CHAPTER IV

MASS LOSS AND NUTRIENT MINERALISATION FROM ALDER LITTER IN RELATION TO THE MICROBES AND ISOPODS
INTRODUCTION

Decomposition of litter under natural conditions is regulated by a number of variables including the litter's physical properties, climate, microbes, macro and microfaunal responses. In spite of the complexity of the process two most important attributes are the prevailing environmental conditions and the decomposers community. Rate of litter decomposition differs in sites with different soil types (Witkamp, 1960).

Decomposition processes are intimately coupled to mineralization and immobilization of nutrients. Mineralization is the conversion of organic molecules to inorganic ionic states readily available for plant use. It is carried out by a diverse range of soil organisms including bacteria, fungi and invertebrate animals. These organisms release inorganic N, P, S and many other elements from soil organic matter. In natural ecosystems, these processes are the major ways excluding biological N fixation in which the essential elements are made available to the plant.

The soil on which the litter decomposes may also influence the process by acting as a reservoir of micro-
organisms which colonize the litter. In forest soils decomposition of organic plant debris to yield inorganic plant nutrients is performed largely by fungi, bacteria and actinomycetes (Jensen, 1974) and can become a rate determining step in the nutrient cycling process with the potential to alter ecosystem primary productivity (Miller et al. 1979).

The release of nutrients from forest litter through natural decomposition process is recognized as being a very important part of the nutrient cycle whereby essential mineral elements tied up in the plant biomass are made available for further plant growth. The decrease in dry weight of plant litter is a composite measurement attribute to leaching decomposition by microorganisms and animals; fragmentation by biotic and abiotic breakdown processes and export.

Fungi are considered to be the most important primary microbial decomposers of lignified litter because of their ability to degrade lignin (Ander and Erikson, 1978, Kirk, 1971).

The soil fauna may affect rate of mass loss from decomposing substrate, directly by ingestion and indirectly by grazing on microbes. The affects of substrate communi-
tion are major phenomena in forest systems, where a large fraction of mass loss can be attributed directly or indirectly to the presence of soil fauna.

Faunal effects on litter decomposition have been investigated using litter bags with varying mesh size (Edwards and Heath, 1963; Heath et al. 1964; Madge, 1969) by treatment of substrate with insecticides (Kurcheva, 1960) or a combination of both (Witkamp and Crossley, 1966, Cromack, 1973; Ward and Wilson, 1973).

Many workers have studied the role of soil animals in litter decomposition in natural (Edward et al. 1970;
Edward, 1974; Lofty, 1974; Mason, 1974; Wood, 1976; Anderson et al., 1983; Seastedt, 1984) and agriculture ecosystems (Coleman et al., 1984; House and Parmelee, 1985; Coleman, 1985).

Much attention has recently been paid to devise the techniques for studying decomposition of litter (particularly leaf litter) and its rate of decomposition under different climatic zones (Edwards and Heath, 1963; Weighert and Evans, 1964; Witkamp, 1966; Howard, 1967; Van Cleve, 1971; Anderson, 1973; Gosz et al., 1973; Heal and French, 1974; Howard and Howard, 1974; Jensen, 1974; Suffling and Smith, 1974; Wood, 1974).
However, there is need to investigate the role of various groups of organisms in the decomposition of litter and nutrient release. Particularly of isopods and of soil microbes during litter degradation which has received little attention to North East India (Kshattriya, 1990) as most of the work having done in Europe (Edwards, 1974).

The present study aims to evaluate the rate of decomposition of alder leaf litter as influenced by the microbes and isopods in open and closed forest stands of *Alnus nepalensis*.

**MATERIALS AND METHODS**

(i) Rate of leaf litter decomposition

Nylon bag technique of Bocock *et al.* (1960) with two varying mesh size (20 cm x 20 cm; mesh sizes, 1 mm and 3 mm) was followed to estimate the rate of litter decomposition (Details are given in Chapter III).

On each sampling, six leaf litter bags were collected for each of the two mesh size from both the sites, three bags were recovered to assess the loss in litter on dry weight basis. The litter bags were open, carefully separated and washed on 200 μm mesh sieve to clean the adhered soil particles. The litter was dried in a
hot air oven at 60°C until a constant dry weight was obtained. Final dry weight of the litter samples was taken and percentage weight loss was calculated on the oven dry weight basis. The decay constant (K) was calculated using Olson's (1963) decay model with the following formula:

$$\frac{X_t}{X_0} = e^{-kt}$$

Where \(X_0\) = Initial weight

\(X_t\) = Weight after time 't'

K = The annual experimental (base e) decay coefficient.

(ii) pH and moisture content of the litter

The remaining 3 bags were used for the determination of pH and moisture content of the litter (details given in Chapter III).

(iii) Estimation of organic constituent of leaf litter

Cellulose, hemicellulose, lignin, total soluble sugars and total amino acids of litter were estimated by the method of Peach and Tracey (1955).

(a) Cellulose and Hemicellulose

0.5 g of ground litter was treated with 25% KOH
aqueous solution (W/V). The mixture was centrifuged at 3000 rpm for 15 minutes. The decant obtained was used for detection of hemicellulose. The residue left was washed several times with distilled water. Thereafter, it was dried at 105°C in oven for 24 hours and cooled at room temperature in a desiccator and weighed. The amount thus obtained was total cellulose.

The decant obtained was neutralized with equal amount of glacial acetic acid and ethanol. The precipitate was filtered, washed, dried and weighed as above for determination of total hemicellulose. Three replicates were taken in each case.

(b) Lignin

0.5 g of dried litter powder was taken in a test tube and treated with 20 ml of 72% H₂SO₄ and kept in deep freeze for 24 hours. It was then centrifuged and the residue was collected and washed thoroughly to remove the traces of H₂SO₄ present. It was then dried in oven at 105°C for 24 hours. The amount so obtained gave the total lignin content in the leaf litter.

Data on cellulose, hemicellulose and lignin content was expressed on dry weight basis of the litters.
(c) Total sugars and Amino acids

100 mg dried powdered litter was taken in a test tube and treated with 80% ethanol. Occasionally, when any colour developed, it was treated with a pinch of activated charcoal and centrifuged at 6000 rpm. The solution was filtered through a filter paper (Whatman No. 1). The clear filtrate was boiled on a hot water bath to remove the traces of ethanol. To it distilled water was added to make the volume upto 5 ml.

To 3 ml of the above solution 6 ml of freshly prepared anthrone reagent (0.2% in $\text{H}_2\text{SO}_4$) was added slowly by the side of the test tube and shaken gently. The solution was then kept for 3 minutes in the boiling water bath and cooled at room temperature and absorbance of the solution was read at 610 nm in a Hitachi spectrophotometer. Standard curve was obtained from transmittance of varying concentration of glucose solution treated exactly as the samples. From the standard curve the values of the total sugars were expressed as $\mu$g/100 mg dry weight of the samples.

To the rest of 2 ml of the solution, 2.5 ml of citrate buffer (pH 5.5) and 2 ml ninhydrin solution were added. The mixture was kept in boiling water bath for 30 minutes and then cooled at room temperature. A light
purple colour developed in the solution. The absorbance was determined at 540 nm in the Hitachi spectrophotometer. The total amino acids were calculated from the standard curve obtained from transmittance of varying concentration of leucine solution treated exactly as unknown samples. From the standard curve the amount of amino acids in unknown sample was calculated and expressed as μg/100 mg dry weight of the samples.

(iv) Determination of inorganic constituents of the litter

(a) Nitrogen

Total nitrogen in the leaf litters was estimated by Micro-Kjeldahl method (Allen, 1974). 100 mg dried litter was grounded and sieved through a sieve (0.2 mm) was taken in a Micro-Kjeldahl flask. To it 2 g K₂SO₄:HgO (20:1) mixture was added. Now 3 ml of concentrated sulphuric acid was added slowly down the neck while the flask was rotated. The flask was heated on a digestion rack. After the digest became colourless the heating was continued for another 15 minutes. Thereafter, flasks were allowed to cool at room temperature. The digested material was diluted with distilled water and filtered through filter paper (Whatman No. 1). The blank digestion was prepared only with the mixture. Through digestion all the organic nitrogen converts into ammonia which was measured by Indo-
phenol blue method. The nitrogen was calculated by the following formula.

\[
\text{Nitrogen (\%) = } \frac{C(\text{mg}) \times \text{solution volume (ml)}}{10 \times \text{aliquot (ml)} \times \text{sample weight (g)}}
\]

Where, \(C\) = Concentration reading (mg) in the aliquot.

(b) Phosphorus

Oven dried litter was ground and sieved through a sieve (0.2 mm) was used for phosphorus determination. 0.3 g ground material was digested in a triacid mixture (HNO\(_3\), H\(_2\)SO\(_4\) and 60% HClO\(_4\) in ratio of 10:1:4) for the analysis of phosphorus. After digestion the volume was made to 50 ml and filtered through filter paper (Whatman No. 42). Phosphorus in the digested sample was estimated following the molybdenum blue method of Jackson (1967).

\[
\text{Phosphorus (\%) = } \frac{C(\text{mg}) \times \text{solution volume (ml)}}{10 \times \text{aliquot (ml)} \times \text{sample weight (g)}}
\]

Where, \(C\) = Concentration of phosphorus in the aliquot.

RESULTS

Weight loss of litter

Sequential loss of leaf litter of *Alnus nepalensis* was observed (Figs. 12 and 13). Maximum weight loss occurred during the month of June. A steady decrease in mass...
Fig 12. Percentage of original dry weight of leaf litters remaining after different time intervals at two forest stands of *Alnus nepalensis*, (c = closed, o = open)
Percentage of original dry weight of buried leaf litters remaining after different time intervals at two forest stands of *Alnus nepalensis*
Fig 14. Monthly variation in moisture content (O—O) and $P^H$ (●●●) of leaf litters at two forest stands of *Alnus nepalensis*. (c = closed, o = open)
Fig 15. Monthly variation in moisture content (▲-▲) and $^4$H (●-●) of buried leaf litters at two forest stands of *Alnus nepalensis*. 
Table 20 - Decay constant (K), half life and 95% life values for decomposition of Alnus nepalensis leaf litters under field condition.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>K (per year)</th>
<th>Half life (year)</th>
<th>95% life</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Open</td>
<td>Closed</td>
<td>Open</td>
<td>Closed</td>
<td>Open</td>
</tr>
<tr>
<td>Alnus nepalensis</td>
<td>1.198</td>
<td>0.940</td>
<td>0.578</td>
<td>0.737</td>
<td>2.504</td>
</tr>
</tbody>
</table>
Table 21 - Decay constant (K), half life and 95% life values for decomposition of buried leaf litters of *Alnus nepalensis* under field condition.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>K (per year)</th>
<th>Half life (year)</th>
<th>95% life</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Open</td>
<td>Closed</td>
<td>Open</td>
</tr>
<tr>
<td><em>Alnus nepalensis</em></td>
<td>1.197</td>
<td>1.421</td>
<td>0.578</td>
</tr>
</tbody>
</table>
loss was noticed after June, which increased from September to October as compared to the preceding months and a further repression was observed during winter months.

The mass loss of alder leaf litter in coarse mesh bags (3 mm) was slightly higher than that from the normal mesh bags (Figs. 12 and 13). The weight remaining in coarse mesh bag at the end of 11 months was 8% and 5% and 4% and 8% in case of normal mesh bag at the end of 14 months in the open and closed forest stands respectively.

Among the two forest stands, the decomposition of leaf alder litter was faster in low mesh size nylon bags (1 mm) under open forest stand condition \( (K = 1.198) \) than closed ones \( (K = 0.940) \), whereas disappearance of litter was faster in closed forest stand \( (K = 1.421) \) than open forest stand \( (K = 1.197) \) in coarse mesh bags (3 mm) (Tables 20 and 21).

**pH and Moisture content of the leaf litter**

Leaf litter of open forest stand was slightly acidic compared to closed forest stand. The pH ranged from 5.0 to 6.90 in open stand and from 5.5 to 6.95 in case of closed forest stand. In the beginning, the litter was less acidic in both the sites which subsequently became more acidic in winter and at the end of decomposition (Figs. 14 and 15).
Moisture content of litter ranged from 11.5% to 70% in open forest stand and 10.5% to 75% in case of closed forest stand (Figs. 14 and 15). It was minimum during winter months which increased with the onset of rain. However, the moisture content of litter was higher in closed forest compared to open forest ones. However, seasonal pattern was similar on both the stands. The correlation between weight loss of litter and its moisture content was not significant (Tables 22 and 23).

Organic constituents

Both the soluble (total sugars and amino acids) and insoluble (cellulose and hemicellulose) organic constituents in the leaf litter of *A. nepalensis* forest stands decomposed rapidly in the beginning and slow towards the end of the process of decomposition. Leaf litter of closed forest stand contained more amount of soluble compounds than of open forest stand. Maximum changes in total sugars and amino acids were observed during rainy months (Figs. 16 and 17). It was observed that the rate of degradation of soluble components was highest followed by hemicellulose, cellulose and lignin. The decomposition of cellulose and hemicellulose followed a similar pattern in both the forest stands whereas lignin contents increased in the beginning and degradation of lignin started towards the
latter part of decomposition (Figs. 18 and 19). At both the forest stands, the absolute weight loss of *A. nepalensis* leaf litter showed a significant negative correlation with the weight remaining of different organic constituents like cellulose, hemicellulose, sugars and amino acids. However, lignin content was correlated positively with absolute weight loss (Tables 22 and 23).

**Inorganic constituents**

**Nitrogen**

The initial nitrogen content ranged from 0.5 to 1.90% at open forest stand and 0.70 to 2.01% in case of closed stand. Initially, the nitrogen content increased up to the month of June followed by a subsequent decrease till the end of the decomposition in both the cases (Figs. 20 and 21).

**Phosphorus**

In both the stands the level of available phosphorus exhibited a similar trend during the present investigation. The initial phosphorus content ranged from .920 to 0.90% in open forest stand and .025 to 0.075% in closed stand (Figs. 20 and 21). Phosphorus was initially retained in the leaf litters for few months and then gradually released along with the decomposition of litter. The absolute weight loss of both the litters was correlated negatively with nitrogen and phosphorus (Tables 22 and 23).
Fig 16. Monthly variation in total sugars (•—•) and amino acids (△—△) of leaf litters at two forest stands of *Alnus nepalensis*. 
Monthly variation in total sugars (●—●) and amino acids (▲—▲) of buried leaf litters at two forest stands of Alnus nepalensis.
Fig 18. Monthly variation in cellulose (●●), hemicellulose (○○) and lignin (▲▲) content of leaf litters at two forest stands of Alnus nepalensis.
Fig 19. Monthly variation in cellulose, hemicellulose and lignin content of buried leaf litters at two forest stands of *Alnus nepalensis*.
Fig 20. Monthly variation in total nitrogen (●-●) and phosphorus (○-○) content of leaf litters at two forest stands of Alnus nepalensis.
Fig 21. Monthly variation in total nitrogen and phosphorus content of buried leaf litters at two forest stands of Alnus nepalensis.
Table 22 - Correlation coefficient (r) for cellulose, hemicellulose, lignin, total sugars, total amino acids, total nitrogen, phosphorus, fungal population, bacterial population and absolute weight loss in *Alnus nepalensis* litters at two forest stands.

<table>
<thead>
<tr>
<th>Sources of variation</th>
<th>D.F.</th>
<th>Absolute weight loss</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Open</td>
<td>Closed</td>
<td></td>
</tr>
<tr>
<td><strong>Cellulose</strong></td>
<td>12</td>
<td>-0.957***</td>
<td>-0.983***</td>
<td></td>
</tr>
<tr>
<td><strong>Hemicellulose</strong></td>
<td>12</td>
<td>-0.993***</td>
<td>-0.994***</td>
<td></td>
</tr>
<tr>
<td><strong>Lignin</strong></td>
<td>12</td>
<td>0.935***</td>
<td>0.815***</td>
<td></td>
</tr>
<tr>
<td><strong>Total sugars</strong></td>
<td>12</td>
<td>-0.993***</td>
<td>-0.990***</td>
<td></td>
</tr>
<tr>
<td><strong>Total amino acids</strong></td>
<td>12</td>
<td>-0.993***</td>
<td>-0.986***</td>
<td></td>
</tr>
<tr>
<td><strong>Total nitrogen</strong></td>
<td>12</td>
<td>-0.769***</td>
<td>-0.760***</td>
<td></td>
</tr>
<tr>
<td><strong>Phosphorus</strong></td>
<td>12</td>
<td>-0.697***</td>
<td>-0.777***</td>
<td></td>
</tr>
<tr>
<td><strong>Fungal population</strong></td>
<td>12</td>
<td>0.151</td>
<td>0.213</td>
<td></td>
</tr>
<tr>
<td><strong>Bacterial population</strong></td>
<td>12</td>
<td>0.111</td>
<td>0.067</td>
<td></td>
</tr>
<tr>
<td><strong>Moisture content</strong></td>
<td>12</td>
<td>0.045</td>
<td>0.038</td>
<td></td>
</tr>
</tbody>
</table>

*, **, *** p < 0.1, 0.05 and 0.01 respectively.

Without asterisk statistically insignificant at these levels.
Table 23 - Correlation coefficient (r) for cellulose, hemicellulose, lignin, total sugars, total amino acids, total nitrogen, phosphorus, fungal population, bacterial population and absolute weight loss in buried litters of *Alnus nepalensis*.

<table>
<thead>
<tr>
<th>Sources of variation</th>
<th>D.F.</th>
<th>Open</th>
<th>Closed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cellulose</td>
<td>9</td>
<td>-0.981***</td>
<td>-0.980***</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>9</td>
<td>-0.985***</td>
<td>-0.981***</td>
</tr>
<tr>
<td>Lignin</td>
<td>9</td>
<td>0.630**</td>
<td>0.664**</td>
</tr>
<tr>
<td>Total sugars</td>
<td>9</td>
<td>-0.976***</td>
<td>-0.983***</td>
</tr>
<tr>
<td>Total amino acids</td>
<td>9</td>
<td>-0.980***</td>
<td>-0.970***</td>
</tr>
<tr>
<td>Total nitrogen</td>
<td>9</td>
<td>-0.658**</td>
<td>-0.618**</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>9</td>
<td>-0.562*</td>
<td>-0.605**</td>
</tr>
<tr>
<td>Fungal population</td>
<td>9</td>
<td>0.200</td>
<td>0.113</td>
</tr>
<tr>
<td>Bacterial population</td>
<td>9</td>
<td>0.341</td>
<td>0.467</td>
</tr>
<tr>
<td>Moisture content</td>
<td>9</td>
<td>0.465</td>
<td>0.478</td>
</tr>
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</table>

*, **, *** p < 0.1, 0.05 and 0.01 respectively.

Without asterisk statistically insignificant at these levels.
DISCUSSION

From the results obtained, apparently there was not much variation in the rate of leaf litter decomposition on both the forest stands. Moreover, the rate of litter decomposition in fine mesh bag has been found to be slightly faster in the open forest stand compared to that of closed forest stand. This was attributed to the high microbial population encountered in open forest stand, whereas in case of coarse mesh bags, higher mass loss from closed forest stand than from the open stand, may be attributable to the initial higher N content, narrower C/N ratio litter texture and greater arthropod abundance in the litter bags (Anderson, 1973).

Greater mass loss from coarse mesh bags containing alder leaf litter compared to that from fine mesh bags has also been reported by Gupta and Singh (1981) and Reddy and Alfred (1989). It could be due to the influence of mesh size on the access of different sizes of soil animals and greater abundance of certain taxa determining the communication rate. Lesser decomposition in the fine mesh bags may be due to the inability of the soil microfauna to invade the bags. The importance of soil animals in decomposing organic debris by employing varying mesh size litter bags or by using chemicals (Anderson, 1973; Wood,
1976). More weight is lost when all groups of soil animals and microorganisms take part in the decomposition processes. The higher weight losses in the present study in coarse mesh bags (3 mm pore size) compared to fine mesh bags (1 mm pore) can be accounted in the light of the above discussion. The difference in decomposition rate may be assigned to physical nature of plant material (Bhatt et al., 1985), difference in pH, moisture content and substrate quality, which ultimately govern the distribution of microflora (Swift et al., 1979 and Howard and Howard, 1980).

The slow rate of litter decomposition at the initial stages may be due to unfavourable abiotic conditions and low microbial population. The increased rate of litter decomposition in both the cases during June - October may be due to the favourable temperature and water potentials (Stott et al., 1986 and Tiwari, 1988) which might have favoured the luxurious growth of microbes (Nagy and Macauley, 1982; Moore, 1986 and Tiwari, 1988). The concomitant peaks of weight loss, microbial activity and population obtained during rainy season were attributed to the high moisture content of litter and warm conditions prevailing during the same season. This trend may be due to higher initial content of water soluble materials and
simple substrates, the breakdown of the litter by decomposers, especially microflora and the removal of leaf particles by animals through comminution e.g., by Isopods (Anderson et al., 1983 and Swift et al., 1981).

During winter the rate of litter decomposition decreased which may be due to the low temperature and microbial population which resulted in low microbial activity. Shukla (1976) and Harper and Lynch (1981) also found a slow rate of decomposition at low temperature in the field condition. A repression in the litter decomposition rates during winter months may be caused by a combination of factors like temperature and dry environmental conditions and the predominance of slow decomposing litter components such as lignin (Meentemeyer, 1978). William and Gray (1974) observed that during periods of droughts, litter decomposition rates are drastically retarded and the number of saprophagous animals in the litter reduced.

The organic constituents followed almost a similar pattern of distribution in litters in both types of mesh bag of both the forest stands. Generally, the amount of cellulose, hemicellulose, lignin, total sugars and amino acids was maximum in the beginning and minimum at the end of the decomposing process. It has been observed that the rate of hemicellulose breakdown was the fastest followed
by the cellulose and lignin. This trend was similar in both types of mesh bag of both the forest stands. The amount of lignin increased in the beginning and degraded towards the later part of decomposition can be assigned to the active degradation of cellulose and hemicellulose and other simpler forms in the beginning which can be easily utilized by the microbes (Berg et al., 1984). This may also be due to the resistant nature of ligno cellulotic complexes (Summerell and Burges, 1989). The preferential use of sugars, amino acids, cellulose and hemicellulose in the beginning indicates their role in the microbial growth (Harper and Lynch, 1981). Summerell and Burges (1989) have also reported a decrease in the proportion of cellulose and hemicellulose during decomposition which increase in lignin concentration similar to the present investigation.

Rapid degradation of total sugars, amino acids, cellulose and hemicellulose in the beginning of decomposition process was attributed to their simpler chemical nature and improved utilization by the microbes (Harper and Lynch, 1981). This can also be attributed to their highly soluble nature which must have enhanced their leaching along with rain water.

The increase in nitrogen content in the beginning
in both the forest stands may be due to a demand for nitrogen by heterotrophs in which the nitrogen gets immobilized during decomposition (Lousier and Parkinson, 1978). The decrease in nitrogen content during later part of rainy months may be attributed to the leaching of labile nutrients. Similar observations were reported by Kashattriya (1990).

Studies on plant material decomposition have followed the change in N concentration with time (Bocock, 1963, 1964; Latter and Cragg, 1967; Singh, 1969; Wood, 1974; Lambert and Lang, 1980). Shukla and Singh (1984) reported that low moisture condition was not suitable for the leaching of nutrients from the decomposing litters. They further suggested that during the onset of rains the litters were exposed to the attack of the microorganisms. The soluble carbohydrates, protective layers of wax and cutin were washed away during rainy season and this resulted into increased leaching of the minerals (N, P and K) recorded during the present investigation as most of these minerals leached into the soil during rainy seasons.

Higher phosphorus content was obtained at early stage of decomposition. Drop in phosphorus content was noted with the progress of decomposition process. Staaf (1980) ascribed it to preferential retention of P and N while other nutrients are being rapidly lost during decomposition.
The activity of microorganisms and isopods in leaf litter decomposition seemed to be influenced by the micro climatic conditions and the rate of decomposition mainly depended upon the moisture and temperature requirements of the microorganisms involved therein. Similarly litter and soil moisture affected the mass loss and isopod populations.

Thus decomposition of leaf litter is controlled by a multiplicity of factors including those resulting from changes in the forest floor temperature and moisture regimes, substrate quality, and microbial and soil animal populations (Williams and Gray, 1974, Maclean and Wein, 1978).