Litter decomposition, climate and litter quality

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Litter decomposition is controlled by three main factors: climate, litter quality and the nature and abundance of the decomposing organisms. Climate is the dominant factor in areas subjected to unfavourable weather conditions, whereas litter quality largely prevails as the regulator under favourable conditions. Litter quality remains important until the late decomposition stages through its effects on humus formation. Interest in the role of litter decomposition in the global carbon cycle has increased recently since (1) increased atmospheric carbon dioxide will probably affect the chemical quality of litter (especially nitrogen content), and (2) global warming may enhance decomposition rates.

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The size of the organic carbon (C) reservoir in the soil depends upon both plant production and the mineralization of plant residues. The size of the global reservoir is estimated at 1200–2000 Pg (Pg = 10^{15} g), two to three times the estimated amount of C in the biomass and two to three times the quantity of C in the atmosphere. The average global CO_2 flux from soil heterotrophic respiration is estimated to be 68 ± 4 Pg C yr^{-1} based on extrapolations from biome land areas[1]. Mineralization of the annual litter fall contributes to approximately half of the CO_2 output from the soil, and this proportion remains stable because of its relatively constant annual input. Such figures demonstrate the importance of litter decomposition as a direct source of CO_2 to the atmosphere.

Litter decomposition (mass loss) involves two simultaneous and fundamental sets of processes: (1) the concomitant mineralization and humification of lignin, cellulose and other compounds by a succession of microorganisms; and (2) the leaching downward in the soil of soluble compounds whose C and nitrogen (N) are progressively mineralized or immobilized. These processes are controlled by abiotic factors, such as climate, and by biotic factors, such as litter chemical composition and soil organisms. Chemical changes during litter decomposition are illustrated in Fig. 1 (Ref. 2).

This review focuses on changes in the decomposition process that we can expect in response to global warming.

Decomposition process

Litter chemical components can be classified in terms of their availability to the microorganisms' enzyme systems. The degradation of natural polymers (hydrolysis of cellulose and hemicelluloses) by exoenzymes to dimers and monomers, which are the energy-yielding substrates[3], is necessary for their ingestion by microorganisms, such as bacteria and fungi. In lignin, stable bonds require energy for their degradation. It seems that co-metabolism with other, more labile, compounds is necessary for the degradation of lignin to proceed. It has also been found[4] that the ligninolytic enzyme system can be repressed by high levels of NH_4^+ and low-molecular organic N compounds. This repression can be explained by the following interactions: (1) N alters the outcome of competition between potent and less-potent decomposers, including lignin-metabolizing microorganisms; (2) 'ammonia metabolite repression'[4] blocks the production of ligninolytic enzymes, at least in basidiomycetes, whereby recalcitrant lignified cellulose accumulates; and (3) amino compounds condense with polyphenols and other lignin decomposition products to form 'browning precursors'[4] which are toxic and/or inhibitory. In addition to microbial activity, the soil fauna contributes actively to litter breakdown by (1) grinding plant residues and thus increasing the surface area of the detritus, (2) mixing soil organic matter with the mineral horizon, and (3) channelling and improving the soil structure[5].

Enzyme activity normally increases with temperature, but rapidly falls as the temperature rises above an optimum value. Low moisture limits metabolic activity[6], and as soil moisture levels rise, metabolic activity increases until an optimum plateau is reached. Additional water does not affect metabolism until anaerobic conditions arise. At this point, the decomposition rates of some biochemical compounds are reduced, and some processes are completely suppressed, for example, lignin decomposition. It is likely that the optimum response to temperature and moisture is determined largely by the local climate[7] and the type of functional groups of microorganisms. Nevertheless, this aspect has not been thoroughly investigated on a large scale, especially with regard to the combined effects of temperature and moisture. Indirect effects of temperature and moisture, such as cycles of drying and wetting as well as freezing and thawing, influence decomposition rates and the proportions of mineralized and leached compounds. These effects are generally ascribed to the death of some of the microorganisms and to the partial mineralization of the microbial biomass products.

Effect of climate and litter quality on decomposition

Meentemeyer[8] proposed a general decomposition model driven by actual evapotranspiration (AET) as a climatic variable and lignin concentration as a litter quality variable. This model has been used on a regional scale. For some types of litter, the climate is clearly more important – at least in early decomposition stages – than substrate quality as a predictor of decomposition rates over large scales. Meentemeyer and Berg[9] found that AET was a good predictor of mass-loss rates for Scots pine needles along a Scandinavian climatic transect (Fig. 2). Nevertheless, in the same transect, no climatic factor was significantly correlated with mass-loss rates of Norway spruce needles. Also, in the same climatic transect, decomposition rates of highly decomposed

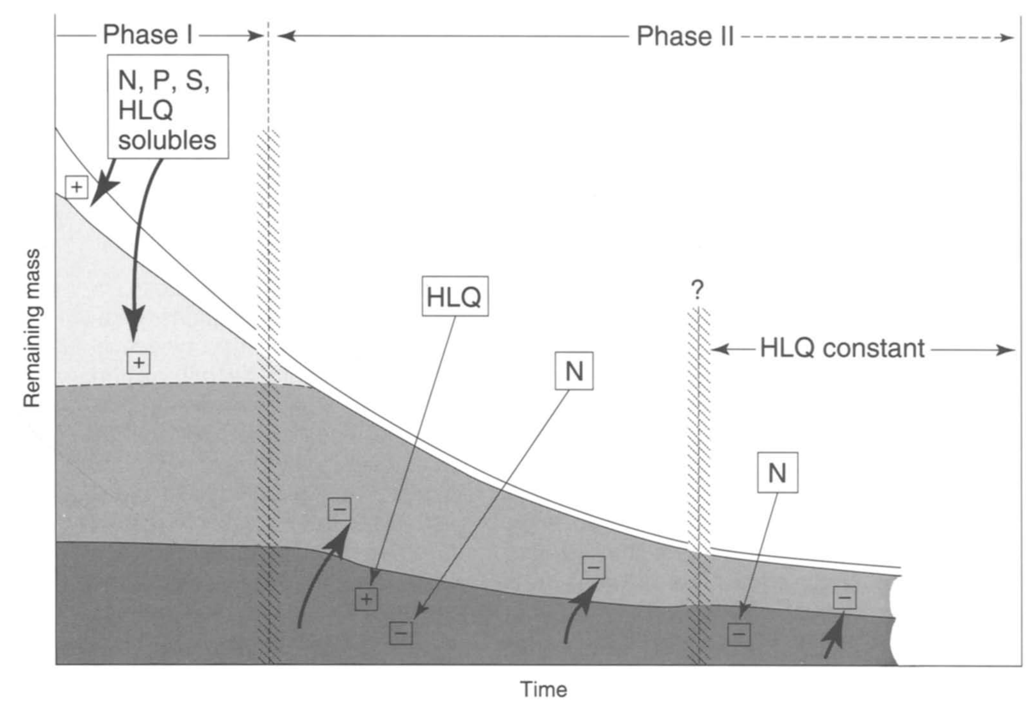

Fig. 1. Suggested model of decomposition of some organic components in Scots pine (*Pinus silvestris*) needle litter. In the early phase (Phase I) of decomposition, high concentrations of nutrients such as N, P and sulphur (S) exert a rate-enhancing influence on mass loss of those compounds of the litter that are not lignified. Also, high concentrations of easily degraded solubles and celluloses influence a high mass-loss rate. In the late stage (Phase II), where mainly lignified material remains, the degradation of litter is ruled by lignin mass loss, which is negatively affected by high N concentrations and positively affected by high concentrations of celluloses in the lignified material. The negative effect of lignin on the degradation rate of cellulose is indicated by the black arrows. (+) indicates a rate-enhancing influence and (–) a negative one. HLQ designates the quotient between holocellulose and lignin plus holocellulose[2]. In order of increasing shading, the plot shows the following fractions: solubles; non-lignified carbohydrates; lignified carbohydrates; lignin.

Scots pine needles depended more on substrate quality than on climate. Furthermore, in a recent study using 39 coniferous forest sites spanning an area from the subarctic to subtropics, including Atlantic and Mediterranean climates, Berg *et al.*[10] also showed AET to be the leading constraint on the mass loss of Scots pine needle litter during the first year of decomposition (accumulated mass loss <50%). However, other climatic factors, such as seasonal distributions of precipitation and temperature, explain part of the variation (Fig. 2), and it is possible to distinguish between the effects of inland (Fig. 2a) and Atlantic climates (Fig. 2b) using AET as a predictor.

During litter decomposition, the relative lignin concentration apparently increases owing to its low degradation rate[11], but also because the conventional lignin analytical methods do not distinguish between true lignin and partially humified products. However, the rate-retarding influence of lignin on litter decomposition appears to depend on climate. Thus, it was found that in late decomposition stages the effect of higher lignin concentrations was low in a harsh climate (e.g. at the Arctic Circle), whereas when the same substrate was decomposed in warmer and wetter regions (European–Atlantic climate), higher lignin concentrations had a predominant effect. The chemical composition of a given litter type, at a given stage of decomposition, depends on the local climatic conditions: at the same level of mass loss the concentration of lignin and lignin-like products is higher at warmer and wetter sites where the initial decomposition rates are high[12]. This could possibly be explained by climatically controlled modifications of the structure of the microbial population and by the humification process. Nonetheless, in these late stages of decomposition, the effect of climate is dominated by the increase of lignin concentration. During these stages there are strong indications that naturally high levels of N have a rate-retarding influence on the litter decomposition rate[13].

In some biomes, AET is not a predictor of mass-loss rate. For instance, it has been reported[14] that, in a subarctic area, much of the mass loss occurs in the winter months under snow cover when AET values are close to zero. Temperatures in the range of –5°C to +1°C are frequent[15] below the snow cover, as an effect of insulation. Snowmelt causes waterlogging in some areas, and as summer approaches these conditions change from semi-aquatic to well drained. Seasonal flooding increases the leaching of organic compounds and nutrients[16]. Schaefer *et al.*[17] reported relatively high decomposition rates in arid and semi-arid regions, which cannot be explained by AET and suggest that abiotic factors, such as fragmentation, may play an important role in the mass-loss process. The primary effect of rainfall would then be to transport fragments downward in the soil[18]. In this dry and warm climate, Vossbrinck *et al.*[19] reported that abiotic breakdown accounted for approximately 40% of the overall mass loss for some litter types. There appears to be a progressive shift in the dominant processes from biotic ones in temperate areas to abiotic ones in arid biomes. As aridity increases, unfavourable surface conditions and the concentration of litter in discontinuous areas hinder the development of the surface decomposer community. Physical fragmentation becomes increasingly dominant in patches on the soil surface where decomposing organisms can act more effectively[20]. Photochemical degradation of lignins may account for a non-negligible part of the total loss[21].

In a wet tropical climate, temperature and moisture are less constraining, and the decomposition rate depends primarily on soil and humus properties and litter quality[22]. Tanner[23], who incubated litter from 15 species in Jamaican montane rainforests, found that, in the first year, decomposition ranged from 27 to 96% depending on the type of humus and the N and phosphorus (P) contents of the leaves. In a literature review, Cuevas and Medina[24] reported that the time required to reach 95% mass loss in various kinds of humid tropical forests ranges from 0.4 to 13.6 years.

The European Mediterranean region constitutes a critical geographical zone because decomposition shifts from being primarily temperature limited in areas close to the Atlantic on the European west coast, to being mainly moisture limited in the southern part of the Mediterranean zone (e.g. towards the semi-arid zones of North Africa). Bottner *et al.*[25] predicted that, for western Europe, the decomposition rates should be highest at the transition between Mediterranean and Atlantic climates where favourable moisture and temperature occur concomitantly. In Mediterranean-type ecosystems, the sclerophylly of the leaves is an indicator of decomposition rates, reflecting a high content of structural compounds[26].

The biodiversity of microbial and animal communities, as well as the duration and the intensity of their activity, is known to depend on climate. The world distribution of soil fauna is temperature-limited in boreal latitudes, moisture-limited in arid zones, and food-limited by microbial competition in the tropics. Although animal activity has been detected at low temperatures in tundra[27], soil invertebrate diversity there is low; for instance, there are no snails, earthworms or millipedes[28]. In a study carried out in an area with a mild and warm (Atlantic) climate, where animals can remain active throughout the year, the decomposition rate of straw over an eight to ten month period was 26–47% greater in the presence of earthworms than in the area from which they had been excluded[29]. In desert systems, microarthropods have been found to increase decomposition rates by up to 50% (Ref. 30). Termites can remain active under dry conditions and are a 'key' group for root decomposition[31]. In Mediterranean ecosystems, animal mortality is high during the dry season, but high diversity and activity lead to high decomposition rates during the milder, wetter periods[32].

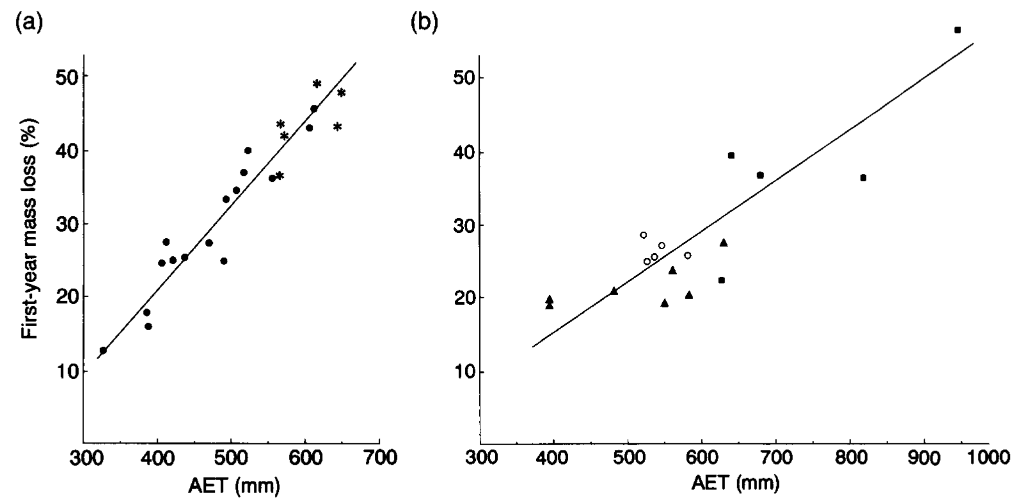

Fig. 2. Bivariate plot of the average first-year litter mass loss versus actual evapotranspiration. (a) Scots pine sites in a Scandinavian–NW-continental transect (filled circles); and pine sites close to the European west coast or sites relatively exposed to Atlantic climate (r^2=0.916, n=22, P<0.001) (asterisks). (b) Pine sites around the Mediterranean (filled triangles); Central European Scots pine sites (Poland) (open circles) with characteristics of an inland climate; and pine sites in eastern inland USA (r^2=0.753, n=17, P<0.001) (filled squares)[10].

Decomposition and global changes

The C stock in terrestrial ecosystems represents the difference between the input from net primary production (in terms of quality and quantity) and the output through decomposition. Considering the strong influence that the chemical and physical climate factors have on both litter quality and decomposition processes, certain responses to predicted climate changes can be expected. (1) Leaf litter N concentrations should decrease as the concentration atmospheric CO_2 rises[33]; since N is one of several factors controlling decomposition rates, subsequent modifications in decomposition patterns are expected[34]. (2) An increased rate of C mineralization is expected in response to the predicted temperature rise. Nevertheless, our knowledge of the thermosensitivity of the decomposer organisms in litter, the organic matter types, and the organic matter compartments, is not clear. (3) N mineralization should also increase in response to a temperature rise, thereby modify the N balance in ecosystems favouring plant nutrition. (4) The effects of a northward shift of vegetation[35] on source–sink relations in soil are hard to predict because of the large inertia of stabilized organic matter.

The biomes where the soils have the highest C concentration are forests and tundras. The largest soil C reservoirs per unit surface area are situated at high latitudes, where litter decomposition rates are low and where accumulation occurs, and in the tropical regions, where high decomposition rates are compensated by high primary production and lead to a relatively high soil C content. The responses of these biomes to global change will be the most substantial.

Experiments have shown that an increase in atmospheric CO_2 can enhance net primary production. Furthermore, in soils where inorganic N is limiting, these studies showed that a CO_2 increase can modify the N distribution in plants and lower N concentrations in the litter[33]. For other nutrients – P, potassium, calcium and magnesium – no significant effects of CO_2 were reported[36]. Thus, in boreal and temperate regions with a low pollution load, a higher production of poor quality litter would favour two counteracting processes: (1) increased litter production would result in soil organic-matter accumulation; and (2) decrease in litter quality would probably increase the production of ligninolytic enzymes, leading, in turn, to increased degradation of recalcitrant compounds. Nevertheless, the extent to which lowering the N level would affect lignin degradation is unknown. In tropical forests, it can be expected that the main change would concern primary production and the effect of increased atmospheric CO_2 on the N concentration in the litter. Nevertheless, in tropical regions, N limitation is generally less crucial than P limitation[37]. Still, because of the high plant diversity and our uncertainty about how plants will respond to an elevation of CO_2, the reliability of any predictions is questionable.

General circulation models predict that the greatest temperature increase (4–6°C) will occur at high latitudes. At low latitudes, in regions with a wet and warm climate, the change in temperature is expected to be low, but cloudiness should increase[38]. In boreal and temperate regions, a temperature rise would decrease the length of the winter, reducing the permafrost areas[39], increasing the decomposition of organic matter and enhancing C and N mineralization. Indirect effects of a rise in temperature would include an increase in N availability and a mitigation of the N dilution resulting from CO_2 fertilization. Nevertheless, the thermosensitivity of soil microorganisms according to biomes remains poorly understood.

Thus, the combined effects of changes in chemical (atmospheric CO_2 increase) and physical factors on the decomposition processes involve a set of responses that can balance each other out to a certain degree. In boreal and temperate climates, it was shown that, generally, during the early stage of decomposition, the climate influence tends to dominate the litter quality factor. By contrast, under wet and warm conditions, climate is less of a limiting factor for decomposition; thus the litter quality will be the key factor.

Future directions

To understand litter decomposition processes and how they would be affected by climatic changes, we need to fill the following gaps in our knowledge.

- Because of the wide range in litter quality, especially concerning broadleaf litters in temperate and tropical zones, there is a need (1) to understand the role of N compounds, of lignin and of lignified cellulose, and their interactions during the late decomposition stages; and (2) to elucidate the role of physical properties (e.g. schlerophylly). Physiologists should provide information concerning the climate-change-induced modifications of physical and chemical properties of the litters of some essential forest species.
- Interactions between C and N that control decomposition pathways have to be clarified with a special focus on C availability and on litter decomposition as a source of inorganic N or as a temporary sink of soil N.
- Other nutrients, for example P and manganese, appear to be just as important and warrant further study to determine their roles.
- Litter decomposition has to be linked to humus formation, with special focus on the factors controlling N availability during late decomposition stages.

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