Comparative study of the mass loss rate of moss litter in boreal and subalpine forests in relation to temperature

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The moss *Hylocomium splendens* shows a very wide distribution in the Northern Hemisphere and may be useful as an indicator of climatic change on a global scale. We aimed to establish a convenient method to estimate the annual rate of litter mass loss of this species. The rate was calculated from the annual litter production rate and the amount of litter accumulated in the field. The litter production rate was estimated by analysis of the moss shoot growth. The rates calculated by this method tended to be larger than estimates obtained by the litter bag method. Using this method, we examined the difference in the litter mass loss rate along the altitudinal and latitudinal temperature gradients. The moss samples were collected from three boreal forests in Canada and four subalpine forests in Japan. At the subalpine sites, the annual rate of litter mass loss was within the range of 10-24% and tended to be smaller with increasing altitude. The rates in the boreal sites were similar to those in the subalpine sites despite lower mean annual temperatures. A significant log-linear relationship was observed between the annual mass loss rate and the cumulative value of monthly mean air temperatures higher than 0° C (CMT). Nitrogen concentration of the litter was positively correlated with mean annual air temperature. Site to site variation in the annual mass loss rate was largely explained by CMT and nitrogen concentration of the litter.

Key words: boreal forest; climate; decomposition; Hylocomium splendens; moss litter; subalpine forest.

INTRODUCTION

Recently, the impact of climatic change on the carbon cycle in the ecosystem has received considerable attention. It has been pointed out that ecosystems with a cool climate, such as boreal, arctic and alpine regions, are especially sensitive to global warming (e.g. Kojima 1994; Grabherr *et al.* 1994). In contrast with tropical rainforests, the bulk of organic carbon in boreal systems is stored in the soil (e.g. Dixon *et al.* 1994). Global warming is thought to reduce soil carbon storage by stimulating the decomposition process. However, considerable uncertainty exists as to the long-term effect of global warming on the decomposition process (e.g. Kojima 1994).

Comparative studies of decomposition rates along climatic gradients may offer some valuable information about the impact of climatic change. A number of authors have studied the rates of litter decomposition along climatic gradients (e.g. Jenny *et al.* 1949; Meentemeyer & Berg 1986; Dyer *et al.* 1990). Recently, Johansson *et al.* (1995) examined the decomposition rates of Scots pine (*Pinus sylvestris* L.) needle litter at 22 sites over a 2000 km-long transect ranging from the Arctic Circle in Scandinavia to northern continental Europe. On Mauna Loa volcano in Hawaii, Vitousek *et al.* (1994) studied the differences in the decomposition rate of *Metrosideros* litter along gradients of altitude, precipitation and substrate age.

One of the difficulties in these comparative studies is that litter decomposition rates often differ significantly even among plant species of the same genus (e.g. Johnson & Damman 1991). According to this, plant species that have a worldwide distribution are suitable for comparative studies of litter decomposition on a wide scale.

Hylocomium splendens (Hedw.) B.S.G. is one of the most abundant moss species in boreal and subalpine forests showing a very wide distribution

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in the Northern Hemisphere (Schofield 1985). Feather mosses, including this species, make a significant contribution to the net primary production of boreal forest ecosystems (Oechel & Van Cleve 1986). Because this species produces an easily identifiable segment each year, the annual growth rate can be easily measured (Tamm 1953; Skre & Oechel 1979). If the decomposition rate can also be easily estimated, this species would serve as a useful indicator of litter decomposition in boreal and subalpine regions.

In this study, we (i) establish a convenient method to estimate the mass loss rate of *H. splendens* litter and (ii) examine the relationship between the mass loss rate and temperature conditions of the habitats. For (i) we estimated annual mass loss rate of the litter using a simple model and compared the estimated values with those obtained by the litter bag method. For (ii) we examined the difference in mass loss rate along the altitudinal and latitudinal temperature gradients.

STUDY SITES AND METHODS

Study sites

The samples were collected from three boreal sites in Canada and four subalpine sites in Japan (Table 1).

Two study sites were set in the boreal forest near Candle Lake in Saskatchewan, Canada. One of the study sites (BSD) was dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) with a few aspen individuals (*Populus tremuloides* Michx.). The tree height ranged from 10 m to 16 m, and some individuals were over 80 years old. The ground water table was not observed at a depth of 70 cm beneath the soil surface. A thick moss layer mainly consisting of *Hylocomium* covered the ground. The other site (BSW) was situated about 30 km northwest of BSD. It was also dominated by black spruce with a scattering of jack pine individuals (*Pinus banksiana* Lamb.). The stand age exceeded 100 years. The ground water level was as high as 40 cm beneath the soil surface. The ground was totally covered with the feather mosses *Pleurozium schreberi* (Brid.) Mitt., *H. splendens* and *Ptilium cristacastrensis* (Hedw.) De Not. This study site was one of the Southern Boreal Forest Super Sites in the Prince Albert area for the Boreal Ecosystem-Atmosphere Study (BOREAS) project.

Sample collection was also carried out in a forest stand (STR) near Stony Rapids in Saskatchewan, about 600 km north of Candle Lake. The dominant tree species in this area was jack pine, with a scattering of small stands of black spruce. *Hylocomium splendens* was mostly found in the black spruce stands.

The study sites in the Japanese subalpine forest were set at four different altitudes – 2400 m, 2200 m, 1800 m and 1700 m – on the northwestern slope of Mt Fuji and named FJA, FJB, FJC and FJD, respectively. The distances between the nearest sites were less than 1.5 km. The dominant tree species were *Tsuga diversifolia* (Maxim.) Masters and *Abies veitchii* Lindley. Various bryophyte species, including *H. splendens*, were found on the forest floor. The species composition of these bryophyte communities in relation to forest succession was described by Nakamura (1984).

At these study sites, the lower part of the moss layer was composed of brown, dead moss shoots mixed with undecomposed conifer litter. This layer

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

	Site			Altitude (m)	Mean annual temperature (°C)*
Name	Location	Latitude	Longitude		
BSD	Candle Lake	53°50'N	105°30′W	500	0.6
BSW ¹	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°24′N	138°42′E	1800	4.6
FJD	Mt Fuji	35°24'N	138°42′E	1700	5.2

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

will from here on be referred as the L layer. Under the L layer, there was a thick FH layer composed mainly of well-decomposed moss shoots and humus. The L layer could be easily separated from the FH layer as fine roots developing in the FH layer aggregated decomposed plant materials. In the boreal sites, an extensive growth of filamentous fungi was observed at the boundary of the two layers.

Methods

Five or six almost pure stands of *H. splendens* were selected in each study site. Part of each stand, $15 \text{ cm} \times 15 \text{ cm}$ in surface area, was cut vertically to the FH layer, and a moss block composed of green shoots and the L layer was collected.

The number of green 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 (1953). These segments and the moss litter in the L layer were dried to a constant weight at 80 °C to obtain the dry weight. The nitrogen concentration of the litter was measured with a CN-corder (Yanaco MT-500, Yanagimoto Co. Ltd, Kyoto, Japan).

The annual mass loss rate of the moss litter was calculated by the simple model proposed by Jenny *et al.* (1949) assuming a constant litter production (*L*) and a constant litter mass loss rate (k') on an annual basis.

Hylocomium splendens produces a new, readily identifiable segment each year (e.g. Tamm 1953). Each segment increases its weight for 1 or 2 years to attain its full size. These fully grown segments constitute the largest age class. The dry weight of these segments are relatively stable for at least one season before they decompose (cf. Tamm 1953; Busby *et al.* 1978). If the annual net production rate and annual litter mass loss rate are constant, the biomass of the largest age class corresponds to the annual litter production L (Skre & Oechel 1979). Therefore, *n* years after the beginning of the decomposition, the weight of the segment (S_n) can be expressed as:

$$S_n = Lr^n \tag{1}$$

where r is the remaining proportion of the litter (r = 1 - k').

The total amount of litter, including the largest

age class accumulated over time n (M_n) , can be estimated as:

$$M_n = L(1 - r^{n+1})/(1 - r)$$
(2)

If *n* is large enough to reach a steady state, the amount of litter at the steady state, (M_m) is given by the following simple equation (Ogawa *et al.* 1961; Olson 1963).

$$M_m = L/(1-r) = L/k'$$
 $k' = L/M_m$ (3)

At the sites examined in this study, the largest age class was the 2-year-old segment. The annual mass loss rate k' was calculated from the total amount of moss litter in the L layer assuming that it approximated M_m . Therefore, the value k' includes the mass loss by fragmentation and incorporation into the FH layer.

The litter bag method was also employed to determine the mass loss rate at BSD and BSW. Moss blocks composed of green shoots and the L layer were collected from BSD on 31 July 1994. The green shoots (0–2-year-old segments) were discarded. Air dried litter, about 3 g in dry weight, was put in a nylon mesh bag (7 cm \times 10 cm, 0.7 mm mesh). In early August 1994, 12 bags with moss litter were placed between the L layer and the FH layer in each study site. They were collected to measure the loss in dry weight on 20 July 1995.

Climatic data

In order to examine the relationship between the mass loss rate and the temperature, monthly mean air temperatures at the study sites were estimated from data recorded at nearby weather stations. Temperatures at the two Candle Lake study sites (BSD and BSW) were estimated from the data recorded at Prince Albert (53°13'N, 105°41'W; 440 m a.s.l.) for 30 years (1961-1990). Since climatic data was not available for Stony Rapids, those recorded at Uranium City, Saskatchewan (59°32'N, 108°43'W) for 26 years (1961-1986) were used. Temperatures at each Mt Fuji study site were estimated from the data recorded at Kawaguchiko (35°29'N, 138°46'E; 860 m a.s.l.) and the summit of Mt Fuji (35°21'N, 138°44'E; 3776 m a.s.l.) for 30 years (1961-1990) using the local environmental lapse rate of $0.59^{\circ}C \ 100 \ m^{-1}$.



Fig. 1. Annual mass loss of *Hylocomium splendens* litter at the two Candle Lake study sites, determined by the litter bag method (\blacksquare ; n = 12) and by the model (\square ; n = 6). Vertical bars represent SE.

RESULTS

Comparison between the two methods

Figure 1 shows the annual litter mass loss of *H. splendens* estimated by the model and the litter bag method at the two Candle Lake study sites. The mean values of annual mass loss at BSD and BSW estimated by the model were 18.6 and 15.2%, respectively. These values were larger than those obtained by the litter bag method (12.2 and 13.1%). The difference in the mass loss rate between the two methods was significant for BSD (*t*-test; P < 0.05), although it was not significant for BSW. However, the mass loss rates of the two study sites, determined by each method, did not differ significantly.

Site to site difference in the mass loss rate

Table 2 summarizes the annual litter production rate, litter accumulation in the field and the annual rate of litter mass loss estimated by the model. The nitrogen concentration of the largest segments (2-year-old segments) is also shown in the table. Annual litter production rate of the boreal sites ranged from 72 to 97 g m⁻² y⁻¹. There was no significant difference in litter production among the three sites. On the other hand, the annual litter production rate in the subalpine sites (27–40 gm⁻² y⁻¹) was almost half of the values in the boreal sites.

In the subalpine sites of Mt Fuji, litter accumulation increased from 167 to 266 g m⁻² as the elevation became higher, while no altitudinal difference was observed in litter production. As a result, the mass loss rate tended to be smaller with increasing altitude, although this was not true for the difference between FJC and FJD. The average mass loss rates were significantly correlated with the annual mean air temperature in a log-linear fashion (Fig. 2). We calculated Q_{10} for the mass loss rate (the proportional increase in mass loss rate for a 10°C increase in temperature) from mean annual air temperatures at the study sites. The Q_{10} value calculated for the subalpine sites was 8.7.

The relationship between the annual mass loss rate and the mean annual temperature was significant even if the data of boreal sites were included (r = 0.795, P < 0.05; Table 3). However, the rate at Stony Rapids (STR) was similar to the rate at FJA despite much lower mean annual temperature in the former site. Similarly, the mass loss rate at BSD at Candle Lake was higher than that at FJA despite a

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

Site	Litter production (g m ⁻² y ⁻¹)*	Litter accumulation (g m ⁻²)*	Annual mass loss (%)*	N concentration (mg g ⁻¹) ⁺
BSD	72 (8) ^a	454 (106) ^{ab}	18.6 (2.6) ^{abc}	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) ^ь	10.1 (0.6) ^c	10.3 (2.0) ^{ab}
FJB	36 (5) ^b	262 (38) ^b	14.1 (1.8) ^{bc}	9.3 (0.6) ^{ab}
FJC	40 (4) ^b	173 (13) ^ь	$24.3(3.2)^{a}$	$14.8(1.1)^{a}$
FJD	39 (7) ^ь	167 (26) ^ь	22.9 (2.4) ^{ab}	13.8 (0.6) ^a

*Values are means with SE in parentheses; n = 5 (STR) or 6 (other sites). *Values are means of three samples with SE in parentheses. Means followed by the same letter within a column are not significantly different (Tukey test, P > 0.05).



Fig. 2. Annual mass loss of *Hylocomium splendens* litter (log scale) as a function of mean annual air temperature. Each value is the mean of five or six samples. The solid line shows the regression line calculated for the Mt Fuji sites: $Y = 8.18 \exp(0.216x)$. \bullet , Mt Fuji; \blacksquare , Candle Lake; \blacklozenge , Stony Rapids.

Table 3 Log-linear relationship between annual mass loss, temperature and nitrogen concentration of *Hyloco-mium splendens* (n = 7)

Linear relation	r	Р
log (mass loss) =		
1.124 + 0.0433MAT	0.795	P < 0.05
0.362 + 0.0122CMT	0.881	P < 0.01
1.069 + 0.0353MAT + 0.0069N	0.798	NS
0.346 + 0.0095CMT + 0.0201N	0.980	P < 0.005

MAT, mean annual air temperature (°C); CMT, cumulative value of monthly mean air temperatures higher than 0°C (°C); N, nitrogen concentration (mg g⁻¹).

lower mean annual temperature at Candle Lake. The Q_{10} for the mass loss rate calculated for the boreal sites was 3.7.

The low mean annual temperatures in the boreal sites are largely due to low temperature conditions in winter. For example, the monthly mean air temperature in January at Candle Lake was -19.8 °C, while that at FJA at Mt Fuji was -10.6 °C. On the other hand, the mean air temperature of the snow-free season (May–October) was higher at Candle-Lake than at the Mt Fuji study sites. Since the temperature conditions under snow cover often differ widely from the air temperature (e.g. Taylor & Jones 1990), air temperatures in winter might have little effect on the annual decomposition rate. In fact, the annual mass loss was related more closely to



Fig. 3. Annual mass loss of *Hylocomium splendens* litter (log scale) as a function of the cumulative value of monthly mean air temperatures higher than 0°C. Each value is the mean of five or six samples. The solid line shows the regression line calculated for all study sites: Y = 2.31 exp (0.028x). \bullet , Mt Fuji; \blacksquare , Candle Lake; \blacklozenge , Stony Rapids.

the cumulative value of monthly mean temperatures higher than 0° C (CMT; r = 0.881, P < 0.01; Table 3; Fig. 3).

Nitrogen concentration of the litter also varied significantly among the study sites. Nitrogen concentration of the 2-year-old segments tended to be smaller with decreasing mean annual air temperature (Fig. 4). The annual mass loss rate (mean value



Fig. 4. Relationship between mean annual air temperature and the nitrogen concentration in the largest (2-yearold) segments of *Hylocomium splendens*. Each value is the mean of three samples. The solid line shows the regression line calculated for all study sites: Y = 1.16x + 7.99; r = 0.911. \bullet , Mt Fuji; \blacksquare , Candle Lake; \blacklozenge , Stony Rapids.

of each study site) was positively correlated with the nitrogen concentration of the litter (r = 0.80; P < 0.05).

The combination of nitrogen concentration with CMT resulted in a highly significant relationship which accounts for 96% of the mass loss. On the other hand, the relationship between annual mass loss rate, mean annual temperature and nitrogen concentration was not significant (Table 3).

DISCUSSION

Applicability of the method

The model used in this study is based on the assumption that the annual mass loss is almost constant. However, this assumption may not be realistic. It is well known that plant litter contains persistent compounds as well as readily decomposable ones. As decomposition proceeds, the content of persistent compounds would increase (cf. Davis 1980). It appeared that the stem of H. splendens is more resistant to decomposition than the leaves, since the lowest (oldest) part of the shoots were composed mainly of the stem. According to this point, the value obtained by the model should be regarded as the average rate of mass loss in the L layer. Another important assumption is that the moss stand is old enough to reach the steady state. The minimum length of time (years) necessary to reach 95% of the maximum litter accumulation (n_{c}) can be calculated by equation 2 for a given k'. If the annual mass loss rates are 10 and 20% (k' = 0.1 and (0.2), n_c is calculated as 28 and 13 years, respectively. The age of the forest trees of the study sites seems to be large enough for the moss stand to reach a steady state.

For the litter bag method, we used the moss litter collected from the L layer as a whole. Therefore, the mass loss rates obtained by the litter bag method can be regarded as the average rate in the L layer. However, the values obtained by the model were larger than those obtained by the litter bag method. This may be partly due to the difficulty in determining the litter accumulation in the field. Some parts of the well-decomposed litter inevitably fragmented and fell from the L layer into the deeper soil layer (FH layer). This would result in an overestimation in the model.

The difference in growth rates between years is another important factor that directly affects the mass loss rate obtained by the model. Tamm (1953) reported that the annual growth rate of *H. splendens* sometimes differed significantly between years. In this study, annual litter production rate was estimated from the biomass of the largest age class of the moss blocks. If the growth condition of the age class was better than usual, this would result in an overestimation of the mass loss rate. However, the annual litter production rates at BSD determined in 1994 and 1995 did not differ significantly (data not shown).

It is also possible that the mass loss rates obtained by the litter bag method were underestimated. Brown and Bates (1990) pointed out several difficulties in the litter bag method for the measurements of moss litter decomposition. The selection of suitable mesh size of the bags is of critical importance. We used bags of relatively small mesh size (0.7 mm) to minimize the loss of small particles. This might result in an underestimation of the mass loss rate since the effects of large decomposers were excluded. In addition, the moisture condition in the bags might be different from that in natural conditions.

These data suggest that special care should be taken when mass loss rates estimated by the model are compared with those determined by the litter bag method. However, the former approach seems to be useful as long as it is used for comparative studies. We can rapidly estimate the annual mass loss rate by analyzing moss blocks collected at one time. In addition, the litter production rate data may give us some useful information about environmental conditions at the forest floor.

Site to site differences in the mass loss rate

The annual mass loss rates obtained in this study were much faster than those reported for mosses in maritime Antarctica (Davis 1980), but within the range of mass loss rates of *Sphagnum* in peatlands (e.g. Johnson & Damman 1991). Similar mass loss rates were reported for *Dicranum polysetum* Sw. in a mature Scots pine forest (Berg 1984) and for *Calliergonella cuspidata* (Hedw.) Loeske in Dutch chalk grasslands (van Tooren 1988). At Mt Fuji, Nakatsubo (1990) reported a much slower mass loss rate (about 10% for 3 years) for *Racomitrium lanuginosum* (Hedw.) Brid. growing in an open lava field near FJA. This is probably due to the xeric conditions prevailing in the lava field and/or the lower nitrogen concentration of *R. lanuginosum* (Nakatsubo 1990).

In the subalpine sites, the annual mass loss tended to decrease with increasing altitude. This suggests that altitudinal change in temperature largely controlled the decomposition rate. In fact, the mass loss rates were significantly related to temperature in a log-linear fashion. Since the decomposition process is affected by the moisture condition as well, the effects of moisture may not be eliminated. However, it is assumed that moisture fluctuation is more pronounced in the green surface layer than in the brown (litter) layer of the moss stand. Despite the fact that the moss production rate is sensitive to moisture conditions (e.g. Nakatsubo *et al.* 1989), the annual litter production rate did not differ significantly among the subalpine sites.

The Q_{10} values obtained in this study were much larger than those obtained for soil respiration in previous studies (e.g. Rosswall et al. 1975; Tate et al. 1993). Recently, however, Vitousek et al. (1994) reported similar large Q_{10} values, ranging from 4 to 11, for the decomposition of Metrosideros leaf litter on Mauna Loa. The large Q_{10} values obtained in this study may be partly due to the cool climatic conditions at the study sites. Kirschbaum (1995) pointed out that the temperature sensitivity of soil (litter) respiration decreased with increasing temperature. He estimated that the Q₁₀ of decomposition was almost 8 at 0°C. Our data as well as the Kirschbaum (1995) study may suggest that decomposition in cool climatic regions is especially sensitive to temperature increase.

The mass loss rates at the Candle Lake study sites and Stony Rapids were comparable to those at Mt Fuji despite lower mean annual temperatures at the former sites. When data from the boreal sites were included, annual mass loss was related more closely to the cumulative value of monthly mean air temperatures higher than 0°C (CMT). This supports the earlier assumption that air temperatures in winter have little effect on the annual decomposition rate.

Annual precipitation was much lower in the boreal sites (<400 mm) than in the subalpine sites (>14000 mm). However, marked suppression of the mass loss rate was not detected in the former sites. This may be partly due to the high water table in the boreal sites.

Climatic conditions not only affect soil microbial activity but also change litter quality, which in turn affects the decomposition rates. Berg et al. (1995) reported that concentrations of nitrogen, phosphorus, sulfur and potassium in Scots pine needle litter increased with increasing actual evapotranspiration and decreasing latitude. In this study, the nitrogen concentration of the litter was positively correlated with the mean annual air temperature. This change in nitrogen concentration might have resulted from the difference in nitrogen availability and/or the physiological response of the plant to different climatic conditions. A positive correlation was also observed between annual mass loss and the nitrogen concentration of the litter. This is in contrast with the study of Johansson et al. (1995) who found no significant correlation between first-year mass loss and nitrogen concentration in Scots pine needle litter.

In this study, site to site differences in the mass loss rate of *H. splendens* litter was largely explained by the temperature conditions in the snow-free season (CMT) and the litter quality (nitrogen concentration). However, considerable uncertainty still exists as to the mechanism involved. The mechanism by which temperature condition affects the litter quality is not clear. The community structure of soil microorganisms may also change with changing temperature. In order to assess the long-term effect of the climatic change on decomposition, improvement of our understanding about these effects seems to be necessary.

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