

Accumulated organic matter, litterfall production, and decomposition tell us the status of litter dynamics in forests

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Abstract

Litterfall dynamics in forests are assessed by estimating biomass production and decomposition. However, there have been few studies on how litter dynamics impact the health and management of ecosystems. Here, a new approach to measure and assess ecosystem function is presented based on conventional methods using littertraps, litterbags, and the mass on the forest floor. To assess the status of litter dynamics, the decay rate (k) was estimated from a litterbag experiment, and removal rates (k_r) were determined from mass balance on the forest floor at 21 sites on three mountains in South Korea. The k_3 (organic mass ratio of O_i and $O_e + O_a + A$ horizons in November) values in an equilibrium state in South Korea were within the range of $k \pm 0.174$ when considering the annual variation of litterfall production. This study also suggests that sampling sites for these types of studies should be in the middle, not at the ends, of steady slopes on the forest floor.

Key words: accumulated organic matter, assessment of litter dynamics status, decay rate, decomposition, forest floor, litterfall, Olson's model, removal rate

INTRODUCTION

Nutrient input and output in ecosystems is important for nutrient cycling. The rate of litterfall and decomposition as an important pathway for the transfer of litter mass and minerals to the soil surface in forest ecosystem has been quantified by many researchers (Gosz et al. 1973, Birk and Simpson 1980, Hobbie et al. 2006). Litterfall is dominant among the aboveground components of nutrient input (Kim and Chang 1989, Shin et al. 2011), and litter production in forest ecosystems varies with community structure and nutrient conditions. Temperature, precipitation, soil, light, and other environmental factors can also have an impact (Barbour et al. 1999). Litterfall generally increases during succession and has been shown to peak at various times depending upon the region and forest type: 14 years in eastern Guatemala (Ewel 1976), 46 years in *Alnus* plantation in the eastern Himalaya (Shar-

ma and Ambasht 1987), and the period of crown closure in Douglas-fir stands as the time of maximum wood productivity (Turner and Long 1975).

Forest litter decomposition rates are known to be influenced by macro- and microclimate variables (Edwards 1975, Insam 1990), as well as by the chemical composition of the litter (Meentemeyer 1978, Melillo et al. 1982, Gallardo and Merino 1993, Rustad 1994, Laskowski et al. 1995, Hobbie et al. 2006). On a global scale, rates of litter decomposition are regulated by climate (Johansson et al. 1995). However, within a particular climatic region, litter chemistry was known to be the best indicator of decomposition rates (Taylor et al. 1991, Aerts 1996). Litter lignin content is negatively related to mass loss and is positively correlated to the calcium content (Hobbie et al. 2006). Soil microbes biologically decompose most lit-

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ter and microclimate or microenvironmental conditions are also important factors for decomposition (Yavitt and Fahey 1986).

Decomposition rates are also related with succession. This rate was found to peak at 30 years in an *Alnus* plantation in the eastern Himalayas (Sharma and Ambasht 1987) and in a 24-year-old stand of Douglas firs, where temperature and moisture conditions were most favorable (Edmonds 1979). However, Ewel (1976) reported that loss of dry weight occurs at a generally consistent rate regardless of the age of the forest.

In a forest, litter production and decomposition are responsible for the formation of the forest floor; this formation is a long-term process that is indicative of the nutrient cycling rate (Johansson et al. 1995). Litter accumulates on the soil surface until litterfall equals litter decomposition; after which, the amount of litter accumulated on the soil surface oscillates around some mean steady-state value (Ewel 1976). Litter decomposition rates and forest floor characteristics yield information about the quality of litter as well as the rates of nutrient cycling within an ecosystem (Knoepp et al. 2000).

Ecosystem functional processes (e.g., productivity and decomposition) are generally known as important indicators of ecosystem stability or homeostasis (van Voris et al. 1980, Odum 1985, Rapport et al. 1985). Decomposition is a function of an ecosystem that includes a robust food chain supporting the desired biota, an adequate nutrient pool for desired organisms, and adequate nutrient cycling to perpetuate the ecosystem (Schaeffer et al. 1988). It is an important indicator of ecosystem stability involving the interaction of vegetation, soil nutrient availability, micro- and macro-fauna, and microbial populations (Knoepp et al. 2000). If decomposition is impaired, the ecosystem is functionally impaired (Schaeffer et al. 1988). Decomposition rates can provide an accurate prediction of soil and site quality or productivity (Johansson 1994). Increasing rates of litter decomposition accelerate nutrient cycling rates within the site and indicates increased soil quality (Johansson et al. 1995). However, it is not easy to assess the status of nutrient dynamics based on production and decomposition without long-term monitoring. Gessner and Chauvet (2002) suggested a method for evaluating ecosystem health using a decomposition rate k (impacted)/ k (reference) ratio in stream ecosystems. In the present study, another complementary approach for assessing ecological integrity of forest ecosystems is proposed, which compares decomposition rates calculated by litterbag methods and the mass balance on the forest floor along with real and the theoretical mass remains.

In general, littertraps and litterbags are used to measure litter input and output on the forest floor. However, these methods have inherent problems, including large variation in litterfall from year to year, difficulties in accounting for very small litter fragments, short experimental periods, and the accessibility of the litterbag to organism (Knutson 1997). To avoid these problems, Knutson (1997) estimated annual production and decomposition of litter by examining unconfined litter using the disappearance from a litter layer as a measure of decomposition. However, it is still not easy to examine all unconfined litter, and many studies have used the litter amount in each litter layer (e.g., O_i , O_e , O_a , and A horizon based on Brady and Weil 2008) to estimate decomposition rates in deciduous forests with the assumption that there was a steady state of litter input and output (Chang and Ko 1982, Chang and Kim 1983, Chang et al. 1987, Hobbie et al. 2006). However, decomposition rates estimated by the litterbag method and mass balance on the forest floor are based on different assumptions that do not often correlate.

For the litterbag method, decomposition rates can be estimated by an exponential decay model, with k being the parameter from the exponential equation:

$$X_t = X_0 e^{-kt},$$

where X_0 is the initial % weight; e the nature log constant; and k ($1/y$) the decomposition constant (Olson 1963, Swift et al. 1979). This can be converted to:

$$k = -1/t \ln(X_t/X_0).$$

In the forest floor, the decomposition rate can be estimated by mass balance assuming there is a steady state as follows (Olson 1963, Hobbie et al. 2006):

$$k_i = L/F,$$

where L is the annual litterfall organic mass, and F is the forest floor organic mass ($O_i + O_e + O_a + A$ horizon organic mass). If litter dynamics in a forest floor are in a steady state, the k value should be the same or similar to the k_i value. If the litterfall input on the forest floor is larger than the output, k_i should be less than k .

Organic accumulation (OAcc) with continuous litterfall can be expressed by the equation:

$$OAcc = (L/k) (1 - e^{-kt}),$$

in which the value of $(1 - e^{-kt})$ is close to 1 when k is larger than 0.25 and t is longer than 30 years, and $OAcc \cong L/k$. This OAcc is the theoretical organic accumulated mass on the forest floor at a steady state arrived at using current litter bag k values and current litterfall. This theoretical

value can be compared to the actual organic mass on the forest floor (OMFF) to determine if current litter dynamics are faster, slower, or equal to those in recent decades over which the forest floor mass accumulated.

Here, I suggest a hypothesis: a comparison of k and k_i will indicate the status of litter dynamics in forests. If k and k_i or OMFF and OAcc are similar, then litter dynamics are assumed to be in equilibrium or a steady state. If the litter bag-derived k values (indicative of current conditions) are smaller than k_i calculated from actual forest floor data (integrated over past decades), then the OAcc estimated using current inputs and outputs will be greater than the OMFF actually measured, which means that, therefore, in the past, litter output has been relatively greater than litter input, as compared to that ratio currently. In contrast, if $k > k_i$, then the estimated OAcc will be less than the actual OMFF, and in the past, litter output has been relatively less than litter input, as compared to that ratio currently. Field data from forests on three well-conserved mountains that have been a part of the national parks in South Korea for more than 30 years are also presented to demonstrate how to apply this new approach. Loss or gain of litter mass would be expected to differentially affect germination and establishment of plants, soil invertebrates and vertebrates, and the exchange of CO_2 with atmosphere, the carbon cycle, etc. (Schaeffer et al. 1988, Vitousek 1994, Knoepp et al. 2000, Gessner and Chauvet 2002). This study may play an important role in predicting litter-mass trajectories (steady state, increasing, or decreasing forest floor organic matter) into the future.

MATERIALS AND METHODS

Study site

I tried to find sites in a steady-state condition, which means that anthropogenic disturbances were not detected, and in the broad spectrum of sites, I tried to provide enough variation in factors, such as slope, altitude, aspect, and dominant species, that determine forest floor mass, litterfall, and decomposition. Twenty-one sites on three mountains in the southwestern part of South Korea (Jirisan, Deogyusan, and Gyeryongsan) covering low to high altitudes and including representative forest species were selected (Table 1). Altitudes of the study sites ranged from 221 m a.s.l. in Gyeryongsan to 1,567 m a.s.l. in Deogyusan. Slope aspects of the study sites varied, and slopes ranged from 18–43°. Dominant species of trees in the sites were *Carpinus laxiflora* (2 sites), *C. tschonoskii* (2 sites),

Fraxinus mandshurica (2 sites), *Quercus serrata* (3 sites), *Q. mongolica* (3 sites), *Q. variabilis* (2 sites), *Q. acutissima* (1 site), *Pinus densiflora* (3 sites; Pd1, Pd2, Pd3), and *Stewartia koreana* (1 site). Basal areas in the study sites ranged from 16.3 m²/ha to 50.2 m²/ha (average, 30.9 m²/ha). The density of trees larger than 5 cm diameter at breast height ranged from 494 trees/ha to 1,856 trees/ha (average, 958 trees/ha). The average basal area of the trees was largest at the Qs1 site in the *Q. serrata* community and smallest at the Fm2 site in the *F. mandshurica* community.

The climate of the region is summer monsoonal. Mean annual precipitation was 1,400 mm in Jirisan; 1,270 mm in Deogyusan; and 1,350 mm in Gyeryongsan, and more than half of the precipitation falls between May and August. The mean annual temperature was 12.5°C in Jirisan, 11.5°C in Deogyusan, and 12.3°C in Gyeryongsan. Soil types were silt loam or silt clay loam. Soil pH of the upper 5 cm ranged between 4 and 5 (Korea National Park Service 2002, 2004a, 2004b).

Litterfall

Rectangular litter traps with a 1-m² internal surface area were used to intercept litterfall. The bottom of the traps was a 1-mm mesh stainless steel screen. The traps were fixed 1 m above the soil surface. Two traps in Jirisan and three each in Deogyusan and Gyeryongsan were placed at each site within 50 m × 50 m quadrats. Fallen litter was harvested in the 4th week of August and November in Jirisan during 2001–2003, and the 4th week of February, 3rd week of April, and 4th week of May, July, September, and November in Deogyusan and Gyeryongsan during 2005–2008.

Litter decomposition experiments

Even though litter includes dead leaves, twigs, logs, fine roots, and soil microorganisms, dead leaf was the most abundant source of litter (Korea National Park Service 2002), and I used dead leaves as litter in this experiment. For each site, litter from the site for litterbags was obtained by collection of the litter on the O_i horizon of the forest floor in early November. The litter was mixed and air dried. Nylon litterbags measuring 20 cm × 20 cm with a mesh size of 1 mm were prepared. Litterbags were filled with 15 g of air-dried litter. The bags were anchored on the O_e layer of the forest floor with heavy gauge wire and covered with litter. Litterbags were randomly sampled in four replicates at each collection time (1, 6, 9, 12, 24, and 36 months) at each site. Samples of the initial litter and

Table 1. Characteristics of the study sites

Site	Mountain	Latitude, longitude	Altitude (m, a.s.l.)	Aspect	Slope (°)	Topographic character	Dominant species*	Basal area* (m ² /ha)	Tree density* (No./ha)	Basal area/Tree (m ² /tree)
Cl1	Jirisan	N 35°20'02", E 127°35'33"	750	W	32	Middle of steady slope	<i>Carpinus laxiflora</i>	27.1	1,468	0.018
Cl2	Jirisan	N 35°16'49", E 127°33'34"	890	E	24	Middle of steady slope	<i>C. laxiflora</i>	29.4	540	0.054
Ct1	Jirisan	N 35°16'35", E 127°33'43"	800	E	31	Middle of steady slope	<i>C. tschonoskii</i>	25.6	696	0.037
Ct2	Jirisan	N 35°16'35", E 127°33'43"	800	E	34	Middle of slope (hollow area)	<i>C. tschonoskii</i>	25.7	684	0.038
Fm1	Deogyusan	N 35°31'18", E 127°46'13"	895	E	31	Middle of steady slope	<i>Fraxinus mandshurica</i>	25.3	592	0.043
Fm2	Jirisan	N 35°19'34", E 127°35'22"	850	NE	34	Middle of steady slope	<i>F. mandshurica</i>	17.5	1,856	0.009
Pd1	Deogyusan	N 35°56'35", E 127°42'56"	557	SE	27	Middle of steady slope	<i>Pinus densiflora</i>	20.2	1,108	0.018
Pd2	Gyeryongsan	N 36°21'16", E 127°13'20"	285	W	26	Valley	<i>P. densiflora</i>	34.2	1,110	0.031
Pd3	Gyeryongsan	N 36°21'37", E 127°11'29"	221	SE	27	Middle of steady slope	<i>P. densiflora</i>	35.3	1,010	0.035
Qa	Gyeryongsan	N 36°20'28", E 127°12'10"	326	E	18	Middle of steady slope	<i>Quercus acutissima</i>	32.5	900	0.036
Qm1	Deogyusan	N 35°51'33", E 127°44'49"	1,567	SE	21	Middle of steady slope	<i>Q. mongolica</i>	30.4	638	0.048
Qm2	Deogyusan	N 35°57'02", E 127°41'37"	949	SE	19	Middle of steady slope	<i>Q. mongolica</i>	50.2	831	0.060
Qm3	Deogyusan	N 35°48'30", E 127°41'24"	828	NW	27	Middle of slope (prominent area)	<i>Q. mongolica</i>	26.9	525	0.051
Qm4	Gyeryongsan	N 36°21'47", E 127°12'46"	549	NE	22	Middle of steady slope	<i>Q. mongolica</i>	41.2	1,550	0.027
Qm5	Gyeryongsan	N 36°20'58", E 127°13'13"	279	N	43	Middle of steady slope	<i>Q. mongolica</i>	26.8	850	0.031
Qs1	Deogyusan	N 35°51'54", E 127°46'24"	871	SE	21	Middle of steady slope	<i>Q. serrata</i>	32.3	494	0.066
Qs2	Deogyusan	N 35°48'35", E 127°41'45"	756	NE	36	Middle of slope (prominent area)	<i>Q. serrata</i>	24.8	638	0.039
Qs3	Gyeryongsan	N 36°22'03", E 127°12'49"	404	E	38	Ridge	<i>Q. serrata</i>	49.5	1,140	0.043
Qv1	Gyeryongsan	N 36°21'02", E 127°12'33"	711	S	39	Broad Valley (hollow area)	<i>Q. variabilis</i>	47.9	960	0.050
Qv2	Gyeryongsan	N 36°19'40", E 127°15'49"	483	NE	39	Middle of steady slope	<i>Q. variabilis</i>	29.5	1,140	0.026
Sk	Jirisan	N 35°19'41", E 127°35'21"	800	NE	30	Middle of slope (hollow area)	<i>Stewartia koreana</i>	16.3	1,392	0.012

W, west; E, east; N, north; S, south.

*Data from the Korea National Park Service (2002, 2004a, 2004b).

all samples recovered from each site were ground in a Willey Mill, passed through a #40 mesh screen, and analyzed for moisture content (dry for 24 h at 105°C) and ash-free weight (ignition for 4 h at 550°C).

Estimation of litter removal rate by mass balance

Litter was collected in two 20 cm × 20 cm quadrats on the forest floor in each 20 m × 20 m plot during the last week of November when almost all deciduous leaves have senesced in South Korea. Litter was divided into those on O_i (L) horizon and those on O_e (F), O_a (H), and A horizons (Coleman et al. 2004, Brady and Weil 2008). The collected litter was air dried and ground in a Willey Mill to be passed through a #40 mesh screen. Ground litter was ignited in a furnace at 550°C for 4 h. The following calculations were performed with the ash-free mass.

Hobbie et al. (2006) suggested calling the estimated decomposition rate by mass balance on the forest floor (k_1) the “removal rate”; therefore I call k_1 (k_1 , k_2 , and k_3) the “removal rate.” The removal rate, k_1 , on the forest floor was calculated assuming that there was a continuous litterfall

mass (L), following Olson (1963):

$$k_1 = L/F,$$

where F is the forest floor mass at a steady state. Since litterfall was not fixed on the forest floor, litter mass on the forest floor was not the same as that collected in the littertrap. The ratio of annual litterfall to autumn litterfall was relatively constant in ecosystems where dominant species are the same (Table 2). Therefore, L was calculated from the organic mass on the O_i horizon, and the autumn/annual litter production ratio in Table 2 can be represented with the equation:

$$L = O_i \times (\text{annual litterfall}/\text{autumn litterfall}).$$

Since litterfall is relatively discrete in temperate forests, another removal rate (k_2) was calculated using Olson's equation for discrete autumn litterfall (Hobbie et al. 2006):

$$k_2 = -\ln(1 - O_i/T),$$

where T is the maximum forest floor organic mass ($T = O_i + O_e + O_a + A$). With this formula we can calculate the proportion of organic matter in the upper layer as com-

Table 2. Average annual and autumn litter production over 3 y (2001-2003) in the Jirisan sites and over 4 y (2005-2008) in Deogyusan and Gyeryongsan sites

Site	Annual litter production (g/m ²)		Autumn litter production (g/m ²)	Autumn/Annual litter production	Concentration of ash-free matter in autumn litter (%)
	Average	SD			
Cl1	373.7	114.4	357.5	0.96	95.0
Cl2	443.6	118.4	366.8	0.83	92.3
Ct1	316.4	137.9	260.1	0.82	94.5
Ct2	383.1	60.3	376.8	0.98	85.7
Fm1	416.9	42.5	316.9	0.76	94.1
Fm2	281.5	54.3	260.8	0.93	94.7
Pd1	538.4	61.5	211.6	0.39	96.1
Pd2	538.7	46.4	262.1	0.49	96.8
Pd3	637.1	70.4	249.3	0.39	94.4
Qa	497.2	15.7	312.4	0.63	95.1
Qm1	323.4	34.8	204.2	0.63	93.7
Qm2	475.5	134.4	312.9	0.66	93.7
Qm3	428.9	30.9	299.6	0.70	93.8
Qm4	398.2	91.9	237.9	0.60	95.2
Qm5	427.0	103.1	270.9	0.63	95.8
Qs1	447.1	54.6	315.8	0.71	93.7
Qs2	488.8	75.0	322.2	0.66	91.9
Qs3	474.7	181.2	296.1	0.62	95.4
Qv1	508.8	121.3	369.7	0.73	80.8
Qv2	453.5	58.7	322.3	0.71	94.4
Sk	258.6	135.0	239.4	0.93	94.7

pared to that in all layers and that minus 1 to get the value of the mass lost. For the comparison with other removal rate data from South Korea, k_3 was calculated using the equation:

$$k_3 = O_i / (O_e + O_a + A),$$

which is an adaptation of Olson's exponential decomposition equation (Kim and Chang 1966, Chang and Kim 1983, Chang et al. 1987). If O_i mass of recently fallen litter is greater than the organic mass in all the other layers below it, then k is fast (perhaps even greater than 1 per year). If O_i is less than the accumulated mass in all the other layers below it, then k is slower than in the example above.

Analysis

All data on mass loss were converted to ash-free mass because we could not remove all soil particles from the decomposed litter and forest floor mass. Olson's negative exponential decay model was used to calculate the litterbag decay constant, and all regression analyses were done by MS Excel (MS Excel 2000; Microsoft Cooperation, Redmond, WA, USA). Pearson's correlation coefficients were also calculated using MS Excel. The theoretical organic matter remaining on the forest floor (TOM) was calculated using the equation:

$$TOM = L/k.$$

I compared k , k_1 , k_2 , and k_3 values to each other and also to the actual organic matter on the forest floor and TOM. The status of litter dynamics at each study site was determined through this comparison.

RESULTS

Litterfall production

Litterfall in Jirisan was collected only in August and November, and the ratios of autumn to annual litterfall in Deogyusan and Gyeryongsan were applied to the other months in order to obtain estimates of annual litterfall in the same or similar species stands. Annual litterfall in the litter traps (Table 2) ranged from 259 g/m² at Sk in Jirisan to 637 g/m² at Pd3 in Gyeryongsan (434 ± 91.6 g/m²). The amount of autumn litterfall was 39-49% of the annual litterfall in evergreen *Pinus* forests and greater than 60% of the annual litterfall in deciduous forests. Litterfalls at Cl1, Sk, Fm2, Ct1, Ct2, and Cl2 sites in Jirisan were collected only in August and November, and the autumn litterfall

was 82-98% of the annual litterfall, which were higher than the others.

Litterbag experiment

Negative exponential decay models provided accurate descriptions of the litterbag data (Table 3). All regressions were significant ($P < 0.05$), and the fits were very good (mean, $r^2 = 0.918$; median, $r^2 = 0.926$; range, 0.761 to 0.991). Decay constants were very similar when the sites were close and the dominant plant species were the same, such as the case of the Ct1 and Ct2 sites. However, decay constants were very different when the sites were far apart from each other, such as the case of the Qs1, Qs2, and Qs3 sites, or when the dominant species were different, such as in the Qm2 and Pd1 sites. Decay constants were generally small in *P. densiflora* forests but those in the Qm3, Qm4, Qm5, Qs2, and Qs3 sites were even smaller than those of the *Pinus* forest.

Table 3. Negative exponential models and decay constants (k ; 1/y) of the study sites.

Site	Decay equation	Correlation coefficient (r^2)	Decay constant (k)
Cl1	$y = 100e^{-0.3216x}$	0.960	0.322
Cl2	$y = 100e^{-0.4306x}$	0.901	0.431
Ct1	$y = 100e^{-0.4462x}$	0.773	0.446
Ct2	$y = 100e^{-0.4882x}$	0.966	0.488
Fm1	$y = 100e^{-0.3677x}$	0.975	0.368
Fm2	$y = 100e^{-0.354x}$	0.909	0.354
Pd1	$y = 100e^{-0.2879x}$	0.956	0.288
Pd2	$y = 100e^{-0.2998x}$	0.932	0.300
Pd3	$y = 100e^{-0.3085x}$	0.991	0.309
Qa	$y = 100e^{-0.3614x}$	0.917	0.361
Qm1	$y = 100e^{-0.3315x}$	0.761	0.332
Qm2	$y = 100e^{-0.4306x}$	0.943	0.431
Qm3	$y = 100e^{-0.2777x}$	0.904	0.278
Qm4	$y = 100e^{-0.2914x}$	0.897	0.291
Qm5	$y = 100e^{-0.2676x}$	0.974	0.268
Qs1	$y = 100e^{-0.3834x}$	0.965	0.383
Qs2	$y = 100e^{-0.2877x}$	0.803	0.288
Qs3	$y = 100e^{-0.2479x}$	0.891	0.248
Qv1	$y = 100e^{-0.352x}$	0.982	0.352
Qv2	$y = 100e^{-0.3336x}$	0.920	0.334
Sk	$y = 100e^{-0.4028x}$	0.968	0.403

Litter on the forest floor and removal rates

Ash-free mass ranged from 232 g/m² to 1,076 g/m² (485 ± 218.7 g/m²) for the O_i horizon, and from 467 g/m² to 5,197 g/m² (1,881 ± 1,152.0 g/m²) for the other (O_e, O_a, and A) horizons (Table 4). The litter amount of the O_i horizon was not significantly related with autumn litterfall (correlation coefficient $r = 0.214$), indicating the movement of litter after it had fallen on the forest floor. Even though the ash-free mass of the O_i horizon in the *Pinus* forest was small, those of the O_e, O_a, and A horizons were relatively large. Removal rates k_1 , k_2 , and k_3 were different at all sites. k_1 was the largest; k_2 was the smallest; and k_3 was in between. The ranges of k_1 , k_2 , and k_3 were 0.176–1.067/y (0.479 ± 0.246/y), 0.049–0.717/y (0.282 ± 0.173/y), and 0.125–0.853/y (0.322 ± 0.174/y), respectively. The largest removal rates were observed in the Qs2 site at 1.067 (k_1)/y, 0.717 (k_2)/y, and 0.853 (k_3)/y.

Table 4. Litter on the forest floor and mass balance-derived constants at the study sites

Site	Ash-free matter (g/m ²)		Removal rates		
	O _i horizon	O _e , O _a and A horizon	k_1	k_2	k_3
Cl1	1,076	3,404	0.382	0.122	0.316
Cl2	747	2,413	0.324	0.144	0.310
Ct1	818	1,949	0.510	0.150	0.420
Ct2	568	2,501	0.231	0.143	0.227
Fm1	433	1,026	0.555	0.341	0.422
Fm2	580	2,487	0.252	0.107	0.233
Pd1	481	1,912	0.662	0.248	0.252
Pd2	232	1,848	0.258	0.256	0.125
Pd3	262	1,477	0.454	0.359	0.177
Qa	336	792	0.675	0.487	0.424
Qm1	381	941	0.810	0.295	0.405
Qm2	497	1,444	0.401	0.285	0.344
Qm3	328	545	1.044	0.580	0.602
Qm4	432	2,950	0.245	0.127	0.146
Qm5	329	1,803	0.287	0.213	0.182
Qs1	406	1,243	0.463	0.307	0.327
Qs2	398	467	1.067	0.717	0.853
Qs3	312	713	0.702	0.510	0.438
Qv1	421	3,224	0.180	0.147	0.131
Qv2	305	1,159	0.371	0.330	0.264
Sk	846	5,197	0.176	0.049	0.163

$k_1 = L/F$, where L is the continuous litterfall mass; and F is the forest floor mass, $k_2 = -\ln(1 - O_i/T)$, where $T = O_i + O_e + O_a + A$, $k_3 = O_i/(O_e + O_a + A)$.

DISCUSSION

It is known that litter production in deciduous temperate forests shows discrete annual production in the autumn (Olson 1963). However, the present study found that about 30% of the annual litter production occurs during the other seasons (also Sharma and Ambasht 1987, Kim and Chang 1989). The amount of litterfall is highly variable according to time and space, and this variability should be estimated for comparison (Sharma and Ambasht 1987, Knutson 1997). Long-term data sets need to be used for making this type of estimate. This is highlighted by the finding in which the standard deviation for our three-year data from Jirisan ranged from 16% to 53% of the mean, and those of the four-year data from Deogyusan and Gyeryongsan ranged from 3% to 38% of the mean.

When litter falls on the forest floor, it can move by wind or gravity. Movement depends on several factors, including the intensity and direction of wind, micro-topography, and density of shrubs (Lee and Cho 2000). Thus, the amount of litterfall produced in autumn as measured by the litter trap was different from the litter on the O_i horizon of the forest floor in late autumn. Comparison of annual litter production should be done on litter trap-based data because the litter amount on the O_i horizon differs according to micro-scale environments, and the litter amount on a forest floor at a specific site may not be representative of the whole forest ecosystem.

Hobbie et al. (2006) calculated k_1 and k_2 based on Olson's models. They used annual litter production and litter amount on the O horizons to calculate k_1 . To calculate k_1 from mass balance estimates, the annual litter production data should be corrected with annual deposition data because the fallen litter does not remain fixed in any particular spot. This can be calculated with the equation $L = O_i \times (\text{annual litterfall}/\text{autumn litterfall})$. If the annual litterfall data is converted to annual deposited amounts, the conversion factor should be determined by comparing the autumn litterfall and litter amount in the O_i layer at the end of autumn. If the O_i data from autumn is converted to the annual deposited amounts, the conversion factor should be determined by comparing the autumn litterfall and annual litterfall. Knutson (1997) calculated a conversion factor in the deciduous forests of northeast Iowa as the ratio of litter mass in the quadrat to the litterbox on the forest floor, and the mean of conversion factors from 1984 through 1993 was 1.5 (range, 1.32 to 1.75; SD, 0.150). In the present study, the latter conversion factor was used, and the mean ratio of annual litterfall and autumn litterfall was 1.48 (range, 0.95 to 2.56; SD, 0.453).

Hobbie et al. (2006) suggested that calcium is responsible for the difference between k and k_1 , and found that litter calcium was significantly related to k_2 . However, this was not the case for this study because calcium in the soil was not correlated with the difference between k and k_1 (Korea National Park Service 2002, 2004a, 2004b). The removal rates calculated by mass balance for many litter types were not always slower than the decay rates calculated from litterbags.

Even though decomposition in the litterbags was measured for only 2 or 3 years, the decay rate (k) may not change with time because it was calculated using a regression equation of exponential decrease. Therefore, the decay rates may not have slowed with time as the relative amount of recalcitrant materials in the litter increased, which was suggested by Hobbie et al. (2006). If the litterbag decay constant (k) and mass balance removal rates (k_1 , k_2 , and k_3) are compared, k is unrelated to k_1 , as was previously described by Hobbie et al. (2006). However, there were significant relationships among the removal rates themselves. Regression equations were $k_2 = 0.5639k_1 + 0.0119$ ($r^2 = 0.7368$, $P < 0.01$); $k_3 = 0.5845k_1 + 0.0422$ ($r^2 = 0.7813$, $P < 0.01$); and $k_3 = 0.8015k_2 + 0.0961$ ($r^2 = 0.634$, $P < 0.01$). The k_1 values were calculated from annual litterfall (L). Litter quality is different in each season, and in spring and summer, litter is more likely to be decomposed than in autumn and winter. The k_1 might over-estimate the actual removal rate. The k_2 values were calculated from the maximum accumulated biomass (T) and did not include disappeared biomass before; so, the actual removal rate might have been under-estimated. The k_3 values were in between k_1 and k_2 , and were calculated through autumn litterfall and other remaining mass. Spring and summer litterfall is decomposed quicker than autumn litterfall because N and P contents are high and have little implication on accumulated mass. Other accumulated mass, except O_1 , has much higher content of recalcitrant matter than O_1 mass. If there is a small amount of accumulated mass, this recalcitrant matter will not give much implication on the decomposition rate. Therefore, the k_3 values may be a good indicator of decomposition rate. A significant relationship among the removal rates themselves means that the comparison of k with any one of k_1 , k_2 , or k_3 may have the same result. Here, it is recommended that k_3 is used because this variable can be easily determined based on the litter on the forest floor at the end of autumn or early winter and may accurately represent the actual removal rate.

Assessment of the state of litter dynamics

In this study, the decay rate and several types of removal rate were calculated. If litter dynamics on the forest floor were in a steady state, the decay rate (k) and removal rate (k_1) should be similar. However, they were similar at some sites and different at others. Some difference might have resulted from the differences in methods because a smaller fraction than mesh size was assigned to decomposed matter in litterbag method but the removed fraction at the site was only assigned to decomposed matter in mass balance estimates. Nevertheless, this difference is natural where the litter dynamics at the study site were not in equilibrium. Olson's equation $k_1 = L/F$ assumes that there is a steady state between input and output. Kim and Chang (1966) also assumed the steady state of litter input and output to calculate k_3 . Thereafter, many studies were done in South Korea (Chang and Ko 1982, Chang and Kim 1983, Chang and Chung 1986), and Chang et al. (1987) presented a decay map for South Korea that reflects latitude, altitude, and dominant species. However, k and k_1 were not similar at many sites in the present study. This means that litter input and output was not in equilibrium at those sites. As mentioned earlier, the litterfall amount on the O_1 horizon in autumn is not the same as the fallen amount in autumn at many sites because of micro-scale environmental differences, such as the location of the study site on a slope. This might be responsible for the difference between the decay rate and removal rate.

The use of a diagram showing the relationship between k and k_1 is suggested (Fig. 1). In the diagram, a diagonal line is drawn to indicate a 1:1 relationship, and two additional lines are included on either side of the diagonal line to represent one SD of the k_3 values. One SD of the annual litter fall was less than 38% of the mean for 4 years, and k_3 closely represents the uncertainty of removal rates in the studied communities. If a site was between the two dotted lines, the litter dynamics on the forest floor would be defined operationally in equilibrium. However, this does not mean that they actually are. If a site was located in a faster removal zone, past long-term removal rates would be higher than the present decomposition rate. This might be true in old forests because these areas will tend to be inhabited by species resistant to decomposition with succession (Odum 1960, Kazakou et al. 2006, Cortez et al. 2007). Consistent species composition that has not changed remarkably might have resulted from lower input than output. If a site is located in a slower removal zone, the past long-term removal rate will be lower than the present decomposition rate. Litter removal in slower

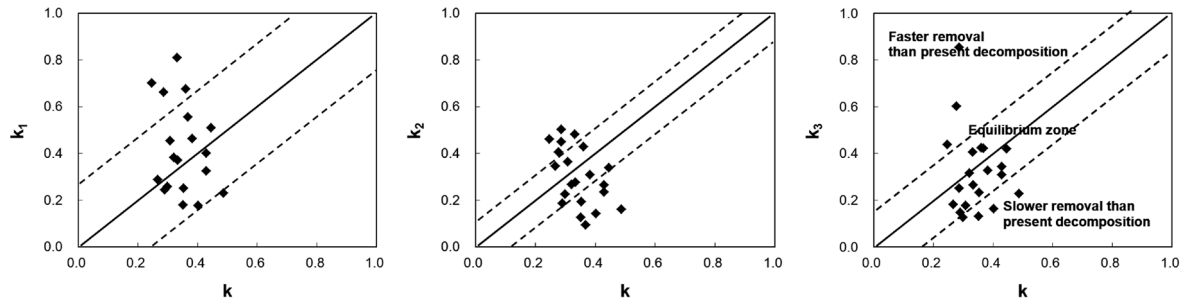


Fig. 1. Zoning the state of litter dynamics on the forest floor according to the litterbag-based decay rate, k (1/y), and mass balance removal rate, k_i (1/y). Dotted lines were drawn above and below the diagonal line to represent ± 1 SD of the k_i values. One SD of the k_1 , k_2 , and k_3 values in this study were 0.2636, 0.1250 and 0.1743, respectively.

removal zones will exceed the litter input, and a balance between removal and input will be achieved. From this analysis, the state of litter dynamics can be determined, and future changes can be predicted.

In the present study, all 21 sites contained well-conserved and stable ecosystems, and these should have been in equilibrium. However, only 14 sites were in equilibrium: four sites (Ct2, Pd2, Qv1, and Sk) were in a slower removal zone, and three sites (Qs2, Qs3, and Qm3) were in a faster removal zone. This was probably due to the location of the litter collection sites: four sites were in a valley, and three sites were on a ridge. Litter is blown by wind from ridges to valleys where it accumulates. This implies that litter should be collected at sites located in the middle of steady slopes to calculate the mass balance (k_i). This study also suggests that the range of variation of k_3 in the equilibrium state is $k \pm 0.1743$ in South Korea.

The other way to assess the state of litter dynamics on a forest floor is to compare the remaining mass on the forest floor with the theoretical mass remaining on the forest floor. Here, the theoretical mass remaining can be calculated based on Olson's exponential decay equation: $dm/dt = m_0 e^{-kt}$. If the mass input is in equilibrium, the mass remaining in the equilibrium state is an integral of this equation at $t = \infty$; $m = m_0/k$, where m_0 is the annual input on the forest floor. The m_0 can be the actual input at the litter collection site and can be calculated from the conversion factors that were used to calculate k_1 .

If the OAcc/TOM ratio at a site is larger than 1, then accumulation would exceed decomposition. If the OAcc/TOM ratio were smaller than 1, the removal rate would be larger than the input rate. There are two possible mechanisms of higher accumulation than expected from the decay rate (k). One is the change in litter quality over time. The other is the larger input or production of litterfall than of decomposed or removal amounts. However, the

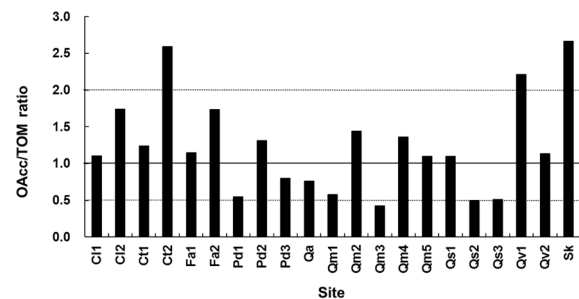


Fig. 2. Ratio of real and theoretical organic matter remaining on the forest floor (TOM) at each site. The theoretical organic matter remaining was calculated assuming that there was a steady input of organic matter and a constant decay rate (k). OAcc, organic accumulation.

data in this study indicates that there should be a reasonable range of deviation of the OAcc/TOM ratio because of the annual variation in litterfall. The OAcc/TOM ratio in the equilibrium state based on the k_3 - k diagram ranged from 0.4 to 2.7 (Fig. 2). The Ct2 and Sk sites were in a hollow area and have highest the OAcc/TOM ratios.

Even though decomposition is driven by the environment on both regional and micro-site scales, the substrate quality of litter, the composition of the decomposer community (Parton et al. 1987, Aerts 1996, Cornelissen 1999), and the magnitude of species-driven differences may be much larger than previously thought and greater than climate-driven variations (Cornwell et al. 2008). Litter quality changes with succession (Cornwell et al. 2008). In general, fast-growing, poorly-defended species of angiosperms produce litter with a high decomposability; whereas, slower-growing, better-defended species produce poor-quality litter with low decomposition rates (Cornelissen et al. 1999). Among the sites in the present study, Pd1, Pd2, and Pd3 were dominated by the gymnosperm *P. densiflora*, while other sites were dominated by angiosperms. Decomposition of gymnosperms is gener-

ally slower than that of angiosperms (Chang et al. 1987, Cornwell et al. 2008). However, the OAcc/TOM ratios of Pd1 and Pd3 were lower than 1, meaning that removal was faster than input. The OAcc/TOM ratios of some sites dominated by angiosperms were larger than 1. Therefore, litter quality changes with succession do not affect the OAcc/TOM in this study.

In this study, the range of decay rates (k) among the sites was small, even though the sites were dominated by different species. However, the range of removal rates was relatively large. This does not reflect the difference in decomposition rates but rather differences in input and output on a small scale. The range of ash-free litter on the O_1 horizon was large, but the input amount was not solely responsible for the OAcc/TOM ratio. Microenvironmental factors such as rock coverage, soil texture, moisture content, and topography might be responsible for the input/output difference.

In conclusion, the present study shows that litterfall dynamics on the forest floor can be understood through the comparison of k and k_i and the OAcc/TOM ratio. However, the mechanism of litter dynamics cannot be understood only through conventional experiments, and, therefore, further research on microenvironmental factors that affect the litter output/input in different ecosystems is required.

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