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Litter quality in a north European transect versus carbon storage potential

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Abstract

Newly shed foliar plant litter often has a decomposition rate of ca 0.1–0.2% day^{-1}, which decreases greatly with time and may reach 0.0001 to 0.00001% day^{-1} or lower in litter material in the last stages of decay. The decrease in decomposability (substrate quality) varies among species and is complex, involving both direct chemical changes in the substrate itself and the succession in microorganisms able to compete for substrate with a given chemical composition. In late stages, the decomposition appears very little affected by climate, suggesting that climate change will have little effect on late-stages decomposition rates. Here, we apply a model for the late stages of litter decomposition to address the question of climate-change effects on soil-C storage. Decomposition of litter turning into soil organic matter (SOM) is determined by the degradation rate of lignin. In the last phases of decay, raised N concentrations have a rate-retarding effect on lignin degradation and thus on the decomposition of far-decomposed litter and litter in near-humus stages. The retardation of the decomposition rate in late stages may be so strong that decomposition reaches a limit value at which total mass losses virtually stop. At such a stage the remaining litter would be close to that of stabilized SOM. The estimated limit values for different species range from about 45 to 100% decomposition indicating that between 0 and 55% should either be stabilized or decompose extremely slowly. For no less than 106 long-term studies on litter decomposition, encompassing 21 litter types, limit values were significantly and negatively related to N concentration, meaning that the higher the N concentration in the newly shed litter (the lower the C/N ratio) the more litter was left when it reached its limit value. Trees growing under warmer and wetter climates (higher actual evapotranspiration, AET) tend to shed foliar litter more rich in N than those growing under colder and drier climates. A change in climate resulting in higher AET would thus mean that within species, e.g., Scots pine, a higher N level in the foliar litter may result. Further, within the boreal system deciduous species appear to have foliar litter richer in N than have conifers and within the conifers group, Norway spruce has needle litter more rich in N than, e.g., Scots pine. Thus, a change of species (e.g., by planting) from pine to spruce or from spruce to a deciduous species such as birch may result in a higher N level in the litter fall at a given site. In both cases the result would be a lower limit value for decomposition. The paper presents an hypothesis, largely based on available data that a change in climate of 4° higher annual average temperature and 40% higher precipitation in the Baltic basin would result in higher N levels in litter, lower decomposition and thus a considerable increase in humus accumulation.

Introduction

The accumulation of soil organic matter (SOM) is a slow process that often spans generations of scientists, thereby complicating the study of SOM accumulation. Still, a long-term buildup of SOM appears to take place in natural and undisturbed sys-tems. Thus, Wardle et al. (1997) found thick mor humus layers under growing trees that had accumulated continuously for more than 2900 years. On a more short-term basis, Berg et al. (1995b) described and quantified the buildup of a humus layer over a period of 110 years using data from decomposing foliar litter.

In their model for plant litter decomposition, using Scots pine needles, Berg and Staaf (1980) recognized different decomposition stages with different properties, before the litter eventually turns into humus (cf Berg and Matzner, 1997). This model has been applied across a climate transect and the mass-loss rates compared for different decomposition stages, and Johansson et al. (1995) describe how litter incubated in different climates actually reached the same decomposition rate in a late decomposition stage. For very late decomposition stages of the same litter type, Couteaux et al. (1998) estimated extremely low decomposition rates (magnitude of $10^{-5}\%$ day^{-1}) for the stabilized part of the litter as well as for humus from the same site. Based on the results of Howard and Howard (1974), Berg et al. (1996) estimated limit values (i.e. the point when decay virtually ceases) for the decomposition of litter. These results have been supported by an increasing number of studies (Berg, 2000) and validated using N as an internal marker (Berg et al., 2000a, b).

No less than 106 such limit values for decomposing foliar litter from natural forest systems have been estimated. Using litters representing a wide range in chemical composition, Berg et al. (1996) and Berg (2000) found a highly significant negative relationship between limit values and initial N concentrations in litter. The concept 'limit values' makes it possible to quantify the remaining, recalcitrant mass in the very late stages of decomposition as well as to quantify SOM buildup (cf Berg et al., 1995).

The recalcitrance of lignin to decomposition often has been ascribed to the structure of the molecule itself. It has been found, however, that the concentration of N may have a strong influence on the degradation rate, in part by repressing the formation of lignolytic enzymes (Eriksson et al., 1990), and in part due to chemical condensation reactions (cf Nömmik and Vahtras, 1982). These findings from laboratory studies were applicable to lignin in decomposing litters with different N levels; higher N concentrations led to lower lignin mass-loss rates (e.g., Berg and Ekbohm, 1991). There are also negative relationships between respiration and N levels in humus (cf Fog, 1988; Berg and Matzner, 1997). The present paper has, therefore, focused on interactions between N and lignin as the primary control of late stage mass-loss rates.

A change in climate in northern Europe is expected to result in an increase in temperature and higher precipitation (e.g., Johannesson et al., 1995). Such a change may also lead to increased N concentration in foliar litter within, e.g., Scots pine (Berg et al., 1995a), or to generally higher foliar N levels if conifers are replaced by deciduous species. Here we hypothezise that an increase in temperature and precipitation will lead to a larger fraction of recalcitrant litter material and a higher storage rate for SOM because the foliar litter will have higher N concentrations under such a change in climate. Further, higher N levels will increase the recalcitrant fraction of the decomposing litter.

Our hypothesis contrasts with a more traditional view that higher temperature and higher N content support a higher plant litter decomposition rate irrespective of the type of C compounds (cf Garten et al., 2000).

Discussion

A conceptual model for rate-regulation of plant litter decomposition and final stages of decomposition

The basic model for litter decomposition

Both from the point of view of chemistry and substrate quality (decomposability), fresh litter is very different from older, partly decomposed litter. Based on their studies on Scots pine needle litter, Berg and Staaf (1980) set up a model dividing the decomposition into two phases, with an early and a later stage in which the increasing lignin concentrations during decay suppress the decomposition rates (e.g., Fogel and Cromack, 1977; McClaugherty and Berg, 1987) and in which lignin degradation is suppressed by raised N-levels (cf Eriksson et al., 1990). Also the concentrations of N increase linearly with accumulated mass loss (cf Staaf and Berg, 1982). As decomposition proceeds the litter thus becomes enriched in lignin and N (Berg and Staaf, 1980). Berg and Matzner (1997) developed the model further and included a final stage in which the decomposition may slow down and approach a limit value (cf Fig. 1a,b).

The negative relationship between decomposition rate and lignin concentration changed with climate with a more rate-retarding effect the warmer and wetter the climate (the higher the AET) and in a climate-transect study Berg et al. (1993) and Johansson et al. (1995) observed that the slope of this negative relationship was steeper and the intercept was larger with increasing annual actual evapotranspiration (AET) among sites. Thus, as the decomposing litter approaches humus the response of decomposition to climate variation decreases but the response to lignin concentration increases. In fact, the effect of climate (annual average temperature ranging from 0.5 to 8 °C and AET from 357 to 559 mm) on decomposition rate

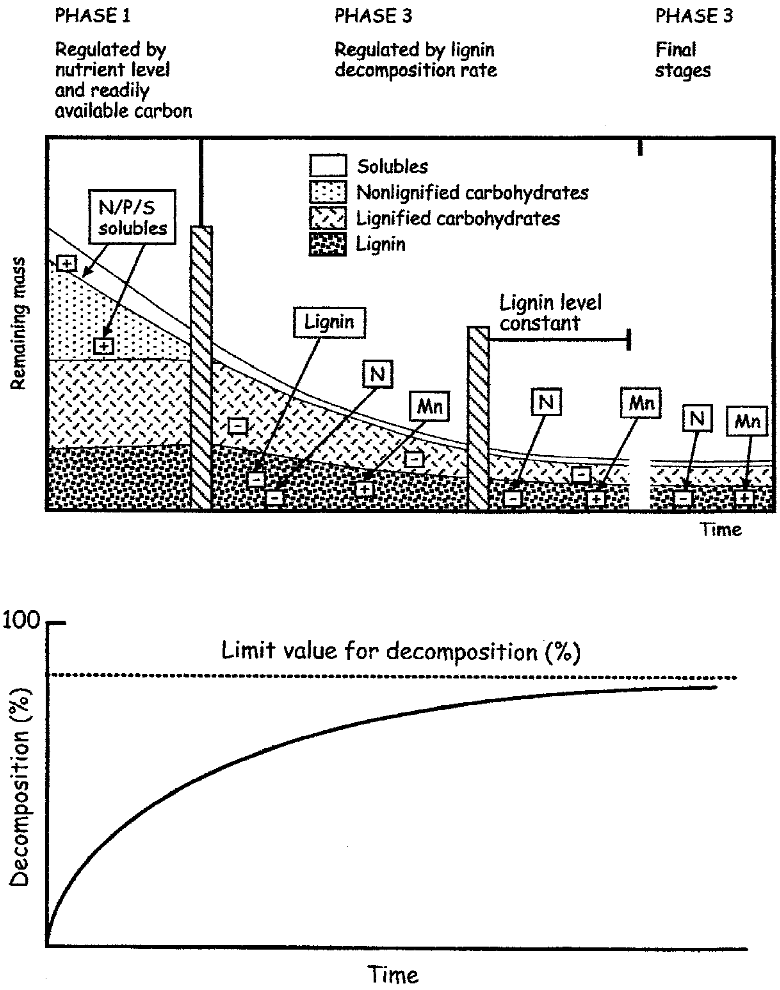

Figure 1. (A) Model for chemical changes and rate-regulating factors during decomposition. Modified from Berg and Matzner (1997). (B) Asymptotic model for estimating limit values for plant litter decomposition. Limit value indicated by the dashed line. Redrawn from Berg and Ekbohm (1991).

was not measurable in the late stages of decomposition. These measurements using litter bags represent decomposition of organic matter in undisturbed systems. A similar result was obtained by Strömgren et al. (1999) in a soil-warming experiment. After a period of 4 years during which the growing season soil temperature was maintained at a temperature 5 °C higher than in the control the CO_2flux from the forest floor was similar in the control and the heated plots. This finding supports the observation of Johansson et al. (1995) that in the near-humus stages, factors other than climate dominate humus decomposition rates. It must be emphasized that the disturbance caused by creating the experiment of Strömgren et al. (1999) initially gave a higher respiration rate in the heated plots.

Nitrogen concentration is critical for lignin degradation

During late stages of plant litter decomposition there is a significant and negative relationship between litter N concentration and lignin mass-loss rate. The lignin decomposition rate is lowest for N-rich litters and highest for N-poor ones (cf Berg et al., 1982). Berg and Ekbohm (1991) also found a clearly significant and negative relationship between N concentration and lignin decomposition, in seven chemically different types of litter, mainly of different species. They found a highly significant negative linear relationship between lignin decomposition and litter N concentration (R^2 = 0.677). The observation of the repressing effect of N has not been limited to mass-loss measurements. Increased N concentrations in humus (both as ammonium and as total N) also suppress respiration (CO_2) from humus (Berg and Matzner, 1997).

The empirical relationship of N as a rate-suppressing factor could be explained by two mechanisms that also help to explain why mass-loss rates of the sulfuric acid lignin fraction differed among litters. For several fungal species, low-molecular N compounds repress the formation of lignolytic enzymes (Eriksson et al., 1990; P. Ander, pers. commun.). As a further rate-regulating phenomenon, products of lignin degradation may react with ammonia or amino acids to form recalcitrant complexes (e.g., Nömmik and Vahtras, 1982). The results of laboratory experiments indicate that the concentration of ammonium/ammonia could be rate-limiting to this type of reaction (Axelsson and Berg, 1988).

Either one or both of these mechanisms may decrease decomposition rates of sulfuric acid lignin. Also, in partly decomposed litter, lignin exists as native lignin or moderately modified lignin. At least within a certain range of litter mass loss, there does not appear to be any extensive synthesis of entirely new products and Nordén and Berg (1990) did not find any new peaks in the aromatic resonance region when applying high resolution ^{13}C NMR to needle litter samples in decomposition stages from 0 to 70% accumulated litter mass loss (a near-humus stage for this type of litter).

Final stages of decomposition: limit values versus litter chemical composition

Berg (2000) estimated a total of 106 limit values for foliar litter decomposing in natural systems, and found a highly significant and negative relationship against litter N concentrations (R^2 = 0.323; P<0.001) (Fig. 2a; Table 1). These limit values represented 21 different species and within, e.g., Scots pine and Norway spruce, also a good variation in chemical composition. The possible causal relationships were discussed above. The low R^2 value of 0.323 may have resulted because the data set included limit values for litter decomposing in very different ecosystems with different soil types and climates which potentially influence the limit value. Thus, for each species when the average limit value was estimated and compared to the average N concentration (Fig. 2b; Table 2) the relationship clearly improved (R^2=0.761; n=8; P<0.01).

Table 1. Correlations between limit values, and initial concentrations in litter of N, Mn, and Ca respectively (from Berg (1998; 2000))

Nutrient	r	R^2	n	$P<$
Natural systems				
N	−0.568	0.323	106	0.001
Mn	0.519	0.269	83	0.001
All deciduous litter				
Mn	0.618	0.382	13	0.05
Ca	0.675	0.456	18	0.01
N	−0.438	0.192	30	0.05
All coniferous litter				
N	−0.660	0.436	86	0.001
Mn	0.513	0.263	74	0.001
Scots pine litter alone				
N	−0.683	0.466	42	0.001
Mn	0.485	0.235	35	0.01

Table 2. Mean values for limit values for decomposition and N concentration for eight litter types (from Berg, 2000) (cf. Fig. 2B)

Litter type	Average values for		n
	N conc. (mg g^{-1}) (SE)	Limit value (%) (SE)	
Scots pine (brown needles)	4.19 (0.19)	81.3 (1.21)	23
Scots pine (green needles)	12.18 (0.91)	67.2 (3.38)	8
Lodgepole pine	4.0 (0.19)	94.91 (1.94)	7
Norway spruce	5.44 (0.37)	74.07 (3.59)	15
Silver fir	12.85 (0.33)	51.5 (1.36)	4
Common beech	11.9 (2.17)	59.12 (3.81)	5
Pyrenean oak	12.2 (1.80)	60.3 (3.95)	4
White birch	9.55 (1.37)	77.7 (7.8)	4

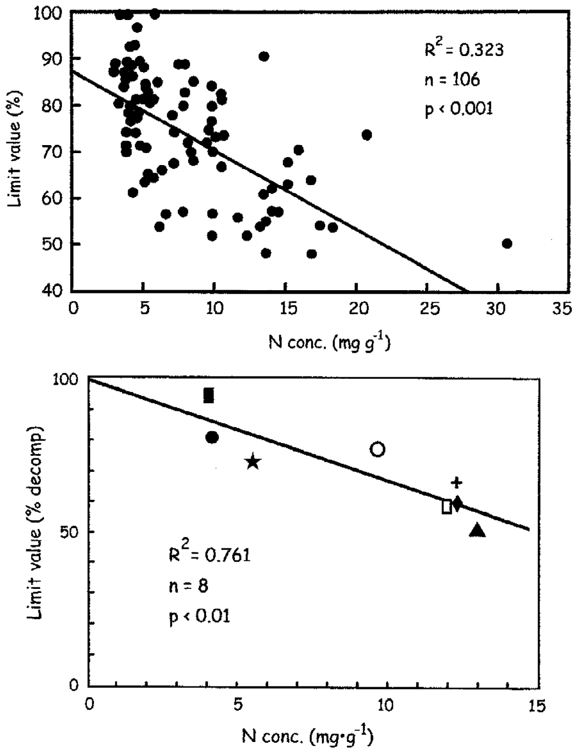

Figure 2. Linear relationship between limit values for decomposition and initial concentrations of N in foliar litter (from Berg 2000). (A) Available data from natural forests systems versus N concentration. (B) The relationship between mean limit values and N concentrations of eight different foliar litter types; (●) Scots pine, brown needles, (○) Scots pine, green needles, (■) lodgepole pine, (⋆) Norway spruce, (□) silver fir, (+) white birch, (▲) common beech, (◆) oak spp.

Litter chemical composition in transects and at a given site

Natural variation among species

Factors that determine litter chemical composition for a given tree species may be related to climate and soil nutrient supply (cf Berg et al., 1995a). In a study carried out at several sites Johansson (1995) found for paired stands of Scots pine and Norway spruce that the litter chemical composition was clearly different with the Norway spruce needle litter having significantly higher N concentration. Further, in a comparison between Norway spruce and white birch the birch leaves were found to have higher levels of N. Reurslag and Berg (1993) investigated available data from European forests and found (cf Table 3) that deciduous litter in general had higher N levels than coniferous litters.

Table 3. Concentrations of N and lignin in foliar litter of some common tree species in Europe. All available literature data were used. Under each average value the range in values is given

Litter type	Concentration (mg g^{-1})		Ref
	N	Lignin	
Coniferous needle litter			
Scots pine			
	4.8	317	(1,2)
	2.6–9.0	219–348	
Lodgepole pine			
	4.5	373	(2)
	3.4–7.9	357–391	
Austrian/Corsican pine			
	7.8	—	(2)
	6.4–8.5		
Norway spruce			
	7.7	317	(2,3,5)
	4.5–14.2	277–350	
Silver fir			
	13.0	427	(4)
	12.3–13.6	356–512	
Deciduous leaf litter			
Common beech			
	9.91	393	(2,4,5)
	5.6–16.8	284–513	
Grey alder			
	27.5	264.0	(2)
	25.8–30.7	—	
White birch			
	9.5	288.9	(2)
	7.5–13.4	263–330	
Mountain ash			
	8.17	184	(2)
	7.12–9.22	—	
Trembling aspen			
	7.68	199.0	(2)
	7.2–8.2	—	
European maple			
	5.07	—	(2)

1. Berg et al. (1995a); 2. Reurslag and Berg (1993); 3. Berg et al. (2000); 4. Berg (1998); 5. Matzner (1988).

Variations within freshly fallen Scots pine needle litter in a climatic transect

Scots pine needle litter showed a clear increase in concentrations of N, P, S, and K with increasing temperature and precipitation. In their comparison of needle litter collected at 31 sites Berg et al. (1995a) used actual evapotranspiration (AET) (cf Meentemeyer, 1978) as

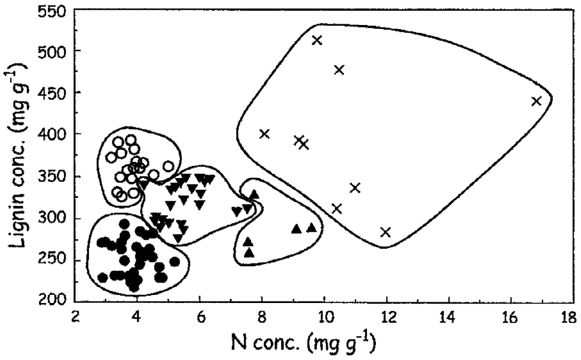

Figure 3. Concentrations of lignin and N in newly shed foliar litter of Scots pine (●), lodgepole pine (○), Norway spruce (▼), white birch (▲) and common beech (**X**). All available data. Redrawn from Berg (1998; 2000).

a climate index and obtained a highly significant relationship to litter N concentration. The range in N concentrations was from 2.5 mg g^{-1} in northern Sweden to 9.0 in south Poland. The concentration of N in litter may reflect that of the green leaves and needles (Staaf and Berg, 1981) and under warmer and wetter conditions the green needles will have higher N concentrations to allow for a higher photosynthesis (A. Eriksson, pers. commun.). Aerts (1997) pointed out the triangular relationship between, climate, litter quality, and decay rates, and Berg et al. (2000a, b) found a linear relationship between concentrations of N in litter and in humus at the sites used by Berg et al. (1995a). We used available data for foliar litter to develop this relationship and with a relationship between AET and litter chemical composition both within a species and among species the effect of a climate change on litter chemical composition could be predicted.

How much do some critical chemical components vary between litter types within a region?

When plotting available data on concentrations of N and lignin for foliar litter, Berg (1998; 2000) found that the litter types actually formed distinct groups despite the fact that the litter was collected over large regions. Thus for Scots pine, lodgepole pine, Norway spruce, and white birch sampling was made on a Scandinavian basis and for beech available west European data were used. Thus, Scots pine needle litter formed a homogeneous group that did not overlap with the lodgepole pine or Norway spruce groups (Fig. 3). In this comparison, Scots pine needle litter was characterized as having simultaneously low concentrations of both N and lignin and lodgepole pine litter formed another homogeneous group, with low N and high lignin concentrations. Norway spruce needles formed a group that had higher N concentrations than those of the two pine species and lignin concentrations that were in-between. The birch leaves had lignin concentrations similar to those of the spruce needles but generally higher N concentrations. The leaves of common beech formed an extreme group, with very high concentrations of both N and lignin; in this case the data were collected in south Sweden and south Italy. Berg (1998) concluded that the grouping patterns and the variability for samples collected over a large region were similar to those obtained for samples of Scots pine, lodgepole pine and Norway spruce litter collected in nearby stands over a range of years.

Variation across a transect of European coniferous litter

We compared all data for N concentration in pine needle litter (Scots pine, lodgepole pine, stone pine, maritime pine, Corsican pine, and Monterey pine) with average annual AET (R^2=0.548; n=40; Fig. 4a). In these samples there were no relationships with latitude. Even among sites with very low N deposition (northern Scandinavia and some coastal sites on the Iberian peninsula) but with varying AET values, litter N concentration was still related to AET (R^2=0.763: n=19).

We also compared all data for coniferous foliar litter for Europe to AET and obtained a highly significant relationship (R^2=0.381; n=60), which in addition to the above pine species included Norway spruce, Sitka spruce, silver fir, grand fir, and Douglas fir. Adding available data for deciduous foliar litter did not change the relationship (R^2= 0.354; n=68; Fig. 4B) and the data for deciduous litter alone formed a significant relationship (R^2=0.829; n=8) between N and AET.

These patterns suggest two possible scenarios. A change in climate (AET) may in part change the N concentration in litter of a given species at a given site. In addition, a change in tree species, adapted to a warmer and wetter climate may increase the N concentration of the falling litter. Using the equations for the linear relationships we could see a response in N concentration to climate that differed among the groups consisting of pines, spruce, and deciduous trees (Fig. 5) indicating that for pine, for example, a climate change would have a smaller effect on N concentration than for spruce or for deciduous litter.

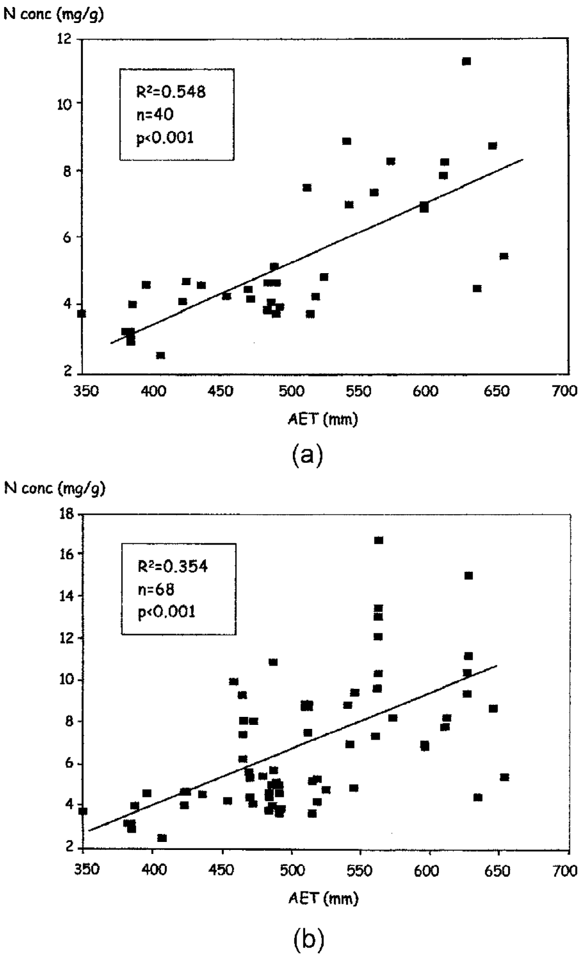

Figure 4. The relationship between climate as indexed by actual evapotranspiration (AET) and N concentration in foliar litter. (A) Different pine species at sites across Europe. (B) All available data on coniferous and deciduous litter across Europe.

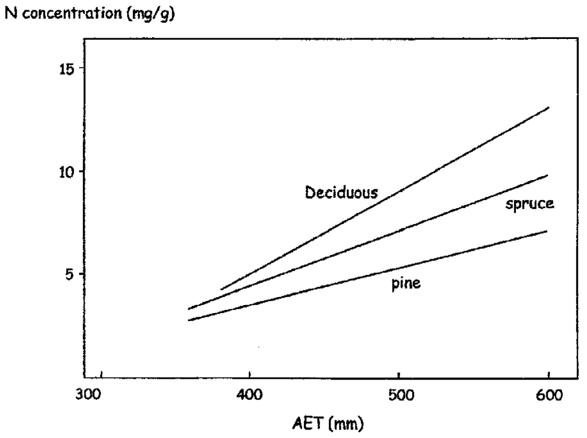

Figure 5. Relationships based on data from Fig. 4B giving the increase in N concentration with increasing AET for pine species, for spruce and for deciduous species.

A possible climate scenario for Scandinavia and the Baltic basin

We applied an increase of 4°C in mean annual temperature, evenly distributed over the year and an increase in precipitation of 40%, also evenly distributed over the year thus simplifying an existing prediction (cf Johannesson et al., 1995). Annual actual evapotranspiration (AET) was calculated (cf Meentemeyer, 1978) for several representative sites in Scandinavia and mainland Europe for which we had data on initial chemical composition of litter (Johansson et al., 1995) as well as for limit values (Berg et al., 2000a, b; Berg, 1998). Applying the above climate change, AET was calculated within the range of sites, and we obtained an average increase of AET of 27%, with minor variation about the mean. Since these forested systems are energy limited a rather constant change in AET resulted.

Is there a relationship between climate, litter N concentration, and limit value?

If we accept the above relationships suggesting that plant litter formed at sites with higher AET will have a higher N content, such litter during decomposition would reach a lower limit value (Fig. 2), leaving more recalcitrant material. Using that information and combining available data on estimated limit values, N concentrations and the climate index AET estimated for these sites, we regressed limit values against AET. First we used data on Scots pine only (Fig. 6A). With 20 data points this negative relationship was highly significant and indicated that within this range of AET the limit values fell from ca 90% to less than 80%. In this geographical region (Arctic Circle to south Sweden) there was an increase in N concentration in the Scots pine litter with increasing AET, but we cannot exclude the possibility that climate is also influencing the limit value. In order to generalize the finding from Scots pine we used all available data for Europe, encompassing Scots pine, lodgepole pine, Norway spruce, common beech and white birch (Fig. 6b). With a range in AET from ca 350 to 560 mm there was a highly significant and negative relationship (R^2=0.487; n=47; P<0.001) with the limit value decreasing from ca 95 to nearly 60%. Geographically the data covered the range between the Arctic Circle and south Italy and N concentrations ranged from 31 mg g^{-1} in leaves of grey alder to about 2.6 mg g^{-1} in Scots pine needles giving a range with a factor of more than 10 in our material.

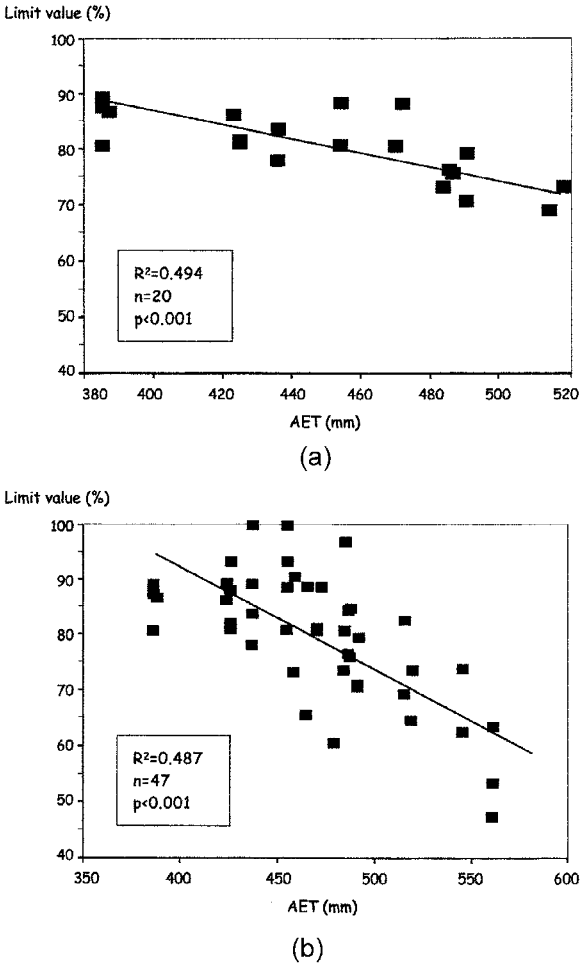

Figure 6. A relationship between limit value for litter decomposition and the climate index AET. The litter originated in all cases from the site at which decomposition was studied. (A) Scots pine litter decomposing at sites along Sweden. (B) Available data for foliar litter on a European basis.

Table 4. An estimate of potential annual increase in humus layers using functions based on Scots pine data only and all available data. For this comparison that illustrates the effect of a changed substrate quality we used an example of a site with AET of 470 mm that after a climate change increased to 588 and a constant annual litterfall of 2000 kg ha^{-1}

AET (mm)	Limit value (%)	SOM accumulated (kg ha^{-1} year^{-1})	Relative increase (%)
Scots pine data			
470	79.1	416	
588	68.0	640	54
All available data			
470	79.4	416	
588	58.1	838	100

We applied an increase in AET of 27% in the Baltic basin to the functions based on Scots pine data and all available data (Fig. 6). The graphs are based on decomposition of local litter from trees grown under different AET, and thus different N levels (cf Fig. 4), which then produce different limit values. For each decomposition experiment limit values have been estimated. The graphs of AET and limit values thus show the resulting effect of a raised N level causing a lower limit value for decomposition.

For our comparison we used the AET value of 470 mm for a given site at which the AET would be 588 mm after a full climate change. In order to compare the effect of just a changed substrate quality on humus accumulation we used the arbitrary value for litterfall of 2000 kg ha^{-1}. Such an assumption is not entirely correct since a higher litterfall also would be a consequence of a changed climate (Berg and Meentemeyer, unpubl.). Increased AET for Scots pine (cf Fig. 6a) gives an increase in needle litter N and the limit value decreases from 79.1 to 68% (Table 4) which means that the annual humus accumulation increased from 416 to 640 kg ha^{-1}, namely a bit more than 50% (Table 4). Using the function (cf Fig. 6b) for all available data the annual increase was ca 100%. In a period of 110 years the accumulated humus at a Scots pine site was 15400 kg ha^{-1} (Berg et al., 1995b) giving a humus layer of ca 6 cm thickness. An increase based on the Scots pine data (Fig. 6A) increasing the accumulation rate by 54% would lead to a somewhat thicker humus layer.

Conclusions and summarizing comments

Field experiments have shown that litters of different quality tend to decompose to a 'limit value' at which further decay virtually ceases and the litters become part of the humus pool. This limit value for litter in late stages of decay has been shown to be strongly and inversely related to initial N concentration of newly shed litter. With higher N levels (a lower C/N ratio), more recalcitrant litter remains. The limit value thus reflects a part of the litter/humus layer that is rather resistant to degradation.

The initial N concentration of litters is positively related to climate as indexed by average annual AET.

In warmer and/or wetter climates within the Baltic and northern European regions, litter with a higher N is produced. The effect is more pronounced for spruce versus pine and deciduous species versus either spruce or pine. This suggests that any climatic change would generate effects on decay dynamics that are not obvious. A warmer and wetter climate 'should' produce systems with a greater mass in late stages of decay.

While it is true that decay rates of litters in early stages of decay can be related to weather and climate, the late stages of decay seem to be largely disconnected from direct control by climate. Instead, the indirect control of climate on initial N concentration seems to dominate. This helps to explain the confounding result of the negative relationship between AET and limit values for different litters: in high AET environments, more of the recalcitrant litter remains. This does not preclude the possibility that over long periods of time decomposer organisms could develop with different efficiencies in metabolism.

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