Seasonal variation in CO₂ production of leaf litter from different deciduous forests at the early decomposition stage

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Abstract

We collected leaf litter from a deciduous broadleaf forest and a larch forest in Hokkaido, Japan naturally without using litter traps or litter bags. The litter collection was conducted every month from October 2001 through October 2002 except in the snowy season. We measured the CO₂ production rate of the litter samples through microbial respiration using the chamber method in a laboratory under different temperature and moisture conditions to investigate the seasonal pattern and temperature and moisture responses of CO₂ production at the early stage of litter decomposition. Seasonal variation was found in the CO₂ production rate per unit of litter dry weight (P_{dw}), or the litter decomposition rate, for both broadleaf and larch litters. Although seasonal patterns differed somewhat according to temperatures and species, P_{dw} reached the minimum in June. The moisture sensitivity of P_{dw} decreased with time and reached the minimum in summer for both broadleaf and larch litters, whereas the seasonal pattern of the temperature sensitivity (Q_{10}) was not clear. The seasonal pattern of P_{dw} was explained by its C:N ratio for broadleaf litter. For larch litter, however, the relationship between P_{dw} and the C:N ratio was complicated because of fresh litterfall supplied gradually before defoliation. The temperature and moisture sensitivities of P_{dw} changed in parallel with the C:N ratio for both broadleaf and larch litters, respectively. These facts suggest the importance of litter chemical quality in the early decomposition process of fresh litter and the validity of the C:N ratio as an index of litter quality.

Key words: C:N ratio, litter decomposition, microbial respiration, moisture sensitivity, temperature sensitivity

1. Introduction

Decomposition of plant litter is a dominant process for the flow of carbon and nutrients in most terrestrial ecosystems. Therefore, a full understanding of plant litter decomposition is essential to understanding and evaluating the global carbon balance and nutrient cycles.

Litter is decomposed through three physical and chemical processes: leaching by water, fragmentation by soil animals, and chemical alteration through activity of microorganisms (Chapin *et al.*, 2002). The decomposition processes progress roughly in two stages after rapid mass loss by leaching (Aerts, 1997; Chapin *et al.*, 2002). Labile and moderately labile compounds such as sugars, amino acids and cellulose are mainly

decomposed during the early stage lasting for a few years. Leaf litter frequently loses over 30% of its mass in the first year. In the latter stage, the recalcitrant compound of lignin is the dominant substrate for decomposition. The latter decomposition process occurs quite slowly (Aerts, 1997; Berg, 2000; Chapin *et al.*, 2002). Litter decomposition is regulated by three factors: physical environment, litter quality, and the nature and abundance of microbial communities (Coûteaux *et al.*, 1995). Effects of the physical environment, such as temperature and precipitation, on litter decomposition rates are stronger in the early stage (Berg, 2000). Although early decomposition rates are strongly affected by litter concentration of water soluble nutrients and carbohydrates, later decomposition rates are related to lignin concentration (Berg, 2000; Gartner and Cardon, 2004). Litter with low nitrogen concentration has a tendency to be decomposed slowly because nitrogen is generally insufficient in fresh litter for the growth

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of microorganisms (Chapin *et al.*, 2002), whereas high nitrogen concentration in litter constrains the final litter decomposition (Berg, 2000).

The mechanisms of plant litter decomposition are relatively well understood, as mentioned above, using plentiful knowledge and findings from numerous field and laboratory studies. However, there is little information in reference to seasonal variation in the environmental dependence of litter decomposition during the early stage. Such information will be necessary to elucidate the early litter decomposition process with greater certainty. This study measured the CO₂ production rate as the decomposition rate of leaf litter collected from two different deciduous forests under different temperature and moisture conditions. Measurements were taken monthly during the snow-free season. Based on these measurements, we investigated responses of the CO₂ production rate of fresh litter to temperature and moisture and their seasonal patterns.

2. Materials and Methods

2.1 Site description

We examined leaf litter samples from two adjacent deciduous forests in Tomakomai, Hokkaido, Japan: a natural broadleaf forest and a Japanese larch (*Larix kaempferi*) plantation. These forests have identical soil types, which are classified as volcanogenous regosol with high water permeability and poor nutrients. The broadleaf forest belongs to Tomakomai Experimental Forest, Hokkaido University. The dominant tree species of the broadleaf forest are oak (*Quercus mongolica* var. *grosseserrata*), magnolia (*Magnolia obovata*), Japanese elm (*Ulmus davidiana* var. *japonica*), maple (*Acer mono*), and heartleaf hornbeam (*Carpinus cordata*). The larch forest is located in Tomakomai Flux Research site (Tomakomai FRS), established in Tomakomai National Forest, and planted in 1957-59. In the larch forest, some deciduous broadleaf trees, such as birch (*Betula ermanii* and *Betula platyphylla* var. *japonica*) and Japanese elm, have invaded into the gaps. Individual spruce trees (*Picea jezonensis*) have grown sparsely. Basal area densities at a breast height of larch, broadleaf trees, and spruce were 19.0, 4.1, and 0.4 m² ha⁻¹, respectively (Hirano *et al.*, 2003a); the occupation of larch trees in the forest was 81% on a stem-area basis. Both broadleaf and larch trees usually begin to foliate in late April, whilst defoliation of broadleaf trees occurs in October, about half a month earlier than larch trees. The annual mean air temperature is 6.5°C; the

monthly means are below 0°C from December through March. The annual precipitation is about 1200 mm. Snow covers the ground for about four months from early December through early April. In both forests, the monthly mean litter temperature ranged between about 2°C in November and about 18°C in August in the growing season of 2002.

2.2 Litter collection

Litter collection was conducted naturally, without using litter traps or litter bags. Sixteen samples of leaf litter were collected directly from each forest floor once a month from October 2001 to October 2002, except during the snowy season between December and March. Leaf litter under one year of age, which was mainly provided through defoliation in October and November, was only collected carefully within a framework area of 0.042 m². The framework was placed temporarily on the ground at 16 positions determined randomly in each forest every month. Litterfall in the growing season was also included in the litter samples. In the larch forest, only larch litter was collected. Although the collected litter included the slightly and moderately decomposed organic horizons, or O_i and O_e horizons, the highly decomposed one, the O_a horizon, was excluded because of difficulty in distinguishing the O_a horizon from the A horizon (Federer, 1982). Litter samples were enclosed in plastic bags immediately after collection and stored in a cool dark room for a few days until laboratory experiments began. If samples were too wet because litter was collected after heavy rain, the samples were dried moderately inside.

2.3 Analysis of Litter quality

Carbon (C) and nitrogen (N) concentrations (weight percentage) were determined from oven-dried litter samples using an N-C analyzer (NC900; Shimadzu Corp., Japan); replication was five. The C:N ratios calculated from both concentrations were used as indexes of litter quality.

2.4 Measurement of CO₂ production rate

The CO₂ production rates of the litter samples were measured using the closed chamber technique in an incubator (BNC-110; Tabai Espec Corp., Japan) at four temperatures: 3, 12, 21, and 30°C. The measuring system included four chambers with a volume of 0.00771 m³. Sixteen samples from each forest were divided into four groups for four temperatures, and four samples in each group were enclosed individually in a different chamber; thus replication was four for each temperature. Each chamber was equipped with

an infrared gas analyzer (GMD20; Vaisala, Finland) to measure CO₂ concentration in the chamber headspace. The chambers were closed for 12 min and opened for 3 min automatically at intervals of 15 min. The closing and opening was controlled by a data logger (CR10X; Campbell Scientific Inc., USA) using solenoid valves and an air pump. CO₂ concentration was measured every 5 s, with the data logger for the last 7 min in periodic 12 min closing because of considerable CO₂ concentration fluctuation during the first few minutes. The mean increase rate of CO₂ concentration for 7 min was calculated using linear fitting to obtain the CO₂ production rate of each litter sample, namely microbial respiration rate. When the chambers were opened, the chambers were ventilated with outside fresh air to decrease CO₂ concentration. Humidity of the outside air was regulated with a bubbler to prevent litter samples from dewing or excessive drying. The measurements were conducted for 14 h at each constant temperature in a dark condition. The fresh weight of the litter samples was measured every hour to monitor the change of litter moisture, as litter samples gradually dried through ventilation during the measurement process. After the measurement process, litter samples were desiccated in an oven at 84°C for 24 h and weighed to determine their dry weight. Litter moisture based on dry weight (θ , g (water) g (dry weight)⁻¹) was calculated hourly from fresh weight and dry weight. Thus, the data of litter CO₂ production rates were averaged hourly to match the moisture data. The CO₂ production rates were normalized using litter dry weight. Litter samples were renewed for each temperature condition because they dried and may have reduced labile carbon considerably during the 14 hour measurement process (Fierer *et al.*, 2003).

2.5 Analysis of temperature response of litter CO₂ production

The following simple exponential equation was applied to analyze the relationship between litter CO₂ production rates normalized by dry weight (P_{dw} , nmol g⁻¹ s⁻¹) and temperature. Moreover, the Q_{10} value, which was obtained from a fitted constant of the equation, was used as an index of the temperature sensitivity of P_{dw} .

$$P_{dw} = a \cdot \exp(b \cdot T) \quad (1)$$

$$Q_{10} = \exp(10 \cdot b) \quad (2)$$

In these equations, T represents temperature (°C), and a and b are fitted constants.

3. Results and Discussion

3.1 Temperature and moisture responses of litter CO₂ production

Here we combine all data regardless of seasonal variation to obtain the general relationship between P_{dw} and temperature or moisture. Figure 1 shows the temperature dependence of P_{dw} , in which θ is confined within 1–2 g g⁻¹ to eliminate the moisture dependence of P_{dw} (Fig. 2). The P_{dw} of both broadleaf and larch litters increased exponentially with temperature. The relationships drawn by Eq. (1): r^2 were over 0.96 in both cases. Values of Q_{10} were 1.9 and 1.3 for broadleaf and larch litters, respectively, considerably smaller than those from microbial respiration rates in forest soils (Boone *et al.*, 1998; Fang and Moncrieff, 2001). Although litter decomposition is generally faster in broadleaf trees than in conifer trees (Chapin *et al.*, 2002), P_{dw} showed no significant difference between broadleaf and larch litters.

Figure 2 shows how the relationship between P_{dw} and θ . P_{dw} of both broadleaf and larch litters increased almost linearly with θ . The rate of increase was higher at higher temperatures and was very low at 3°C. Q_{10} also increased with θ , from 1.2 to 1.9 for broadleaf and 1.2 to 1.4 for larch between θ classes of 0.0–0.5 and 2.5–3.0 g g⁻¹, respectively. However, these results are obtained under relatively dry conditions. Another experiment indicated that P_{dw} of larch reached a plateau

Fig. 1. Relationship between the rate of litter CO₂ production per unit dry weight (P_{dw}) and temperature for broadleaf and larch litters. All data were used within the moisture range of 1–2 g g⁻¹. Vertical bars denote standard deviations. An exponential equation was fitted; r^2 was over 0.96 for both broadleaf and larch litters.

around 5 g g^{-1} in θ (data not shown). The saturation relationship was probably caused by the inhibition of oxygen supply at high moisture.

3.2 Seasonal variation in litter CO_2 production

Seasonal variations in P_{dw} are shown in Fig. 3 for four temperatures. Hourly mean data of P_{dw} were averaged within the moisture range of $1\text{--}3 \text{ g g}^{-1}$ for each month to increase the number of samples. Mean litter moisture for each point plotted on the figure ranged from 1.4 to 2.0 g g^{-1} for broadleaf and 1.7 to 2.3 g g^{-1} for larch; it was slightly higher in summer. Although P_{dw} depends on litter moisture (Fig. 2), the moisture effect on P_{dw} would be small in Fig. 3 because the range of moisture was limited. The seasonal pattern differed somewhat according to temperature for broadleaf. P_{dw} was largest

at $2.5 \text{ nmol g}^{-1} \text{ s}^{-1}$ in October 2001, immediately after defoliation, under 30°C conditions. P_{dw} continued to decrease until July and increased from July through October 2002. At 21°C , P_{dw} was almost constant at $1.1\text{--}1.3 \text{ nmol g}^{-1} \text{ s}^{-1}$ from October through June, and decreased to $0.7 \text{ nmol g}^{-1} \text{ s}^{-1}$ in July. P_{dw} increased to the previous level in October. At 12°C and 3°C , P_{dw} decreased gradually from October through July and increased from July through October. For larch, P_{dw} decreased in June, and increased from June through October under all temperature conditions. By comparison with P_{dw} in November, P_{dw} decreased by 45–65% in July for broadleaf litter and 30–40% in June for larch litter. Experiments using litter bags showed that litter dry mass decreased exponentially at the early

Fig. 2. Relationship between the rate of litter CO_2 production per unit dry weight (P_{dw}) and moisture at four temperatures for (a) broadleaf and (b) larch. Data were categorized into moisture classes of 0.5 g g^{-1} between 0 and 3 g g^{-1} . Standard deviations were within the range of $0.1\text{--}0.6 \text{ nmol g}^{-1} \text{ s}^{-1}$ (CV: 20–60%) and $0.2\text{--}0.6 \text{ nmol g}^{-1} \text{ s}^{-1}$ (CV: 30–70%) for broadleaf and larch, respectively.

Fig. 3. Seasonal variations in the rate of litter CO_2 production per unit dry weight (P_{dw}) at four temperatures for (a) broadleaf and (b) larch, from October 2001 through October 2002. Data were used within the moisture range of $1\text{--}3 \text{ g g}^{-1}$. Each symbol denotes the mean of four replications; standard deviations were within the range of $0.02\text{--}0.30 \text{ nmol g}^{-1} \text{ s}^{-1}$ (CV: 3–35%) and $0.03\text{--}0.40 \text{ nmol g}^{-1} \text{ s}^{-1}$ (CV: 3–40%) for broadleaf and larch, respectively.

decomposition stage because cell solubles, cellulose and hemicellulose were broken down (Chapin *et al.*, 2002; Berg, 2000). The breakdown of such labile and moderately labile compounds would reduce P_{dw} in June or July. Although we did not measure the amount of litterfall, the increase of P_{dw} from July or August was probably due to fresh litterfall supplied gradually before defoliation; this is supported by a seasonal variation in litter quality (Fig. 8). Skambracks and Zimmer (1998) reported that the CO₂ production rate of litter consisting of alder, birch and oak was 1.0–1.5 nmol g⁻¹ s⁻¹ at 15°C. Also, Hoornes *et al.* (2002) reported the rate of 1–6 nmol g⁻¹ s⁻¹ at 20°C for some grassland and peatland species. P_{dw} obtained in this study was slightly smaller

than those rates.

Figure 4 shows seasonal variations in leaf litter density on the forest floor, which is defined as the dry weight of leaf litter accumulating within a ground area of 1 m². For the larch forest, larch litter was only counted. In the broadleaf forest, much fresh litterfall was provided on the forest floor through defoliation in October 2001. Litter density began to decrease in June, and reached a minimum in September. In October 2002, litter density increased, but did not reach the level of the previous October because of delayed defoliation in 2002. In the larch forest, larch litter density reached a maximum in November because of larch defoliation. The litterfall of larch needles accounted for about 70% of total leaf litterfall in 2003 (ECONIXE, 2004). Although fresh litterfall was supplied gradually even in the growing season, litter density continued to decrease until October.

Seasonal variation in the CO₂ production rate of leaf litter based on a ground area (P_a) is shown in Fig. 5 for four temperatures; P_a is the product of P_{dw} and litter density. The monthly mean litter temperature increased from 7–8°C to about 18°C between April and August, and it decreased to 2–3°C in November for both the forests in 2002; it was 11–13°C in May. Hirano *et al.* (2003b) measured soil respiration continuously in the broadleaf forest using a modified profile method. That study showed an exponential relationship between the soil respiration rate and soil temperature. Results therein estimated the soil respiration rate as about 2 and 6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 12°C and 21°C, respectively. P_a was 0.25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in May at 12°C and 0.17 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in August at 21°C. The comparisons of P_a with

Fig. 4. Seasonal variations in litter density on the floor of the broadleaf and larch forests, from October 2001 through October 2002. For the larch forest, only larch litter was counted. Each symbol denotes the mean of 16 replications. Vertical bars denote standard deviations.

Fig. 5. Seasonal variations in the rate of leaf-litter CO₂ production per unit ground area (P_a) at four temperatures on the floor of the broadleaf and larch forests, from October 2001 through October 2002. For the larch forest, only larch litter were counted. Data were used within the moisture range of 1–3 g g⁻¹. Each symbol denotes the mean of four replications.

Fig. 6. Seasonal variations in Q_{10} of P_{dw} for broadleaf and larch litters, from October 2001 through October 2002. Data were used within the moisture range of 1–3 g g⁻¹.

Fig. 7. Seasonal variations in the slope of linear relationship between P_{dw} and moisture at 21°C for broadleaf and larch litters, from October 2001 through October 2002. Linear regression was applied within the moisture range of 0–3 g g⁻¹.

the soil respiration rate suggest that the contribution of litter CO₂ production through microbial respiration to total soil respiration was 12% in May and 3% in August. In addition, total soil respiration including broadleaf litter respiration was estimated at about 2 and 6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 12°C and 21°C, respectively, in the larch forest (Liang *et al.*, 2004). P_a of larch litter was 0.12 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in May at 12°C and 0.12 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in August at 21°C, which suggests that the CO₂ production of larch litter accounted for 6% and 2% of total soil respiration in May and August, respectively.

Q_{10} of P_{dw} showed no clear seasonal variation for broadleaf litter and its value fluctuated between 1.8

and 2.1 (Fig. 6). For larch litter, Q_{10} decreased from 1.5 to 1.3 between June and July. That low Q_{10} value continued until October. As shown in Fig. 2, there was a positive linear relationship between P_{dw} and θ under relatively dry conditions. We calculated the slope of the linear relationship for each month within the θ range of 0–3 g g⁻¹ to investigate the moisture sensitivity of P_{dw} ; the unit of the slope is nmol g (water)⁻¹ s⁻¹. Figure 7 shows seasonal variations in the slope at 21°C; linearity was significant ($p < 0.05$) in each month. For broadleaf, the slope decreased from 1.7 to 0.2 from October through July, whereas the slope increased between August and October. For larch, the slope increased from October through November and decreased from April through June. The slope maintained a low value between 0.2 and 0.3 between June and October. These results indicate that the moisture sensitivity of P_{dw} generally decreases with time and is lower in summer for both broadleaf and larch species. Moreover, the sensitivity was higher in broadleaf litter than that of larch, except in July and August.

3.3 Effects of litter quality on litter CO₂ production

Seasonal variation in the C:N ratio of litter accumulation is shown in Fig. 8 along with respective C and N concentrations. The C:N ratio was larger for larch litter than that for broadleaf litter except in July and October, whereas the Q_{10} and slope values were smaller for larch (Figs. 6 and 7). Under the initial condition immediately after defoliation, C concentration was higher in larch litter than broadleaf litter, whereas N concentration was lower for larch, resulting in a larger C:N ratio. A large C:N ratio of fresh litter was reported for Japanese larch (Son *et al.*, 2004). The initial N concentration of 1.06% in larch litter was compatible with that measured at other Japanese larch forests (Osono *et al.*, 2003; Son *et al.*, 2004). Moreover, the C and N concentrations and a C:N ratio of broadleaf litter were within the range of those of other broadleaf species (Arunachalam *et al.*, 1998; Wedderburn and Carter, 1999; Read and Lawrence, 2003). C concentration decreased in April for both broadleaf and larch litters. The decrease in C concentration was probably due to leaching (Arunachalam *et al.*, 1998). C concentration continued to decrease until July and increased from July through October in larch litter, whereas it remained almost constant in broadleaf litter. N concentration increased from April through July and from May through August in larch and broadleaf

Fig. 8. Seasonal variations in (a) C:N ratio, (b) C concentration and (c) N concentration of broadleaf and larch litters, from October 2001 through October 2002. Each symbol denotes the mean of five replications. Vertical bars denote standard deviations.

litters, respectively; it decreased between August and October and in October for larch and broadleaf litters, respectively. As a result, the C:N ratio continued to decrease from May through September for broadleaf litter and from April through July for larch litter. The decrease in the C:N ratio with time was measured in many tree species at the early decomposition stage (Arunachalam *et al.*, 1998; Wedderburn and Carter, 1999; Moro and Domingo, 2000). On the other hand, increasing C concentration and decreasing N concentration increased the C:N ratio from July through October in larch litter. These variations during summer

and autumn were probably caused by fresh litterfall before defoliation.

In general, fresh leaf litter with a larger C:N ratio was decomposed slowly at the early stage because the growth of microorganisms is constrained under the condition of low N concentration (Enrquez *et al.*, 1993; Berg, 2000; Moro and Domingo, 2000). Consistent with previous studies, P_{dw} of broadleaf litter was higher than that of larch litter with higher C:N ratio under high temperature conditions (Fig. 1). In addition, higher sensitivities of P_{dw} to temperature and moisture were observed in the broadleaf litter. However, under low temperature or moisture conditions, P_{dw} of larch litter was higher than that of broadleaf litter. As a result, there was no distinct difference in CO₂ production between broadleaf and larch litters, whereas large differences in C:N ratio do exist between these litters. This fact implies that the temperature and moisture conditions can affect the relationship between the C:N ratio and the decomposition rate.

Figure 9 shows the relationship between P_{dw} and the C:N ratio. For broadleaf, P_{dw} showed a positive linear relationship ($p < 0.05$) with the C:N ratio under each temperature condition. This relationship shows the time evolution of P_{dw} of fresh litter supplied in October. P_{dw} decreased as the C:N ratio decreased (Figs. 3 and 8). The slope of the linear relationship between P_{dw} and the C:N ratio increased with temperature. Also, P_{dw} changed linearly with C or N concentration, whereas their linearity (r^2) was lower than using the C:N ratio. For larch litter, however, data were divided into two groups. The right-hand data shows the time course of decreasing P_{dw} with the decreasing C:N ratio from November through June, whereas the left-hand data show the increasing P_{dw} with the increasing C:N ratio from July through October (Figs. 3 and 8). The relationship was shifted from the right-hand side to the left-hand side between June and July, and returned to the right-hand side in November. This clockwise rotation was probably caused by N-rich fresh litterfall supplied gradually in summer and autumn before defoliation.

There was a positive linear relationship ($p < 0.05$) between Q_{10} of P_{dw} and the C:N ratio for both broadleaf and larch litters (Fig. 10). Moreover, the slope of the linear relationship between P_{dw} and θ increased linearly ($p < 0.05$) with the C:N ratio at 21C for both broadleaf and larch litters (Fig. 11). Nevertheless, that linear relationship was not significant at lower temperatures. Moisture sensitivity of P_{dw} of the broadleaf

Fig. 9. Relationship between P_{dw} and C:N ratio at four temperatures for (a) broadleaf and (b) larch. Data were used within the moisture range of 1–3 g g^{-1} . Each symbol denotes the mean of four replications. A positive linear relationship was found at each temperature for broadleaf litter ($p < 0.05$).

Fig. 10. Relationship between Q_{10} of P_{dw} and C:N ratio for broadleaf and larch litters. Data were used within the moisture range of 1–3 g g^{-1} . A positive linear relationship was found for each of broadleaf and larch ($p < 0.05$).

litter was about three times higher than that of larch litter at 21°C. These facts show that the sensitivities of P_{dw} of a leaf litter to temperature and moisture are related to the C:N ratio, and the sensitivities are higher when the leaf litter has a larger C:N ratio. The C:N ratio can be a measure of relative freshness of litter (Fig. 8). Thus, the significant relationships with the C:N ratio in Figs. 10 and 11 suggest that the sensitivities of litter CO_2 production to temperature and moisture reduce as litter decomposition progresses.

4. Conclusions

This study revealed seasonal variations in CO_2 production of leaf litter through microbial respiration

Fig. 11. Relationship between the slope of linear relationship between P_{dw} and moisture at 21°C and C:N ratio for broadleaf and larch litters. Data were used within the moisture range of 0–3 g g^{-1} . A positive linear relationship was found for both broadleaf and larch ($p < 0.05$).

for both broadleaf and larch at the early decomposition stage. Although the seasonal patterns differed somewhat according to temperature and species, P_{dw} reached the minimum in June. The moisture sensitivity of P_{dw} decreased with time and reached the minimum in summer for both broadleaf and larch litters, whereas the seasonal pattern of the temperature sensitivity (Q_{10}) was not clear. The seasonal pattern of P_{dw} was explained by its C:N ratio for broadleaf litter. For larch, however, the relationship between P_{dw} and the C:N ratio was complicated because of fresh litterfall supplied gradually before defoliation. The temperature and moisture sensitivities of P_{dw} changed in parallel

with the C:N ratio for both broadleaf and larch litters, respectively. These facts suggest the importance of litter chemical quality in the early decomposition process of fresh litter.

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References

- Aerts, R., 1997: Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.
- Arunachalam, A., Maithani, K., Pandey, H. N. and Tripathi, R. S., 1998: Leaf litter decomposition and nutrient mineralization patterns in regrowing stands of a humid subtropical forest after tree cutting. *For. Ecol. Manage.*, **109**, 151–161.
- Berg, B., 2000: Litter decomposition and organic matter turnover in northern forest soils. *For. Ecol. Manage.*, **133**, 13–22.
- Boone, R. D., Nadelhoffer, K. J., Canary, J. D. and Kaye, J. P., 1998: Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature*, **396**, 570–572.
- Chapin, F. S. III., Matson, P. A. and Mooney, H. A., 2002: *Principles of Terrestrial Ecosystem Ecology*. Springer, New York, pp. 436.
- Coûteaux, M-M, Bottner, P. and Berg B., 1995: Litter decomposition, climate and litter quality. *Tree*, **10**, 63–66.
- ECONIXE Co., Ltd., 2004: Report of the forest research in the Tomakomai FRS. pp. 24 (エコニクス(株), 2004: 北方林の温室効果ガスフラックス観測等に係る調査区の植物調査業務報告書(平成15年度)).
- Enríquez, S., Duarte, C. M. and Sand-Jensen, K., 1993: Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C:N:P content. *Oecologia*, **94**, 457–471.
- Fang, C and Moncrieff, J. B., 2001: The dependence of soil CO₂ efflux on temperature. *Soil Biol. Biochem.*, **33**, 155–165.
- Federer, C. A., 1982: Subjectivity in the separation of organic horizons of the forest floor. *Soil Sci. Soc. Am. J.*, **46**, 1090–1093.
- Fierer, N., Allen, A. S., Schimel, J. P. and Holden, P. A., 2003: Controls on microbial CO₂ production: a comparison of surface and subsurface soil horizons. *Global Change Biol.*, **9**, 1322–1332.
- Hirano, T., Hirata, R., Fujinuma, Y., Saigusa, N., Yamamoto, S., Harazono, Y., Takada, M., Inukai, K. and Inoue, G., 2003a: CO₂ and water exchange of a larch forest in northern Japan. *Tellus*, **55B**, 244–257.
- Hirano, T., Kim, H. and Tanaka, Y., 2003b: Long-term half-hourly measurement of soil CO₂ concentration and soil respiration in a temperate deciduous forest. *J. Geophys. Res.*, **108**(D20), 4631, doi: 10.1029/2003JD003766.
- Hoorens, B., Aerts, R. and Stroetenga, M., 2002: Litter quality and interactive effects in litter mixtures: more negative interactions under elevated CO₂? *J. Ecol.*, **90**, 1009–1016.
- Liang, N., Nakadai, T., Hirano, T., Qu, L., Koike, T., Fujinuma, Y. and Inoue, G., 2004: *In situ* comparison of four approaches to estimating soil CO₂ efflux in a northern larch (*Larix kaempferi* Sarg.) forest. *Agric. For. Meteorol.*, **123**, 97–117.
- Moro, M. J. and Domingo, F., 2000: Litter decomposition in four woody species in a Mediterranean climate: weight loss, N and P dynamics. *Annals Bot.*, **86**, 1065–1071.
- Osono, T., Fukasawa, Y. and Takeda, H., 2003: Roles of diverse fungi in larch needle-litter decomposition. *Mycologia*, **95**, 820–826.
- Read, L. and Lawrence, D., 2003: Litter nutrient dynamics during succession in dry tropical forests of the Yucatan: Regional and seasonal effects. *Ecosystems*, **6**, 747–761.
- Skambracks, D. and Zimmer, M., 1998: Combined methods for the determination of microbial activity of leaf litter. *Eur. J. Soil Biol.*, **34**, 105–110.
- Son, Y., Jun, Y., Lee, Y., Kim, R. and Yang, S., 2004: Soil carbon dioxide evolution, litter decomposition, and nitrogen availability four years after thinning in a Japanese larch plantation. *Commun. Soil Sci. Plant Anal.*, **35**, 1111–1122.
- Wedderburn, M. E. and Carter, J., 1999: Litter decomposition by four functional tree types for use in silvo-pastoral systems. *Soil Biol. Biochem.*, **31**, 455–461.

異なる落葉樹林のリターの分解初期段階における CO₂ 発生速度の季節変化

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要 約

2001年10月～2002年10月の積雪期を除いて毎月、北海道の落葉広葉樹林とカラマツ林において、リタートラップやリターバッグを用いずに、自然条件の林床から直接リーフリターを採取した。分解の初期段階(最初の一年間)における微生物呼吸によるリターのCO₂発生(季節変化や環境依存性を調べるために、採取したリターのCO₂発生速度を、異なる温度および含水率の条件で、チャンバー法を用いて実験室で測定した。リターの分解速度を意味する単位乾物重あたりのCO₂発生速度(P_{dw})は季節変化を示した。 P_{dw} の季節変化は温度やリターの種類によって少し異なったが、いずれの場合も P_{dw} は6月に最低になった。 Q_{10} で表される P_{dw} の感温性には明瞭な季節変化がみられなかったが、 P_{dw} の含水率に対する感受性(感湿性)には、落葉広葉樹およびカラマツのリターの両方で

季節変化が認められた。 P_{dw} の感湿性は、落葉からの時間とともに低下し、夏期に最低となった。落葉広葉樹のリターにおける P_{dw} の季節変化は、C:N比で代表されるリターの化学特性で一部説明できた。しかしカラマツのリターでは、夏から秋にかけて少しずつ供給される新鮮なリターフォールの影響を受けたため、C:N比と P_{dw} の関係は複雑であった。なお、 P_{dw} の感温性(Q_{10})および P_{dw} の感湿性は、両者ともにC:N比と同様の季節変化を示した。このことは、リーフリターの分解過程の初期段階における化学特性の重要性を示しているとともに、化学特性の指標としてC:N比が有効なことを示唆している。

キーワード：感温性，感湿性，C:N比，微生物呼吸，
リターの分解