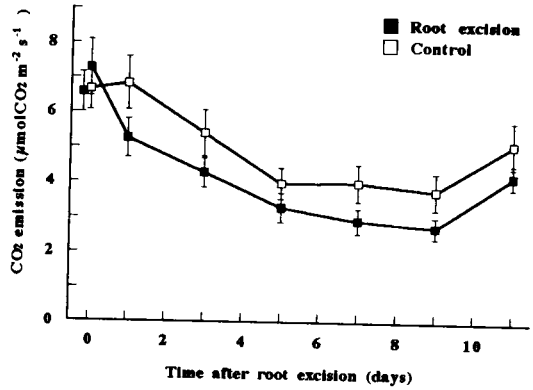

Fig. 7. The effect of root excision on the total soil respiration rate in the field. Vertical bars represent standard errors (n = 6).

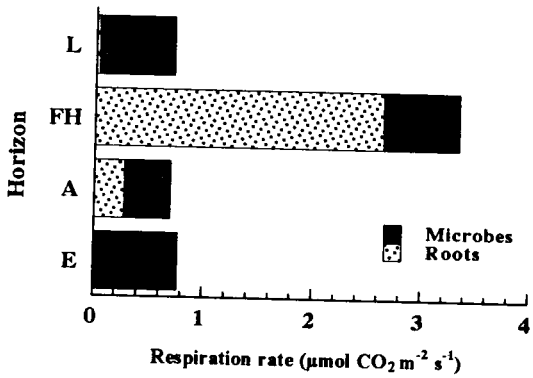

Fig. 8. The contribution of microbes and plant roots to the soil respiration in each soil horizon.

Annual microbial respiration was estimated from the soil temperature using the experimentally obtained Q_{10}. The annual respiration in the L and FH horizons were calculated based on the temperature at 15cm beneath the ground surface. For the A horizon, we used the data recorded at depth of 10cm from the mineral soil surface. It was assumed that soil microbial activity was negligible from December to May. The annual microbial respiration of L, FH and A horizons were estimated to be 105, 108 and 70 gC m^{-2} yr^{-1}, respectively. Using these values and the microbial biomass, turnover time was also calculated after Joergensen *et al.*[5]. The turnover time of L, FH and A horizons were calculated as 80, 253 and 134 days. These values are comparable to those reported by Joergensen *et al.*[5] who measured the turnover rate in the mineral soil of temperature grassland at 15℃. The data indicates that soil microbial activity in the boreal forest is relatively high despite low temperature condition.

3. The relationship between litter mass loss and temperature

(1) Materials and Methods

The moss *Hylocomium splendens* (Hedw.) B. S. G. shows a very wide distribution in the Northern Hemisphere making a significant contribution to the net primary production of boreal forest ecosystems. Because this species produces readily identifiable segment each year, annual growth rate can be easily measured. Thus, this species can be used as a useful indicator of litter decomposition in boreal regions.

The samples were collected from three boreal forest including the study site described above. For comparison, we also examined samples collected from four sites in the subalpine forest of Mt. Fuji (Table 1).

Six or five almost pure stands of *H. splendens* were selected in each study site. Part of each stand, 15cm × 15cm in surface area, was cut vertically to the FH horizon, and a moss block composed of green shoots and the L horizon was collected. The number of shoots in each moss block was counted to obtain the shoot density. Then, the shoots were divided into segments of each age class according to Tamm[6]. These segments and moss litter in the L horizon were dried to constant weight at 80℃ to obtain the dry weight. Nitrogen concentration of the litter was measured with a CN-corder (Yanaco MT-500).

Table 1. Location and mean annual air temperature of the study sites.

Site		Latitude	Longitude	Altitude	Mean annual air*
Name	Location			(m)	temperature (℃)
BSD	Candle Lake	53° 50′ N	105° 30′ W	500	0.6
BSW	Candle Lake	53° 50′ N	105° 30′ W	500	0.6
STR	Stony Rapids	59° 35′ N	105° 45′ W	300	-3.5
FJA	Mt. Fuji	35° 23′ N	138° 43′ E	2400	1.2
FJB	Mt. Fuji	35° 23′ N	138° 43′ E	2200	2.3
FJC	Mt. Fuji	35° 23′ N	138° 43′ E	1800	4.6
FJD	Mt. Fuji	35° 23′ N	138° 43′ E	1700	5.2

* Values were estimated from data recorded at nearby weather stations.

Table 2. Annual litter production, the amount of litter, annual mass loss and nitrogen concentration of the litter of *Hylocomium splendens*.

Site	Litter production* (g m^{-2})	The amount of litter* (g m^{-2})	Annual mass loss* (%)	N concentration† (mgN g^{-1})
BSD	72(8)^{a}	454(106)^{ab}	18.6(2.6)^{ab}	9.8(1.9)^{ab}
BSW	97(6)^{a}	709(113)^{ac}	15.2(2.1)^{abc}	6.0(0.8)^{b}
STR	90(10)^{a}	928(89)^{c}	9.8(0.8)^{c}	4.7(0.9)^{b}
FJA	27(4)^{b}	266(32)^{bd}	10.1(0.6)^{c}	10.3(2.0)^{ab}
FJB	36(5)^{b}	262(38)^{bd}	14.1(1.8)^{bc}	9.3(0.6)^{ab}
FJC	40(4)^{b}	173(13)^{d}	24.3(3.2)^{a}	14.8(1.1)^{a}
FJD	39(7)^{b}	167(26)^{d}	22.9(2.4)^{ab}	13.8(0.6)^{a}

* Values are means with standard errors in parentheses ; n=5 (STR) or 6 (other sites).

† Values are means of three samples with standard errors in parentheses.

Means followed by the same letter within a column are not significantly different (Tukey test, P>0.05).

The annual mass loss of the moss litter was calculated by the simple model proposed by Jenny *et al.*[7] assuming a constant litter production and a constant litter mass loss rate in annual basis. The annual litter production was estimated by the growth analysis after Skre and Oechel[8]. The annual mass loss obtained by this method includes the loss of fragmentation and incorporation into the FH horizon. The values calculated by this method tended to be larger than those obtained by the litter bag method.

(2) Results and Discussion

Table 2 summarizes the annual litter production, the amount of litter accumulated in the field and the annual mass loss estimated by the model. Nitrogen concentration of the largest segments (2-years old segments) was also shown in the table. There was no significant difference in the litter production among the three boreal sites. On the other hand, annual litter production in the subalpine sites were almost one half of those in the boreal sites.

In the subalpine sites of Mt. Fuji, the litter accumulation increased from 167 to 266gm^{-2} as the elevation became higher, while no altitudinal differnce was observed in litter production. As a result, the mass loss rate tended to be smaller with increasing altitude though this was not true for the difference between FJC and FJD. The average mass loss rates were significantly related with the mean annual air temperatures in a log-linear fashion (Fig. 9).

The mass loss rates at the study sites in boreal forests were comparable to those in Mt. Fuji despite lower mean annual temperatures in the former sites. The low annual mean temperatures in the boreal sites are largely due to low temperature condition in the winter season. Mean air temperature of the snow-free season (May - October) was higher in Candle Lake than in the study site of FJA in Mt. Fuji.

Nitrogen concentration of the litter also varied significantly among the study sites. Nitrogen concentration of the 2-years old segments tended to be smaller with decreasing mean annual temperature (Fig. 10). The annual mass loss was positively related with the nitrogen concentration of the litter ($r=0.80$; $P<0.05$).

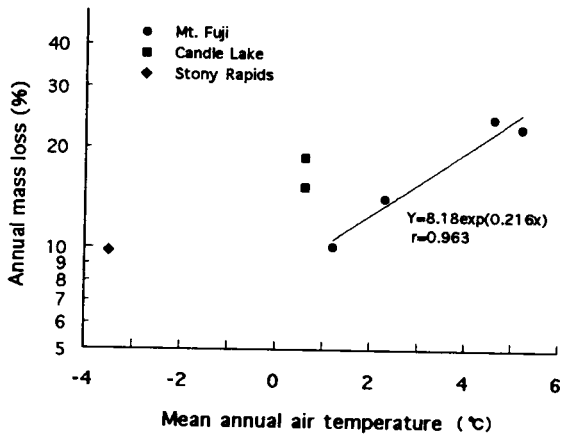

Fig. 9. Annual mass loss of *Hylocomium splendens* litter (log scale) as a function of mean annual air temperature (n = 5～6).

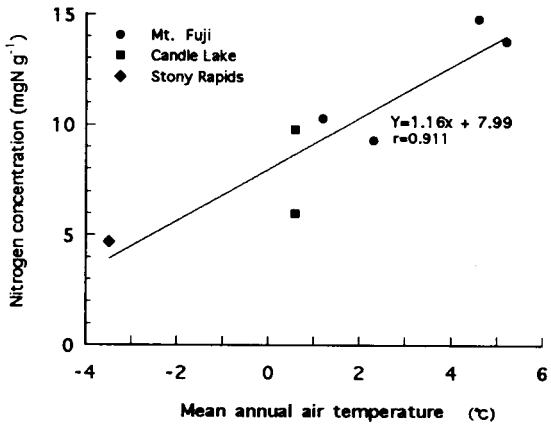

Fig. 10. Relationship between mean annual air temperature and the nitrogen concentration in the 2-years old segments of *Hylocomium splendens* (n = 3).

We calculated an apparent Q_{10} of the mass loss rate (the proportional increase in mass loss rate for a 10℃ increase of temperature) from the altitudinal change of mean annual air temperature. The value calculated for the subalpine sites was 8.7. This value was much larger than Q_{10} values of soil respiration in previous studies[9]. Recently, however, Vitousek *et al.* reported similar large apparent Q_{10} values, ranging from 4 to 11, for the decomposition of *Metrosideros* leaf litter on Mauna Loa, Hawai'i[10]. The large Q_{10} value obtained in this study may be partly due to the cool climatic condition. Kirschbaum pointed out that temperature sensitivity of soil (litter) respiration decreased with increasing temperature[11]. He estimated that Q_{10} of decomposition was almost 8 at 0℃. Our data as well as the study of Kirschbaum[11] suggest that decomposition in cool climatic region is especially sensitive to temperature increase. It must be noted, however, that apparent Q_{10} values are determined not only by the temperature dependence of microbial activity but also by other factors which affect the decomposition process. Climatic condition seems to change the chemical composition of litter as mentioned above. The community structure of soil microorganisms may also change with changing climate. In order to assess the long-term effect of climatic change on decomposition, improvement of our understanding about these indirect effects seems to be necessary.

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