

# Transport and Decomposition of Leaf Litter as Affected by Aspect and Understory in a Temperate Hardwood Forest

Gayoung Yoo, Eun-Jin Park, Sun-Hee Kim<sup>1</sup>, Hye-Jin Lee, Sinkyu Kang, and Downon Lee\*

Environmental Planning Institute, Graduate School of Environmental Studies,  
Seoul National University, Seoul 151-742, Korea;

<sup>1</sup>Department of Environmental Engineering, Donghae University, Donghae 240-713, Korea

Key Words:

Aspect  
Decomposition  
Hardwood forest  
Leaf litter redistribution  
Patch  
Understory

Transport of colored papers and decomposition of leaf litter of *Quercus mongolica*, *Acer pseudo-sieboldianum*, and *Kalopanax pictus* were investigated on three patches differentiated by aspect and understory in a temperate hardwood forest. Two patches are represented by dwarf bamboo (Patch SS) and herbaceous plants (Patch S), respectively, lying on a south-west-facing slope. The other patch (Patch N) is located on a northeast-facing slope with herbaceous plants. Colored papers were placed on the patches to understand the pattern of litter movement on the ground. Papers were more dispersed in Patch S than in the other two patches. Some of the colored papers placed in Patch S moved upward. The results suggest that the litter movement is affected by aspect and that the leaf litter is retained by dwarf bamboo in Patch SS. Decay constant of *Q. mongolica* was significantly ( $p < 0.05$ ) lower than those of *K. pictus* and *A. pseudo-sieboldianum*. Decay rates of *Q. mongolica* were significantly different between Patches N and S and between Patches SS and S ( $p < 0.05$ ). On the other hand, decay rates of the other species were not significantly different among the three patches. The results suggest that aspect and understory exert an influence on redistribution and decomposition of leaf litter and that the effects could be different among the plant species.

Decomposition of leaf litter plays an important role in the functioning of forest ecosystems. Forest productivity is largely dependent on nutrients released from the decomposing litter as a forest ecosystem becomes mature (Odum, 1969; Waring and Running, 1998). The litter also contributes a large amount of carbon to soil respiration (Bowden et al., 1993; Lee et al., 1999). At the global level, it is estimated that decomposition of litter accounts for approximately 70% of total annual carbon flux (Raich and Schlesinger, 1992). The estimate of global soil respiration is  $68 \times 10^{15}$  g C yr<sup>-1</sup>, which is almost 11 times greater than  $5.7 \times 10^{15}$  g C yr<sup>-1</sup> (in 1987) of carbon dioxide released through anthropogenic sources (Watson et al., 1990).

For these reasons, many researchers have investigated litter production and decomposition in forest ecosystems (Lavelle et al., 1993; Aerts, 1997). In particular, decomposition of leaf litter is frequently related to substrate quality, soil temperature, moisture content, nutrient availability, and geographic location (Olson,

1963; Berg et al., 1982; Meentemeyer et al., 1982; Melillo et al., 1982; Dyer et al., 1990; Berg and Ekbohm, 1991; Zhang and Zak, 1995). On the other hand, the redistribution of leaf litter among forest patches was described only in few reports (Welbourn et al., 1981; Boerner and Kooser, 1989; Lee et al., 1999).

When a forest is located in steep slopes and exposed to strong wind, its nutrient dynamics may be significantly influenced by leaf litter redistribution. In a mature forest, for instance, a recipient area (sink) of litter may become nutrient-rich while a donor area (source) is nutrient-limited unless the gain and loss of litter are compensated by other biogeochemical processes. In addition, physical environments of forest floor such as solar radiation, soil temperature and moisture vary with litter redistribution (Kang et al., 2000, Kang et al. 2001). This is also significant to many other ecosystem processes. For example, soil respiration, enzyme activities and methane oxidation were differentiated by aspect and the amounts of leaf litter added to soils (Lee et al., 1998; Lee et al., 1999; Shim and Lee, unpublished data). Similarly, the contents of metals, especially Ca, of O and A horizon

\* To whom correspondence should be addressed.  
Tel: 82-2-880-5650, Fax: 82-2-871-8847  
E-mail: leedw@snu.ac.kr

soils were intimately related to spatial redistribution of leaf litter (Oh et al., 1999).

There are several factors that govern litter redistribution among the patches in a forest floor. Gravity and wind are major driving forces of litter transport. These forces are influenced by slope inclination and direction, and patch location in the slope (Orndorff and Lang, 1981; Boerner and Kooser, 1989). Orndorff and Lang (1981) also reported that leaf litter redistribution was affected by fallen logs and microtopographic depressions. To our knowledge, there has been no report which related litter redistribution to understory type although it seems to exert a major control over litter movement by blocking mass flow. We therefore examined the effects of understory on litter redistribution, which could give clues on nutrient dynamics in forest ecosystems (Welbourn et al., 1981; Boerner and Koost, 1989).

On the other hand, litter decomposition is largely regulated by physical climate factors on a broad regional scale. It varies with altitude, latitude and the location of forest ecosystems (Meetenmeyer et al., 1982; Chang et al., 1987). It is also reported that mass loss of leaf litter is well fitted in a function of actual evapotranspiration and precipitation (Berg et al., 1993).

However, at a smaller local scale, litter quality and underlying native litter are of critical importance in controlling decay rates (Chadwick et al., 1998). Understory type can have effects on the quantity and quality of underlying native litter as well as physical environments such as soil temperature and moisture content (Kang et al., 2000). We observed that aspect and patchy distribution of dwarf bamboo generated three distinct types of patches at the ground level of our study area and thus might cause heterogeneity of soil biogeochemistry. Hence, it was hypothesized that decomposition rate is related to understory type as it can modify soil moisture, temperature and nutrient dynamics directly and indirectly by trapping leaf litter (Lee et al., 1999).

The major objective of this study was to investigate effects of aspect and understory type on redistribution and decomposition rate of leaf litter in a hardwood forest.

## Materials and Methods

The study area lies in a temperate hardwood forest in Kangwon Province, South Korea. The area (latitude 38° 00'~38° 03' N, longitude 128° 26'~128° 30' E, elevation 900-1424 m, area 2,049 ha) has been well protected as it was designated as a Natural Forest Reserve by Korean Office of Forestry in November 1987. This area was also included in a Biosphere Reserve in UNESCO Man and the Biosphere Program in May 1993. As some parts of south-facing slopes are occupied by an evergreen dwarf bamboo (*Sasa borealis*), the ground cover has patchy appearance

over the area. More detailed descriptions of vegetation, geography and microtopography are found in Lee et al. (1997, 1999).

The representative two slopes facing opposite directions and partially covered with dwarf bamboo undergrowth were chosen to examine leaf litter redistribution on the forest floor and to relate the results to soil biogeochemistry. The area is dominated by *Quercus mongolica*, *Acer pseudo-sieboldianum*, and *Carpinus cordata*. We divided the area into three distinct patches by aspect and understory type at the ground level. Two patches are located in the southwest-facing slope of 24%. One is predominantly occupied by herbaceous plants such as *Erythronium japonicum*, *Symplocapus nipponicus*, *Meehaniania urticifolia*, and *Pimpinella brachycarpa* (Patch S) and the other by *Sasa borealis* (Patch SS). The third patch is located in the northeast-facing slope of 28%, and its understory is dominated by *Symplocapus nipponicus*, *Erythronium japonicum*, *Meehaniania urticifolia*, *Anemone koraiensis*, and *Cordalis trutschianinovii* (Patch N).

To identify the main direction of leaf litter movement, 10 colored papers (10×10 cm) were placed in each Patch S, SS, and N on November 12 and December 28, 1994. The locations of papers were traced in May 27, 1995. Distance and direction of the movement from the original points were measured by a tape ruler and a compass.

A litter bag method was employed to determine decomposition rates of the leaf litter (Olson, 1963; Zhang and Zak, 1995). Leaf litter of three woody species, *Q. mongolica*, *A. pseudo-sieboldianum*, and *Kalopanax pictus*, which are relatively abundant, were collected from the forest floor in October 1994 and air-dried in room temperature for 5 days. The initial moisture content of the air-dried leaf litter was determined by drying 10 g of leaf litter at 80°C for 48 h. Litter bags (20×20 cm) were made of terylene net with a mesh size of about 1 mm. Approximately 5 grams of the air-dried leaf litter was weighed in a litter bag. Thirty bags were placed and fasten on the ground of each patch in November 1994. Three bags were retrieved from each patch per plant species every 2 to 3 months. The remaining mass of leaf litter was dried at 80°C for 48 h, particles were brushed off, and weighed. After triplicate data set were randomly arranged for each species and site, annual decomposition rate constants were estimated to fit into the single negative exponential decomposition function (Olson, 1963).

Soil temperature has been hourly monitored in the area 10 cm in depth since December 1995 by using a temperature sensor and data logger (Hobo, Onset computer corporation). The data of soil temperature from Jan 1 1997 to December 31 1997 were taken and analyzed since parts of other annual data set could not intactly collected due to weather and military activities.

Soil was sampled from A horizon (to 10 cm depth) in

**Table 1.** Average distance (m) of colored papers moved

Patch	Dates placed	
	Nov. 12, 1994	Dec. 28, 1994
S	19.7(±4.4), n=9	32.3(±11.6), n=4
SS	0.0(±0.0), n=10	0.0(±0.0), n=10
N	4.5(±2.3), n=10	6.6(±9.4), n=9

The numbers in parenthesis and n indicate standard deviations and the number of paper identified on May 27, 1995, respectively.

three locations randomly chosen for each patch every month from June 1995 to May 1996 when the soil was not frozen. The soil was stored in a plastic bag and transported to the laboratory. Ten grams of fresh soil was weighed in an aluminum dish and dried at 105°C for 24 h. Water fraction was expressed by dividing loss of weight by the weight of dried soil.

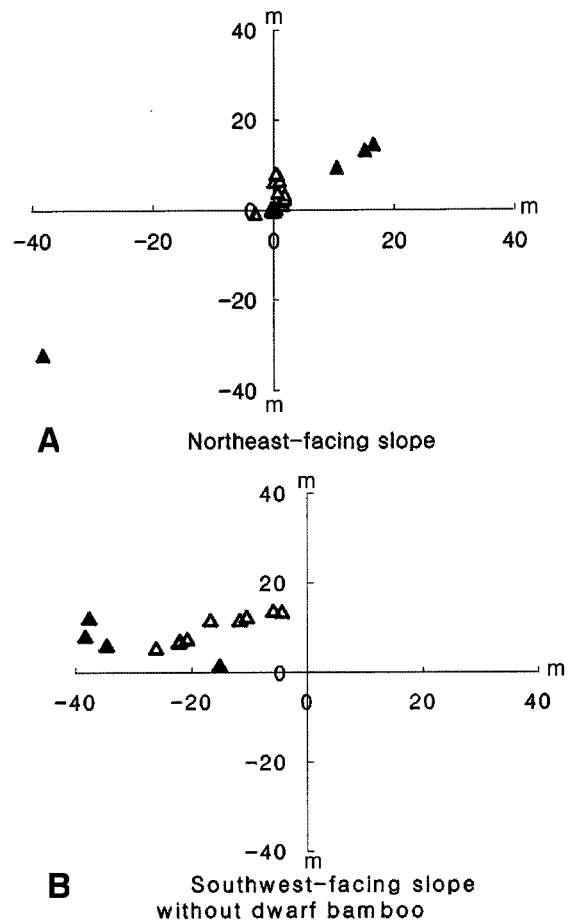
**Results and Discussion**

Initially, we placed colored papers and real leaf litter sprayed with color paint in the three patches. However, the painted leaf litter had low visibility in the spring as it was mixed up with other litter and its color was less conservative due to rapid photolysis and decomposition. Eventually, the paper method made it easy to figure out how leaf litter behaved on the forest floor.

As expected, the colored papers seldom moved when placed in the patch with dwarf bamboo (Table 1). Apparently, our data showed that dwarf bamboo contributed to litter retention on site. Similarly, Speaker et al. (1988) reported that intact riparian shrubs were responsible for retaining 84% of plastic strips placed in a third-order stream.

Interestingly, the colored papers did not merely slide downslope. Rather, some were transported upward except those placed in Patch N in December, which mainly slid downslope (Fig. 1a and b). A similar tendency of litter movement was also observed in this area (Lee et al., 1999). When the leaf litter moving on the ground was trapped by bags open on one side placed on the borders of patches in either directions from mid-September to late November 1997, a significant amount of leaf litter also tumbled upward (Lee et al., unpublished data). In the northeast-facing slope (Patch N), on average, the leaf litter passed the border at the rate of 1,215 g/m northwestward (direction to higher area on the slope), 140 g/m southeastward, 239 g/m southwestward upslope, and 376 g/m northeast downslope. In Patch S of the southwest-facing slope, the leaf litter moved at the rate of 654 g/m northwestward (direction to higher area on the slope), 31 g/m southeastward, 239 g/m northeastward upslope, and 1,263 g/m southwest downslope. The data apparently showed that a significant amount of the leaf litter moved upward at least from September to late November.

Presumably, the movement of leaf litter might be



**Fig. 1.** Distribution of colored papers placed on the northeast- (A, Patch N) and southwest-facing slopes without dwarf bamboo (B, Patch S). The papers were placed on the southwest-facing slope with dwarf bamboo (Patch SS) seldom moved at the original point. Papers were placed on November 12, 1994 (open triangles) and December 28, 1994 (closed triangles). The locations of papers were identified on May 27, 1995.

dominantly governed by the valley wind in the area, because the valley wind scratched forest floor more effectively than did ridge wind (Lee et al., 1999). The movement of leaf litter may be similar to the way in which fire spreads on forested slopes. It is known that upward winds are effective in spreading fire while convective winds inhibit downslope spread (Waring and Running, 1998). Nevertheless, leaf litter tends to slide down by gravitational forces along with surface runoff and wind if it is not retained by ground features. In this sense, dwarf bamboo plays a critical role in conserving leaf litter in the system.

The papers were more dispersed in Patch S than Patch N (Table 1). Papers placed in December were transported over longer distances than those in November. In Patch N, November papers were skewed upward by the forces from ridge and lower valley, but the December papers simply slid downslope. Although it may be related to various factors, e.g. seasonal variation of wind intensity and direction, moisture

**Table 2.** Decomposition rate constant (yr<sup>-1</sup>) of *Quercus mongolica*, *Kalopanax pictus*, and *Acer pseudo-sieboldianum* leaf litter in Patch S, SS, and N

Site	<i>Q. mongolica</i>	<i>A. pseudo-sieboldianum</i>	<i>K. pictus</i>
Patch S	0.16 (±0.03)	0.44 (±0.01)	0.57 (±0.31)
Patch SS	0.39 (±0.02)	0.43 (±0.02)	0.54 (±0.01)
Patch N	0.35 (±0.03)	0.45 (±0.02)	0.55 (±0.04)

content and shape of papers, it is not evident why the papers which were exposed to wind for less period of time moved longer distances. Papers in Patch S moved longer distances than those in Patch N when those were placed in November and December. It is presumed that leaf litter hardly moved in Patch N during the winter due to snowpack, which is persistent on the northern slopes in the study area from December to early April, but not on the southern slopes.

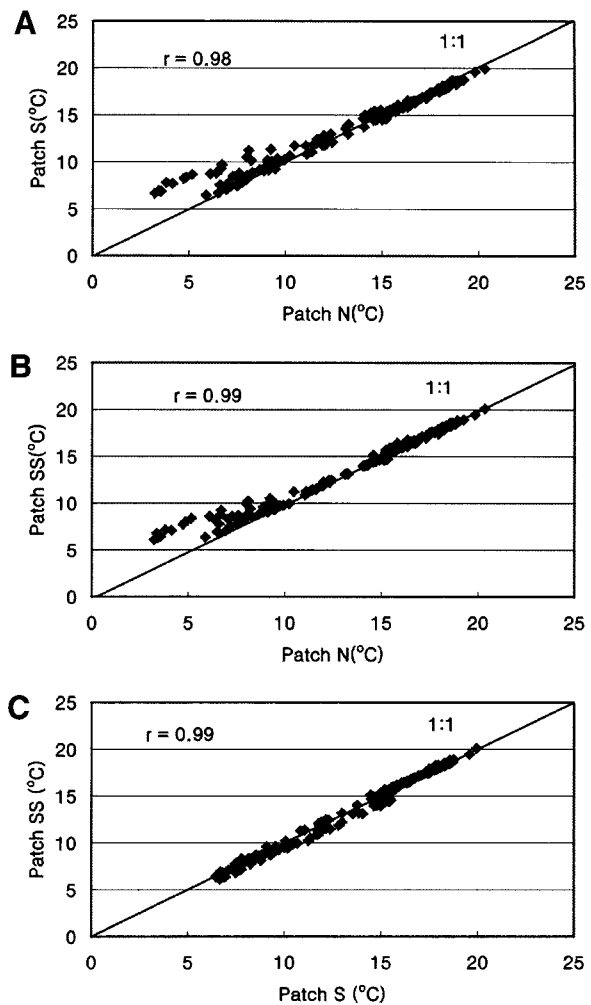
The results are consistent with other data collected in the same study area. Lee et al. (1999) placed litter traps with one side open on the boundary of these patches, and collected the litter for one year. They found that the litter moved from Patch S to Patch N and SS. The results suggest that Patch N and SS were sinks of leaf litter whereas Patch S acted as a source.

Decomposition rates of the three species of litter were shown in Table 2. Chang et al. (1987) reported that the decomposition of *Q. mongolica* was about 0.11-0.21 yr<sup>-1</sup> in Korean hardwood forests, which is comparable to our results. Decomposition rates of *Q. mongolica* were significantly different from the other two species ( $p < 0.05$ ). The differences in the decomposition rates of *K. pictus* and *A. pseudo-sieboldianum* were not significant. The lower decomposition rate of *Q. mongolica* is probably due to the low content of mineral nutrients, especially nitrogen and/or potassium (Table 3). Chadwick et al. (1998) suggested that the initial N and Ca contents of the litter were significantly related to decomposition of the litter.

It has been known that factors influencing decay rates are very complicated. Jansson and Berg (1985) found that the moisture content of the upper soil layers had a dominating influence on litter mass loss rates during early decomposition stages. Aerts (1997) suggested that actual evapotranspiration (AET) is the best predictor for the decomposition constants at the

**Table 3.** Initial concentrations (%) of nutrient elements in leaf litter of *Quercus mongolica*, *Acer pseudo-sieboldianum*, and *Kalopanax pictus* collected in Oct. 1995. The values in parenthesis indicate standard deviation of 3 measurements for a composite sample

Plant species	C	N	S	K	Ca	Mg
<i>Q. mongolica</i>	47.43 (±0.04)	0.88 (±0.08)	0.37 (±0.03)	0.18 (±0.00)	0.90 (±0.01)	0.08 (±0.00)
<i>A. pseudo-sieboldianum</i>	45.73 (±0.53)	0.77 (±0.09)	0.35 (±0.02)	0.28 (±0.00)	1.10 (±0.02)	0.15 (±0.00)
<i>K. pictus</i>	46.99 (±0.14)	1.44 (±0.13)	0.43 (±0.02)	0.64 (±0.00)	1.07 (±0.00)	0.10 (±0.00)



**Fig. 2.** Comparison of daily mean soil temperature among three patches in the growing season, from April 21 to Sep. 20, 1997.

global scale.

Decay rate of *Q. mongolica* in Patch S was significantly different from those in Patch SS and N ( $p < 0.05$ ). However, decay rates of *K. pictus* and *A. pseudo-sieboldianum* were not significantly different among the three patches. This result implies that the effects of aspect and understory may vary with leaf litter species.

In the growing season (April 21-Sep. 20, 1997), there was no significant difference in soil temperatures by daily means between Patch N and S (Fig. 2). However, during the other period of year, there was discrepancy of soil temperature between Patch N and Patch S (Fig. 3), presumably due to thick snowpack of Patch N in the winter. Unlike Patch S, soil temperature rarely fell in Patch N and SS below 0°C even in winter. This indicates that snowpack in Patch N and dwarf bamboo in Patch SS has a damping effect on temperature variation (Kang et al., 2000).

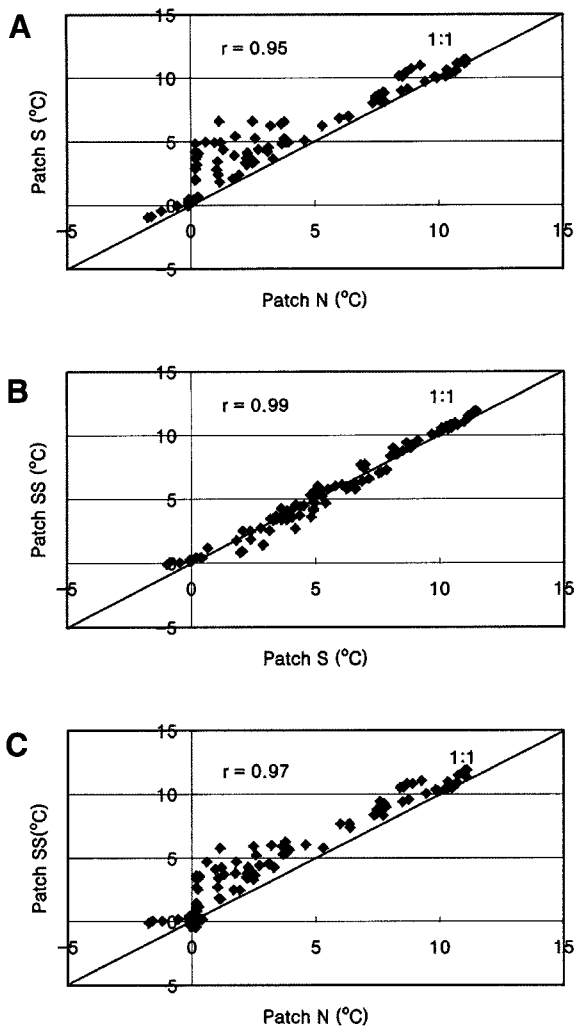


Fig. 3. Comparison of daily mean soil temperatures among three patches from Jan. 1 to April 20 and Sep. 21 to Dec. 31, 1997.

Monthly measurement of soil moisture content showed relatively large discrepancy between the patches (Fig. 4). Patch N had higher soil moisture content than Patch S. It is probably due to less solar radiation in the summer and thicker snowpack in Patch N during the winter. Soil moisture of Patch N was poorly correlated with that of Patch SS.

Presumably, the decay of leaf litter could be controlled by temperature and moisture in the study area. Because litterbags were placed on soil surface, temperature and moisture conditions might favor microorganisms more in Patch N than in the others. In fact, enzyme activities and methane oxidation were the case (Lee et al., 1998; Shim and Lee, unpublished data). Nevertheless, only higher decay rate of *Q. mongolica* leaf litter was observed in Patch N than in Patch S. The result suggests that moisture effect on decay of leaf litter of the other plant species might be dampened by other controlling factors.

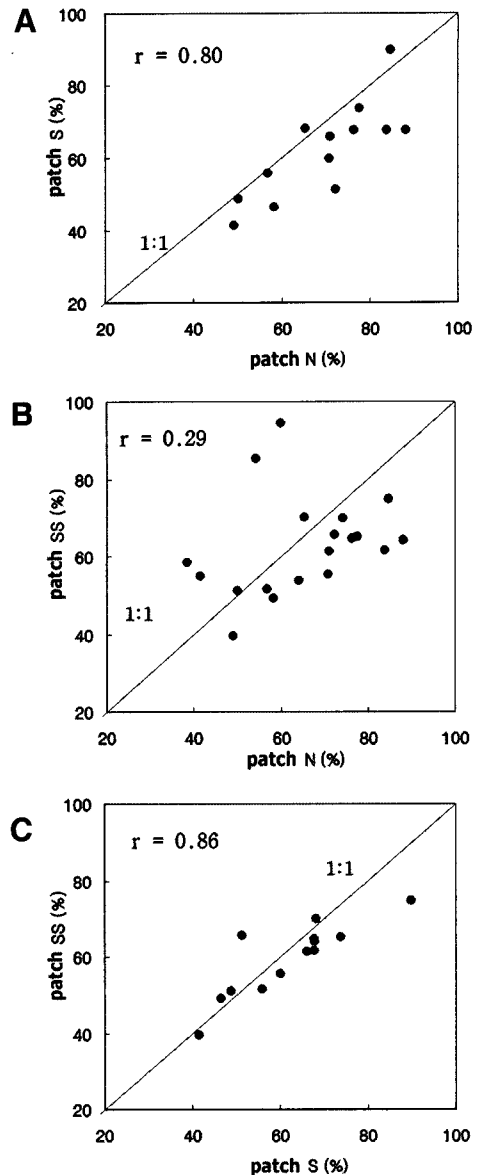


Fig. 4. Comparison of soil moisture contents (g water/100 g soil) among three patches.

Secondly, the different decay rates among the patches may be associated with the underlying native litter layer. The quantity and quality of underlying native litter were reported to influence the decay rates of litter in litterbags (Chadwick et al., 1998). In the three patches, the underlying matrix was different from one another. The amount of leaf litter collected from each patch increased in the order of Patch S, SS, and N (Lee et al., 1999; Oh et al., 1999). The differential quantity of underlying leaf litter was due to aspect and understory as discussed earlier. Greater amounts of leaf litter accumulated in Patch SS than in Patch S as dwarf bamboo trapped litter tumbling over forest floor.

Our data showed that decomposition rates of *Q. mongolica* were different between Patch S and SS ( $p < 0.05$ ). It is suggested that the difference in underlying native litter could explain the differences in decomposition rates in our experiment area.

The third factor that might influence the decay of leaf litter is biological as it is regulated by the soil enzyme activities. Activities of dehydrogenase, urease, phosphatase, and arylsulfatase were highest in Patch N during the growing season (Lee et al., 1998). Oxidation of methane was also higher in Patch N than in the others (Shim and Lee, unpublished data). Future studies on the biological factors may provide an insight into mechanisms governing the decay of leaf litter in terms of aspect and understory.

In summer, aspect and understory exert a substantial control over redistribution, but not conclusively decomposition rate of leaf litter in the hardwood forest ecosystem. These results, together with a similar study (Lee et al., 1999), trigger an approach to quantitative description of redistribution pattern of leaf litter in forest landscape and seasonal fluctuation in the amount of leaf litter entering adjacent streams. It is presumed that the litter movement in a forest landscape can be simulated after a microtopography map is prepared and the distribution of shrubby understory is characterized with aerial photos or remotely sensed images of high resolution. The results will be also useful in understanding spatial and temporal variations of invertebrate populations which feed on leaf litter in forest floors and adjacent streams.

### Acknowledgements

This research was supported by the Korean Science and Engineering Foundation grant KOSEF 94-0401-01-01-03. We are indebted to Mr. Chandra Park for helping us collect data in the field and Mrs. Rosalie Leach and two anonymous referees for providing constructive comments on an early draft.

### References

- Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79: 439-449.
- Berg B, Hannus K, Popoff T, and Theander O (1982) Changes in organic chemical components of needle litter during decomposition. III. Long-term decomposition in a Scot pine forest. *Can J Bot* 62: 2880-2888.
- Berg B and Ekbohm G (1991) Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. *Can J Bot* 69: 1449-1456.
- Berg B (1993) Litter mass loss rates in pine forests of Europe and eastern United States: some relationships with climate and litter quality. *Biogeochemistry* 20: 127-159.
- Boerner REJ and Kooser JG (1989) Leaf litter redistribution among forest patches within an Allegheny Plateau watershed. *Landscape Ecol* 2: 81-92.
- Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM, and Carrison JB (1993) Contribution of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can J For Res* 23: 1402-1407.
- Chadwick DR, Ineson P, Woods D, and Pearce TG (1998) Decomposition of *Pinus Sylvestris* litter in litter bags: Influence of underlying native litter layer. *Soil Biol Biochem* 30: 47-55.
- Chang N, Lee S, Lee B, and Kim H (1987) The decay map and turnover cycles of litters in Korea. *Korean J Ecol* 10: 183-193.
- Cortez J (1997) Field decomposition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity. *Soil Biol Biochem* 6: 783-793.
- Dyer ML, Meentemeyer V, and Berg B (1990) Apparent controls of mass loss rate of leaf litter on a regional scale. *Scand J For Res* 5: 311-323.
- Jansson PE and Berg B (1985) Temporal variation of litter decomposition in relation to simulated soil climate. Long-term decomposition in a Scots pine forest. *Can J Bot* 63: 1008-1016.
- Kang S, Kim S, Oh S, and Lee D (2000). Predicting spatial and temporal patterns of soil temperature based on topography, surface cover and air temperature. *For Ecol and Manag* 136: 173-184.
- Kang S, Kim S, and Lee D (2001) Spatial and temporal patterns of solar radiation based on topography and air temperature. *Can J For Res* (in press).
- Kochy M and Wilson SD (1997) Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. *Ecology* 78: 732-739.
- Lavelle P, Blanchart E, Martin A, Martin S, Spain A, Toutain F, Barois I, and Schaefer R (1993) A hierarchical model for decomposition in terrestrial ecosystems: application to soils and the humid tropics. *Biotropica* 25: 130-150.
- Lee D, Kang H, Lee HJ, and Kang S (1998) Effects of aspects and seasons on soil enzyme activities in a temperate forest. International Workshop on Long-Term Ecological Research and Biodiversity Conservation in East Asia and Pacific Region, Institute of Forestry, Seoul, Korea, pp 13-15.
- Lee D, Yoo G, Oh S, Shim JH, and Kang S (1999) Significance of aspect and understory to leaf litter redistribution in a temperate hardwood forest. *Korean J Biol Sci* 3: 143-147.
- Meentemeyer V, Box EO, and Thompson R (1982) World patterns and amounts of terrestrial plant litter production. *BioScience* 32: 125-128.
- Melillo JM, Aber JD, and Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621-626.
- Mun H and Joo HT (1994) Litter production and decomposition in the *Quercus acutissima* and *Pinus rigida* forests. *Korean J Ecol* 17: 345-353.
- Mun H and Pyo J (1994) Dynamics of nutrient and chemical constituents during litter decomposition. *Korean J Ecol* 17: 501-511.
- Odum EP (1969) The strategy of ecosystem development. *Science* 164: 262-270.
- Oh S, Yoo G, Shim JH, Kang S, and Lee D (1999) Spatial heterogeneity of soil K, Ca, Mg, Fe and Al generated by leaf litter redistribution in a temperate hardwood forest. *Korean J Ecol* 22: 205-210.
- Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322-331.
- Orndorff KA and Lang GE (1981). Leaf litter redistribution in a West Virginia hardwood forest. *J Ecol* 69: 225-235.
- Pardo F, Gil L, and Pardos JA (1997) Field study of beech (*Fagus sylvatica* L.) and melojo oak (*Quercus pyrenaica* Wild) leaf litter decomposition in the centre of the Iberian Peninsula. *Plant and Soil* 191: 89-100.
- Raich JW and Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B: 81-99.
- Speaker RW, Luchessa KJ, Franklin JF, and Gregory SV (1988) The use of plastic strips to measure leaf retention by riparian vegetation in a coastal Oregon stream. *Am Midl Nat*

120: 22-31.

Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scale*. 2nd Ed. Academic Press, San Diego. p 370.

Watson RT, Rodhe H, Oeschinger H, and Siegenthaler U (1990) Greenhouse gases and aerosols. In : Houghton JT, Jenkins GJ, and Ephraums JJ (Eds.), *Climate Change : the IPCC Scientific Assessment*. Cambridge University Press,

Cambridge. pp 1-40.

Welbourn ML, Stone EL, and Lassoie JP (1981) Distribution of net litter inputs with respect to slope position and wind direction. *For Sci* 27: 651-659.

Zhang Q and Zak JC (1995) Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology* 76: 2196-2204.

[Received September 25, 2001; accepted November, 2001]