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Review

Decomposing litter; limit values; humus accumulation, locally and regionally

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A B S T R A C T

Decomposition of foliar litter may be complete or proceed at a progressively lower rate to become zero and a limit value for decomposition may be estimated. Limit values for decomposition have been found to range from 100% accumulated mass loss to 42%, resulting in 'stable' fractions of 0 and 58%, respectively. A limit value does not necessarily mean a complete stop in decomposition but litter mass loss may proceed at a very low rate. An asymptotic function is used to estimate limit value/stable fraction, separating a readily decomposed and a stable residue. The stabilized litter fraction defined as $(100 - \text{limit value})/100$ may be used for estimating the accumulation rate of stable carbon (C) in organic layers.

Rates of C sequestration may be based on two main factors, namely litter fall and size of the stable litter fraction formed during decomposition. A high litter nitrogen (N) concentration may retard the degradation of lignified tissue in the late decomposition stage and the higher the N concentration the stronger the retardation. The enzyme manganese peroxidase (MnP), requiring manganese (Mn) is important for degradation of lignin and the lignified fraction of litter. A high level of Mn in litter supports a more far-going degradation of the lignified tissue and thus results in a high limit value and a small low residue.

Concentrations of N and Mn in newly shed litter are both influenced by site climate, with N increasing and Mn decreasing with increasing mean annual temperature (MAT) and annual actual evapotranspiration (AET). Climate thus becomes an at least indirect regulating factor for the size of the stable fraction.

In a comparison among tree species and genera, pine species (*Pinus* spp.) gave a dominant sequestration rate for organic matter on top of the mineral soil ('primary sequestration'). Coniferous tree species sequestered C faster than deciduous ones. Further, using 'available data' we found a positive relationship between C sequestration rate in organic layers and MAT with rates ranging from 0 to 1106 kg C ha⁻¹ yr⁻¹.

Data suggest that the concept 'steady state' for C accumulation is not a general phenomenon. On the one hand accumulation of carbon in forest stands has been shown to continue for close to 3000 years. On the other hand, for some litter species the decomposition is fast enough to let foliar litter decompose completely in less than a year.

Two approaches to calculate C sequestration rates were compared in a regional case study (Sweden). Using data for stable residue and litter

fall resulted in an annual sequestration of 4.8×10^6 tons of C. Directly measured humus-depth gave 6.7×10^6 tons. The difference, 1.9×10^6 tons corresponded to 30% of the latter approach.

The foliar litter fall increased in linear proportion to AET/MAT and thus also the sequestration increased in linear proportion to AET – in this region mainly based on temperature. Also the C sequestration based on measurements of humus depth increased in proportion to temperature (Tsum) ($R^2 = 0.29$; $n = 548$; $p < 0.0001$).

1. Introduction

When Anderson et al. (1983) estimated humus layers and compared to litter decomposition data they faced an enigma and wrote; 'we have to resolve the paradox that weight losses from the litter bags were inversely related to resource quality and organic matter standing crops.' Studying litter fall, its decomposition and soil organic matter (SOM) in Sarawak, they faced the facts that; (i) the rate calculated using the single exponential for litter decomposition (Jenny et al., 1949) could not explain the accumulation of SOM, (ii) a high initial mass-loss rate was seen at stands with high amounts of accumulated organic matter. In addition, they faced the contradiction that a warm and wet climate, which supports a high initial mass-loss rate, also may be related to a larger stable fraction of the shed litter.

Following decomposition until high accumulated mass loss Berg and Ekbohm (1991) found that the mass-loss rate decreased with accumulated mass loss. They estimated a value for accumulated mass loss at which the decomposition rate was effectively zero or in a state-of-no-change. They called this result 'limit value for decomposition' and

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¹ Music for listening; Lagunenwalzer; <https://www.youtube.com/watch?v=hT9MHIWAAG>

suggested that it indicated a stable residue. Limit values can be calculated using an asymptotic function (e.g. Howard and Howard, 1974; Wieder and Lang, 1982). Berg and Ekbohm (1991) compared decomposition of seven litter types under identical environmental conditions and estimated a set of limit values ranging from c. 50 to 100% accumulated litter mass loss. In the LIDET project an asymptotic function was applied (Harmon et al., 2009; Currie et al., 2010) to 10 litter types incubated at different climates – in all 234 combinations of litter quality and site. The asymptotic model gave significant limit values in 107 studies and explained more than 85% of the variation.

Recently, some compilations for limit values/stable residues have been made, allowing us to look into causal factors. Thus, litter concentrations of manganese (Mn) and nitrogen (N), which have been related to the remaining (stable) fraction have causal relationships as support (Berg et al., 2010; Berg and Matzner, 1997). Also heavy metals have been suggested to have a role for retardation of litter mass-loss rate (Preston et al., 2009a,b) and thus for SOM accumulation.

The build-up of a humus layer is dependent on the inflow of plant litter and the extent of its decomposition and requires the formation of recalcitrant or very slowly decomposing litter residues (Berg and McClaugherty, 2014). In Europe, where forest growth has increased over the last century, increased production of both above- and below-ground litter may lead to further accumulation of SOM (Liski et al., 2002). At the same time increased N deposition has increased the N content of litter, which potentially may have reduced the extent of its decomposition (Hagedorn et al., 2003; Pregitzer et al., 2008) by the stabilisation mechanism suggested by Berg and Matzner (1997).

Litter fall is the largest natural inflow of organic material and nutrients to the forest floor and in most European forests it is dominated by that from the trees. Some large compilations have been published on litter fall. Liu et al. (2004) related litter fall for Eurasia to mean annual temperature (MAT) and found separate patterns among the climatic zones; e.g. in the boreal zone the litter-fall rate was higher in coniferous as compared to deciduous forests. Meentemeyer et al. (1982) used data sets with nearly global coverage and related litter fall to AET, and other climatic variables. In a regional study for Fennoscandia Berg and Meentemeyer (2001) related foliar litter fall to AET and MAT.

Humus – the carrier of plant nutrients – accumulates as a stand grows and ages (e.g. Ovington, 1959; Forrest and Ovington, 1970). In boreal and temperate forests we may find easily distinguishable humus layers, for example mor layers, (FH or LFH layer). We may refer to Fig. 1 and call this ‘primary sequestration’, the one that takes place in e.g. a mor layer, on top of the mineral soil.

Long-term accumulation of SOM takes place in the humus layer of forest soils (Ovington, 1957, 1959) and numerous chronosequence studies have confirmed this (e.g. Wardle et al., 1997; see also Berg and McClaugherty, 2014). Furthermore, ^{14}C dating has indicated that SOM can be 10 000 years old (Paul, 1984; Paul, 1984; Stevenson, 1994), with

the upper limit still not determined. This accumulation is disturbed by fires and clear-felling and other management activities, which may cause a release of part of the accumulated SOM-carbon (SOM-C) (Jandl et al., 2007).

Based on long-term decomposition data it was possible suggested to calculate humus build-up assuming a limit value for decomposition and a stable residue, that depends on litter-quality parameters (Berg et al., 2001; Berg and McClaugherty, 2008).

The stable-residue concept has given us knowledge about the size of the fraction that will remain as slowly degradable, almost recalcitrant soil organic matter (e.g. Berg et al., 1996, 2001; Berg and McClaugherty, 2003). Further, the model for carbon sequestration has been validated against measured values of C accumulation with up to 25 kg SOM-C per meter square (after accumulation over 3000 years) (Berg et al., 2001; Berg and Dise, 2004). Further, the effect of N and Mn on the stable residue (limit value) have been reviewed over a wide spectrum of litter N and Mn concentrations (Berg, 2014a). Until today calculated limit values range between c. 50 and 100% decomposition, the latter number indicating a complete decomposition and thus theoretically no C sequestration should take place. This corresponds to stable fractions of 0.5 and 0.0, or 50 and 0% of the litter fall.

Being relatively simple, the stable-residue approach offers the possibility to calculate and upscale potential C sequestration rates in the humus layer using amounts and quality of foliar litter. Akselsson et al. (2005) made use of this method and carried out an upscaling for the forested land of Sweden obtaining a mean C sequestration rate of $180 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ to be compared to a directly measured value of $251 \text{ kg C ha}^{-1} \text{ yr}^{-1}$.

The aims behind this review is (i) to present the concept of limit value for litter decomposition using causal relationships, (ii) to indicate possible factors that may regulate limit values and the size of the recalcitrant residue, and thus the sequestration of carbon. Further, we discuss and evaluate two regional approaches, both covering the same region – the forested land of Sweden – which gives a case study. (i) In a first approach functions for foliar litter fall were related to AET and average fractions of stable residue for different groups of litter species were used for c. 17,000 $5 \times 5 \text{ km}$ grid cells covering Sweden, (ii) a 41-year study of humus-layer development in which the increasing humus depth was converted to increasing amount of C. Using kriging and $25 \times 25 \text{ km}$ plots the authors used more than 800,000 single measurements from 82,513 plots (over 41 years) to cover the forested land of Sweden.

This paper has a focus on studies carried out in those types of forest soils and ecosystems in which clear and accurate quantitative determinations can be made, which mainly means mor soils in boreal and temperate coniferous forests and the organic layer (Fig. 1). When discussing C sequestration in this paper we refer to the accumulation of C in the SOM layer on top of the mineral soil (Berg et al., 2008).

Fig. 1. A rough definition of the concepts ‘primary’ and ‘secondary’ C sequestration in humus and mineral soil. The arrow labelled ‘primary’ indicates transport of partly decomposed litter to the stable organic layers, thus into a sink for long-term stable material, for example a mor layer. The arrow labelled ‘secondary’ indicates a transport of dissolved organic material into the mineral soil, where it may be precipitated. Such secondary process (secondary sequestration) requires that material from the upper organic layers is solubilized and transported to the mineral soil where it is sequestered. Also root litter will contribute. The figure illustrates a mor humus with clearly defined layers. The layer(s) with primary sequestration in the organic layer are also called A_{01} and A_{02} , or O_e and O_a , or F and H. From Berg et al. (2008).

2. Background

Decomposition of litter may be divided into three stages (Berg and McLaugherty, 2014; Berg and Matzner, 1997). In the *early stage*, the decomposition of non-lignified tissue in newly shed litter may be supported by high concentrations of the main nutrients such as N and phosphorus (P). Whereas the degradation of unshielded holocellulose is stimulated by a high concentration of N, that of acid unhydrolyzable residue (AUR) and lignified tissue is hampered by the same high N (Keyser et al., 1978; Berg and Ekbohm, 1991), but stimulated by Mn (Perez and Jeffries, 1992; Hatakka, 2001). Concentrations of N and AUR increase in linear proportion to litter accumulated mass loss (Berg and McLaugherty, 2014). Similarly, concentrations of Mn appear to increase, varying strongly with litter species (Berg et al., 2013).

In the *late stage*, the degradation of lignified tissue dominates the decomposition process. Nitrogen may have a hampering effect in two possible ways, one being a suppression of the production of lignolytic enzymes (e.g. Keyser et al., 1978; Berg and Matzner, 1997) and the other a recombination of N compounds with reactive groups in e.g. partly decomposed AUR, creating compounds, recalcitrant to biological degradation (e.g. Preston et al., 2009a,b; Knicker, 2004). In a study by Hobbie et al. (2012) the lignolytic enzymes appeared after one year's incubation of litter and their formation was suppressed in N-fertilized plots. Berg and Ekbohm (1991) reported that the degradation of AUR was negatively related to litter N concentration. Such effects on AUR degradation mean that decomposition of the whole remaining litter proceeds at a lower rate – as all remaining litter is lignified. The decomposition process may cease or proceed at a lower rate in high-N litter. Thus, although N may promote a high initial decomposition rate for newly shed litter of some species, it may retard the decomposition of the lignified tissue of litter in late decomposition stages. In contrast, a high level of Mn is necessary for the formation of manganese peroxidase (MnPP), which appears to be the most common peroxidase in white-rot fungi (Hofrichter, 2002). Manganese has been reported to stimulate the degradation of AUR and litter (Berg et al., 2007a,b, 2015). Also, Trum et al. (2015) demonstrated this by using common beech (*Fagus sylvatica*) litter with both experimentally raised Mn and litter with different natural levels.

2.1. Final stage/stable residue

When we want to describe decomposition pattern and a stable residue we may use a function, which includes an asymptote. Wieder and Lang (1982) and later Berg and Ekbohm (1991) presented one;

$$L_t = m(1 - e^{-tk_{init}/m}) \quad (1)$$

where L_t is the accumulated mass loss (in%), t is time in days or years, and k_{init} the decomposition rate at the beginning of the decay – the initial rate. Finally, m represents the asymptotic level, which the accumulated mass loss will ultimately reach (at $k_A = 0$). The initial rate of this function may be indexed k_{init} . A more general index could be k_A , which should be highest at $t = 0$ (equal to k_{init}) and decrease with increasing accumulated mass loss (Fig. 2).

2.2. Size of the stable litter fraction

So far two nutrients have been identified, which directly influence the decomposition of lignified tissue. It appears that N and Mn have opposite effects on the biological degradability of lignin and its transformation products in litter (Berg and Matzner, 1997; Berg et al., 2007a,b, 2010; Berg, 2014a). With c. 150 calculated limit values and thus equally many fractions of stable residue it has been possible to calculate linear relationships between initial litter Mn and N and limit values and thus the stable fraction.

2.3. Litter fall

The build-up of a humus layer is dependent on the inflow of plant litter and the extent of its decomposition. Litter production is dependent on climate and studies on foliar litter fall show a highly significant linear relationship to AET (Table 1) (e.g. Berg and Meentemeyer, 2001) and to MAT (Liu et al., 2003).

2.4. Buildup of an organic (humus) layer

The linear buildup of a humus layer vs time described by e.g. Ovington (1959) and Turner and Long (1975) was followed using gravimetric measurements of the stored organic layer. This approach gives an approximately linear accumulation over time in a given forest stand that is allowed to develop without disturbance. In one approach we may use data for litter fall and the stable litter fraction to calculate the buildup of organic matter. A summation over a number of years gives the stored amount (see Akselsson et al., 2005).

An alternative approach is to measure humus depth over longer periods and with many enough replicates we may register a significant increase (see Berg et al., 2009). In contrast to local studies, regional ones may require simplified and easily administered methods as well as handling of large amounts of data.

For humus accumulation over a region we present a case study using two approaches, namely (i) summation of stable residues over time and (ii) long-term measurements of humus depth. We have used the forested land of Sweden for a comparison. The region encompassed the entire forested land of Sweden, ranging from about 55°N to 69°N, with boreal climate north of c. 60°N and a temperate climate from c. 55 to 60°N. The forested area covers in all c. 23×10^6 ha, and the forests comprise mainly two domestic coniferous tree species, namely Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). The introduced species lodgepole pine (*Pinus contorta* var. *contorta*) has been considered together with Scots pine. Of the deciduous species, silver birch, (*Betula verrucosa* Ehrh.) and downy birch (*Betula pubescens* Ehrh.), and trembling aspen (*Populus tremuloides* Michx.) are of significance over the whole country whereas common beech (*Fagus sylvatica* L.), and common oak (*Quercus robur* L.) cover smaller areas in the southern parts.

3. Limit values and the fraction of stable residue (100-limit value) may vary due to identified influences

The above asymptotic equation (Eq. (1)) may be used to show a variation in limit values and in the corresponding fraction of litter that becomes a recalcitrant residue. So far we have found two main factors that influence the pattern of limit values among various litter types; (i) decomposition of non-lignified and in later stages that of lignified tissue and (ii) nutrients regulating litter late-stage decomposition rates (N, and Mn), which thus may create differences in pattern.

The decomposition rate may decrease relatively fast or slowly, creating different patterns as reflected in the limit values (Fig. 2) and so far a range from 42 to 100% has been observed. Even within a given litter species or within a genus there may be a strong variation in limit values (Berg et al., 2010), creating a high variation in pattern.

3.1. Some comments to the role of AUR vs limit values

The concept AUR includes both native lignin and a mix of compounds that are not hydrolyzable in sulfuric acid, e.g. waxes, cutins, and less-soluble condensed tannins (Preston et al., 2009a). Further, we cannot exclude that part of the AUR is based on new compounds created during decomposition from N and lignin residues (e.g. Knicker, 2004).

AUR concentration in litter has been negatively related to litter mass-loss rate, e.g. annual mass loss (Johansson et al., 1995; Berg et al.,

Fig. 2. As decomposition of litter proceeds and accumulated mass loss increases, the litter mass-loss rate may decrease and a limit value for decomposition is reached, identified as a value for accumulated mass loss, often less than 100%. The limit value may identify a stable litter fraction that decomposes very slowly. The decomposition rate, k_{init} is the rate at time zero. Normally the k value (k_A) decreases as decomposition. From Berg and McClaugherty (2014).

Table 1

Litter-fall functions used for the different tree species. Standard error is given within parentheses. From Akselsson et al. (2005).

Tree species	Litter-fall function	Source
Norway spruce	Fall = $-3650.4 (642) + 12.1 (3.9) \text{ AET}$ $R^2 = 0.47$ $n = 13$	Empirical relationship for spruce Berg and Meentemeyer (2001)
Scots pine	Fall = $-3590 (509) + 11.0 (2.0) \text{ AET}$ $R^2 = 0.48$ $n = 35$	Empirical relationship for pine Berg and Meentemeyer (2001)
Birch species	Fall = $-790 (51) + 5.8 (1.8) \text{ AET}$ $R^2 = 0.79$	Empirical relationship for deciduous species Meentemeyer et al. (1982)
Other deciduous	Fall = $-790 (51) + 5.8 (1.8) \text{ AET}$ $R^2 = 0.79$	Empirical relationship for deciduous species Meentemeyer et al. (1982)

2015). Still, it is possible that AUR is not the important factor *per se* but that its recalcitrance is related to levels of nutrients, such as N and Mn, which have been shown to regulate the biological degradation of AUR and of lignin and thus that of litter. So far only N and Mn have been discussed in that role for litter decomposition (e.g. Berg and McClaugherty, 2014) but we cannot exclude that effects of other nutrients and heavy metals will be discovered. So far no general effect of initial AUR concentration on limit values has been observed (B. Berg, unpubl.). Using available long-term decomposition data ($n = 162$) encompassing 18 litter species (DELILA database; www.eko.uj.edu.pl/deco) as well as *Pinus* litter Berg et al. (2010) did not find any significant relationship between initial AUR and the limit value.

3.2. Effects of N and Mn on limit values – general trends

3.2.1. Nitrogen concentration related to limit values

For several litters with fast initial decomposition, the rate appears to decrease as soon as the late stage is reached. When degradation of AUR/lignified tissue starts, a high N concentration would cause a stronger retardation and a pronounced switch from a high to a low rate for litter decomposition. This has been shown (Berg and Ekbohm, 1991) and is illustrated as limit values decrease with increasing initial N concentration (Fig. 3a). So far that effect has been reported for litter from boreal and temperate climates.

When regressing 149 limit values against initial N concentrations a highly significant and negative relationship was obtained ($R^2 = 0.151$; $p < 0.001$) (Berg, 2014b; Fig. 3a). The possible causal background to this relationship may be found in the suppression of ligninase synthesis

Fig. 3. Relationships (power function) between initial litter concentrations of (A) nitrogen and (B) manganese and the limit value given as accumulated mass loss. In both cases the same set of data was used with 149 decomposition studies and 16 species included (DELILA database, www.eko.uj.edu.pl/deco). Figure from Berg (2014b).

(Keyser et al., 1978; Hatakka, 2001) and in the formation of new compounds from reactions between N and polymer residues (Knicker, 2004). The fact that in this large data set the relationship to N concentration was significant may support a general effect of N over a good number of species, i.e. both deciduous and coniferous litter as well as boreal and temperate ecosystems.

3.2.2. Manganese concentrations related to limit values

Initial Mn concentrations have been positively related to limit values. Using available data Berg (2014b) presented a significant relationship between limit values and litter Mn concentration ($R^2 = 0.184$; $n = 149$; $p < 0.001$; Fig. 3b). The causal background is the role for Mn in manganese peroxidase (MnP) (Perez and Jeffries,

Fig. 4. Limit values for decomposing pine (*Pinus*) needle litter are related to litter Mn concentration. Decomposition studies for four pine litter species Scots pine, lodgepole pine, white pine (*Pinus strobus*), and Aleppo pine (*Pinus halepensis*) were combined into a climatic gradient. Limit values were estimated and a backward elimination procedure removed non-significant factors. Of eight substrate-quality factors, namely water solubles, AUR, N, P, K, Ca, Mg, and Mn and two climatic ones, namely mean annual temperature (MAT), and mean annual precipitation (MAP) only Mn was selected as the single significant factor. Figure from Berg and McLaugherty (2014), based on data from Berg et al. (2010).

Fig. 5. All available data for newly shed pine (*Pinus*) needle litter in a climatic gradient ranging from northernmost Fennoscandia to south Spain and south Italy, with the same litter samples used for both figures. (A); Increasing N concentration with increasing site AET. (B); Decreasing Mn concentration with increasing site MAT. Figure from Berg (2014a).

1992; Hatakka, 2001). In spite of that relationship we may comment on that limit values for specific species, for example litter of Norway spruce (*Picea abies*) (Berg et al., 2000) and of common oak (*Quercus robur*) (Davey et al., 2007) have not given relationships to Mn whereas those of pine species have (Fig. 4).

3.3. Limit values – specific litter genera

When studying specific factors that influence limit values it appears reasonable not to combine litter species or genera, but to use just one species or genus. So far there is no general evaluation of limit values vs. litter nutrients and ideally such an evaluation should be done for single species/genera (e.g. Berg et al., 2010). Even within a genus, e.g. *Pinus* there is a large variation in N and Mn concentrations, which results in a high variation in limit values allowing us to analyze their influences.

To use ‘available data’ may result in unwanted effects, ‘noise’. Reducing the noise by using just one species/genus may improve the level of explanation. In a study on limit values for just pine (*Pinus* spp.) needle litter, Berg et al. (2010), using backward elimination and local litter in a climatic gradient, found that initial litter Mn concentration was the only significant factor for limit values. The backward elimination procedure simply removed non-significant factors stepwise. That data base for pine litter encompassed 56 separate studies with five pine species. As potentially influencing factors they used the sites’ long-term MAT and mean annual precipitation (MAP) as well as substrate-chemistry, viz. concentrations of water solubles, AUR, N, P, K, Ca, Mg, and Mn. Out of these ten factors only Mn was selected and significant with a range in litter Mn concentrations from 0.03 mg g⁻¹ to 3.1 mg g⁻¹. Using the same data set Berg and McLaugherty (2014) applied a quadratic function and obtained an improved relationship (Fig. 4). There was no significance for N in that pine litter data set.

4. Limit values are related to initial litter concentrations of N and Mn. What regulates N and Mn in litter?

The chemical composition of newly shed pine litter varies with climate – at least in part for N and Mn. Highly significant positive relationships for N, P, S, and K vs. the climate indices MAT and actual evapotranspiration (AET) have been reported (Berg et al., 1995). Later, Berg and McLaugherty (2014) showed a positive relationship between N and MAT for eight pine litter species in a gradient from the northern Libya to the Arctic Circle in Scandinavia ($R^2 = 0.389$; $n = 62$; $p < 0.001$) with a range in MAT from -1.7 to 17 °C. They also reported a relationship between N and AET with a range from 350 to 654 mm ($R^2 = 0.636$, $n = 41$; $p < 0.001$; Fig. 5a).

More general relationships over Eurasia for N vs MAT have been reported (Liu et al., 2006). Using standardized data, they confirmed

that MAT ($p < 0.001$) and not MAP gave a highly significant relationship for pine litter ($n = 56$). They also found a highly significant ($p < 0.001$) general relationship ($n = 204$) over Eurasia (Arctic circle to the Equator). A true global data set ($n = 677$) showed a highly significant relationship between litter N and MAT (Kang et al., 2011).

Also Mn may be related to climate indices. Negative relationships between Mn concentrations and AET/MAT have been reported for pine litter (Berg et al., 1995; Berg, 2014a). There is a highly significant negative relationship to MAT for eight pine species ($n = 41$) covering the area from northernmost Scandinavia to North Africa (Fig. 5b). Thus, the higher the MAT/AET, the lower the litter Mn concentration. The highest Mn concentrations were found in Scots pine litter in north Scandinavia (3.67 mg g^{-1}) and the lowest (0.03 mg g^{-1}) for Aleppo pine litter in North Africa. This relationship is empirical.

The changes in N and Mn concentrations with MAT suggest that these two factors reach levels that may retard decomposition rates at higher MAT.

5. Further possible influences on limit values?

A direct relationship between climate indices and decomposition pattern may be complicated to distinguish considering the effects of climate on litter chemistry. However, a study using a unified litter cohort with a constant chemical composition over climatically different sites may help to illustrate such an effect.

For unpolluted litter there are extremely few studies on the dynamics of heavy metals, such as Cu, Pb, Fe, and Zn. Still, as part of the concept substrate quality their possible roles in decomposition cannot be neglected. We may see that for decomposing Scots pine needle litter concentrations of e.g. Pb, Cu, and Fe increase with accumulated mass loss (Berg and McClaugherty, 2014) and we cannot exclude them from having a possible role in the establishment of a stable fraction. This was also commented on by Preston et al. (2009a, 2009b). In fact, during the decomposition process concentrations in natural, unpolluted litter may reach sup-pressing levels as found in a pollution gradient (Berg et al., 1991).

It has been shown that nutrients such as sodium (Na) and potassium (K) may be limiting to the decomposing microorganisms (Kaspari et al., 2009; Kaspari, 2012). Such a limitation would be due to a lack of the nutrients for metabolic reasons. Kaspari et al. (2009) suggested that a limitation of Na may be reasonable at locations at a distance from the sea and thus from sea-spray.

6. Amounts of humus increase in organic layers

6.1. Two main processes necessary for forming an organic layer

The accumulation of stabilized soil organic carbon (SOC) is the net result of; (i) input through litter fall, (ii) that a fraction of the litter becomes stabilized. Once the stable fraction has been formed, a necessary request is the maintenance of the long-term stability. We cannot expect infinite stability, but rather a very or extremely slow degradation.

Litter input to forest soils has numerous components but normally only one has been studied, namely foliar litter fall – the major one. Available data on litter fall and climate shows that foliar litter fall from both pine (*Pinus*) and spruce (*Picea*) species increase linearly with AET. The climatic influence is general and Liu et al. (2004) showed general relationships between MAT and foliar litter fall across Europe and Asia.

Litter may decompose completely at a more or less constant rate or the decomposition may be continuously suppressed and a stable residue be formed (Berg, 2014a), which may range from 0% to 58% of litter mass, the latter value so far being the highest percentage observed.

The two main groups of processes; those resulting in decomposition and those in humus accumulation may be ruled by different conditions and have different optima. Difference in climate should be a primary

influencing factor for the variable amounts of organic matter found on and in the soil. Jenny (1941) considered that the geography of soil organic carbon (SOC) is controlled by temperature and moisture. Considering such a climate dependence there should be relationships also between climatic factors and accumulation rate of C in stabilized SOM (Meentemeyer et al., 1985). We refer to the net accumulation as the product of litter fall and the stable fraction of litter (primary sequestration; Fig. 1).

6.2. For how long does humus accumulate? Is there a steady state?

Accumulation of stabilized SOC in e.g. humus layers has been considered to continue until a steady state is reached – a not very clear concept as regards SOC. Jenny (1980) concluded that “...the SOM regime is often viewed in short perspective as a steady-state system with inputs of C and N balancing their egress.”

Organic layers may grow for not only centuries but millennia, at least in limited areas or niches, and even in systems that are not waterlogged. They may develop profiles which are quite deep. Thus, Wardle et al. (1997) reported that a group of islands in Swedish Lapland, well protected from wildfires, had developed mor-humus layers to a depth of up to 150 cm. This development was found to have taken place over a period of slightly less than 3000 years. Later, Berg et al. (2003) reported humus layers that were more than 1 m deep on Monte Taburno just east of Naples (Italy). The established concept ‘Tangel-humus’ in the Alps and in Central European mountains (Rehfuß, 1990) means organic layers of up to 1 m depth. For the case reported by Wardle et al. (1997) a highly significant linear relationship ($R^2 = 0.993$; $n = 4$; $p < 0.01$) suggests a continued growth also after 3000 years (Berg and McClaugherty, 2014).

As such a growth over millennia may take place, the concept steady state may become less interesting. It appears that at least some ecosystems simply do not develop any kind of steady state for humus layers within reasonable time. Of course such factors as wild fire may be a frequent regulating factor for humus growth and with a high wild-fire frequency, a kind of steady state may develop with a variation regulated by the fire frequency. Still, such a ‘steady state’ will be broken with better fire prevention or possibly by a climate change with increased precipitation.

Kang et al. (2009) found that a group of foliar litters from broad-leaved trees growing at sites with MAT above 14°C and MAP between 1400 and 2800 mm decomposed completely within one year. These litters had N concentrations in the range 9.4 to 31 mg g^{-1} and concentrations of gravimetric lignin (AUR) less than 224 mg g^{-1} . This may allow us to conclude that such litters do not support the formation of an organic layer. Part of the matter may have been leached into the mineral soil, however, and stabilized without leaving a visible humus layer. Such an observation was made in an abandoned agricultural field by Guan et al. (2015), who found a barely measurable increase in stored organic matter on top of the mineral soil, whereas the highest amounts were stored at between 1 and 2 m depth.

One reasonable conclusion is that we may expect several possibilities for humus-layer development and consequently also different patterns. Some extreme examples would be on the one hand that no organic layer is formed in systems in which leaf litter residues never accumulate, but decompose so quickly that no layer is formed. On the other hand more than meter-deep humus layers may be formed – e.g. Tangelhumus.

7. Accumulation of stabilized humus/carbon in organic layers of boreal and temperate forests

As a young stand matures and the stand develops there is a clear increase in organic-layer C. Such observations have been made when sampling single stands over time and stands in chronosequences. It appears today (2017) that this pattern is common at least for several

Table 2

Accumulation rates of SOM-C in forest floors for which the accumulation of C has been followed over time. Either stand age has been known or a chronosequence has been used. The increase rate in the measurement period has been estimated as the slope of the linear function between accumulated amount and time. Table taken from Berg and McClaugherty (2014).

Species	Increase rate (Kg C ha ⁻¹ yr ⁻¹)	MAT	MAP	R ²	p <	Location	Source
Scots pine	380	9.5	517	0.859	0.001	England	(1)
Scots pine	537	9.8	827	0.627	0.001	central Holland	(4)
Scots pine	0	7.2	650	**	ns		(8)
Monterey pine	1032	nd	1450	0.903	0.05	New South Wales Australia	(2)
Loblolly pine	237	12.8–15.6	1020	0.935	0.001	SE USA	(3)
Douglas fir	407	9.4	1440	0.982	0.001		(7)
Norway spruce	1106	5.3	1163	0.816	0.001	Central Germany	(5)
Norway spruce		7.7	600	0.887	0.01		(6)
Norway spruce	340*	5.8–6.8	815–1370	0.88	0.001*	acid soils	(9)
Norway spruce	240*	4.1–7.5	661–1466	0.73	0.001*	calcareous soil	(9)
Common oak	58	7.7	600	0.340	ns		(6)
Common beech	422	5.3	1163	0.609	0.05	Central Germany	(5)

* 6 chronosequences were investigated in the northern, central and southern part of the Alps from eastern Germany to Northern Italy. P values were estimated from data given in papers.

** three samplings over 22 years. ns not significant. nd not determined.

(1) Ovington (1959), (2) Forrest and Ovington (1970), (3) Schiffman and Johnson (1989), (4) estimated from Tietema (2004), (5) Berg (2004), Meessenburg et al. (1999), Meiwees et al. (2002), (6) Vesterdal et al. (2002), (7) Turner and Long (1975), (8) Prietzel et al. (2006). (9) Thuille and Schulze (2006).

coniferous tree species/genera. We may expect that an in-crease takes place also for deciduous stands, although existing information appears clearer for coniferous ones.

We have collected a number of observations for coniferous stands and chronosequences as they develop. It appears for boreal and temperate pine forest ecosystems that a net increase takes place in mor humus layers e.g. for Scots pine (Ovington, 1959; Tietema, 2004) (Table 2).

Stands in a subtropical climate also have shown an increase in amount of sequestered humus with stand age (Table 2). A chronosequence of loblolly pine (*Pinus taeda*) and Virginia pine (*Pinus virginiana*) gave a rapid linear growth of both FH layer and total amount of dead organic matter in the forest floor. A subtropical Monterey pine (*Pinus radiata*) stand (New South Wales, Australia), increased the SOC mass in the forest floor at a rate of 1032 kg C ha⁻¹ yr⁻¹. Using a chronosequence of Douglas fir (*Pseudotsuga menziesii*) stands, Turner and Long (1975) found a linear increase in the forest floor C vs stand age. In a temperature gradient from Central Germany to North Italy, Thuille and Schulze (2006) could relate growth of the C stock in organic layers in Norway spruce forests to stand age (Table 2).

Although the high-rate increase in C in organic layers appears normal, this kind of measurement is made in managed stands, often including a control of number of stems per hectare. Also litter fall is restricted, which may mean that both litter fall and C sequestration are suboptimal as compared to less controlled stands. An exception was a stand of Norway spruce (Table 2) in a temperate forest in Central Germany with an increase in the organic layer of 1106 kg C ha⁻¹ yr⁻¹. That stand was, however, a-normally dense as it had not been thinned.

There is an effect of tree species. Berg and McClaugherty (2014) combined data sets from ten tree species trials in England and Denmark (Table 3). The studies had very similar design, methods, climate, and overlapping tree species/genera. Each quadratic plot (at least 25 × 25 m) had a monoculture. One difference between sites was in type of soil and its richness. The humus layer on top of the mineral soil had accumulated after planting, forming a clearly distinguishable layer. Samples of the O-horizon were compared. Similarities in experimental design and climate allowed data to be evaluated as a block experiment (ANOVA).

At all 10 sites the forest floor was sampled once in stands of known age. Live plants plus branches were removed, leaving foliar litter plus FH-layer material and in both studies ash or C was determined. Berg and McClaugherty (2014) estimated the amount of C by assuming 50% C in the organic matter and recalculated data to give the annual C sequestration. The data set encompassed 75 values for 75 stands, with a range in sequestration rates from 24 to 696 kg C ha⁻¹ yr⁻¹. Berg and

Table 3

Mean sequestration rates for organic carbon in LFH layers in forest stands – planted monocultures. Ash-free humus was determined as one-time inventories. Data for main genera from ten tree species trials in Denmark and England (Vesterdal and Raulund-Rasmussen, 1998; Ovington, 1954) were used and combined. Annual sequestration was estimated. All stands in Denmark were 30 years old and the age of the English ones ranged from 17 to 46. S.D. stands for standard deviation. From Berg and McClaugherty (2014).

Species	Average rate (kg C ha ⁻¹ yr ⁻¹)	SD	n	Significant difference
<i>Coniferous genera</i>				
<i>Pine group</i> (Lodgepole pine, Scots pine, Corsican pine)	470	167.1	11	Pine vs spruce
<i>Spruce group</i> (Norway spruce, Sitka spruce, Serbian spruce)	364	176.1	17	p = 0.068
Douglas fir	266	153.7	10	
Grand fir	189	151.7	9	
<i>Deciduous genera</i>				
Common beech	227	203.9	8	
Common oak, Red oak, Sessile oak	90	77.6	11	
Grey alder, White birch, Chestnut	90	27.3	3	
<i>Main groups</i>				
All coniferous	326	183.6	53	Coniferous vs deciduous
All deciduous	140	150.2	22	p < 0.0001

McClaugherty (2014) compared values for the coniferous and deciduous genera (Table 3). The sequestration rates for the group ‘coniferous’ (n = 53) ranged from 63 to 696 kg C ha⁻¹ yr⁻¹ and within the group ‘deciduous’ (n = 22) from 24 to 642 kg C ha⁻¹ yr⁻¹. The two groups with the averages 326 kg C ha⁻¹ yr⁻¹ (coniferous) and 140 (deciduous) were significantly different at p < 0.0001.

There was a large variation at genus level. The group of pine species (11 values) with Scots pine, lodgepole pine, and Corsican pine had an average rate of 470 kg C ha⁻¹ yr⁻¹ and a range from 125 to 696 kg C ha⁻¹ yr⁻¹. Spruce species encompassed 17 values, with the species Norway spruce, Sitka spruce (*Picea sitchensis*), and Serbian spruce (*Picea omorika*), and gave a mean value of 364 kg C ha⁻¹ yr⁻¹ and the range 151 to 693 kg C ha⁻¹ yr⁻¹. There was an almost significant difference (p = 0.068) between the genera pine and spruce (Table 3).

There was an effect of site temperature on sequestration rate. Using

Fig. 6. Rates for sequestration of carbon in humus layers ($\text{kg C ha}^{-1} \text{ yr}^{-1}$) in coniferous forest stands were related to MAT. MAT ranged from c. 0.1°C in northern Scandinavia to 11°C on Mt Vesuvius, south Italy. The species investigated were lodgepole pine, Scots pine, MontereyMonetary pine, black pine, Sitka spruce, Norway spruce, and Douglas fir. Data was taken from Staaf and Berg (1977), Tietema (2004), Wardle et al. (1997), De Marco et al. (2012), Ovington (1959), Turner and Long (1975), Vesterdal and Raulund-Rasmussen (1998), and Sogn et al. (1999). Figure from Berg and McClaugherty (2014).

gravimetric SOC in organic layers across Europe plus in east Canada, Berg and McClaugherty (2014) compared C sequestration rates and MAT. They used information for the main coniferous genera, namely pine, spruce (Norway spruce), and fir species and found a clearly significant ($p < 0.01$) relationship between C sequestration rate and MAT when combining coniferous species (Fig. 6). Further, using a long-term (41-yr) forest-floor inventory covering the forested land of Sweden, Berg et al. (2009) found a highly significant positive relationship between temperature sum (Tsum) and C sequestration rate ($R^2 = 0.29$; $n = 548$; $p < 0.0001$) – in that case measured humus accumulation, using all plots with both Scots pine and Norway spruce. Temperature sum was calculated from latitude and altitude (www-markinfo.slu.se; Odén et al., 1983). Further data in Section 9.3.

8. Can the ‘stable fraction’ be considered stable?

The concept ‘limit value’ or ‘stable residue’ does not imply a complete stop in decomposition. The stable residue may vary in size and values between 58 and 0% have been reported, the variation to a large part related to litter N and Mn concentrations.

The asymptotic standard error, often in the range from 0.9 to 11.1 (Berg and Ekbohm, 1991), allows for a continued mass loss at a low rate and the limit value may thus indicate a stable fraction with a very low mass-loss rate. Couteaux et al. (1998), used both field incubations and respiration in the laboratory. They used Scots pine needle litter from field incubations and divided this preincubated litter into three main pools of different degradability (respiration rates) and called them ‘labile’, ‘inter-mediate’, and ‘recalcitrant’. In their partly decomposed litter they determined the sizes of these pools and estimated rate constants for decomposition. The recalcitrant pool made up between 79 and 85% of the litter samples with a respiration rate lower than $0.0001\% \text{ day}^{-1}$ ($< 3.6\%$ in 100 years), whereas the labile one had a rate of about $0.124\% \text{ day}^{-1}$, more than 1200 times higher. This experiment with a division of litter into pools also illustrates a potential error source when it comes to measurements of mass-loss rate using respiration.

9. Carbon sequestration – two regional approaches

9.1. Stable-residue approach

Foliar litter fall is proportional to AET and may be scaled up. The dominant coniferous species in Scandinavia are Scots pine and Norway spruce and they thus dominate the litter input (Berg et al., 1999a, 1999b). Birch spp. is less common but still important enough to be considered as one group. Akselsson et al. (2005) combined about six further deciduous tree species to ‘other deciduous species’ as a fourth

one. Data for measured litter fall from these four groups were related to AET and used for the calculation of litter fall. The linear AET-litter fall functions for both species were based on litter-fall measurements on pine and spruce plots. For deciduous litter Akselsson et al. (2005) used data from Meentemeyer et al. (1982)(Table 1).

There appears to be a higher foliar litter fall for Norway spruce than for Scots pine. At an AET of about 500 mm yr^{-1} , e.g. at the southwestern coast of Sweden, the foliar litter fall, as dry organic matter, should be c. $1900 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for pine and $2400 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for spruce. Below an AET of 420 mm yr^{-1} , e.g. in northern Sweden, the annual amounts of litter produced would be less than 1000 kg ha^{-1} for Scots pine and 1400 kg ha^{-1} for Norway spruce.

The stable residue of decomposing litter is part of the SOM build-up. The average limit values and stable fractions for the four groups of litter species were calculated (Akselsson et al., 2005) using available data from litter decomposition studies (Table 4).

The remaining fraction of stable matter was calculated as $(100 - \text{limit value})/100$ and multiplied by litter fall to give the annual SOM build-up (cf. Berg et al., 2001; Berg and McClaugherty, 2003, 2008) for each of the species.

The SOM accumulation may be scaled up. Akselsson et al. (2005) divided the forested land into $5 \times 5 \text{ km}$ plots (grid cells). Each such grid cell had information about area of forested land as well as the fraction of each of the four groups of tree species, namely pine, spruce, birch spp., and ‘other deciduous’. They used average AET for each $5 \times 5 \text{ km}$ grid cell and estimated litter fall for each group of species, using the fraction of each group in the grid cell and equations of Table 1. This information was combined with that for stable fraction (Table 4).

As a last step, C sequestration was calculated by multiplying the derived SOM build-up by the C fraction in litter. Akselsson et al. (2005) assumed a constant C fraction, 0.5. A constant fraction is allowed as their calculations were based on the newly-shed litter, with a minimum of ash. The result is the C sequestration ($\text{kg ha}^{-1} \text{ yr}^{-1}$) in the organic layers of forest soils.

Table 4

Mean values for N and Mn concentrations and limit values for decomposition for three combined groups of litter (data in part from Berg, 1998). The mean values were calculated using one average limit value from each site for pine, spruce, and birch creating a new average value for $n = 32$. For ‘other deciduous’ one average limit value for each of the species aspen ($n = 2$), beech ($n = 5$), and oak ($n = 1$) were used to calculate a mean value. Standard error is given in parenthesis. Table in part from Akselsson et al. (2005).

Litter type	N concn (mg g^{-1})	Mn concn (mg g^{-1})	Limit value (%)	Stable fraction	n
Pine, spruce, birch	6.3 (2.4)	0.93 (0.16)	78.1 (3.8)	0.22	32
Other deciduous	11.5 (3.7)	–	63.8 (4.9)	0.36	2

Fig. 7. A) Actual evapotranspiration and C sequestration rates in Sweden based on a kriging interpolation of 95 sites with modelled AET, using the Thornthwaithe and Mather (1957) water balance procedures. B) Carbon sequestration rates in the organic layers of forest soils for three separate tree species according to the stable-residue approach. The C sequestration rate in a grid is the rate when the fractions of different tree species (with different C sequestration) have been taken into account. Figure from [Akselsson et al. \(2005\)](#).

Carbon sequestration rates in the SOM layers in forest soils in Sweden span from 40 to 410 kg ha⁻¹ yr⁻¹ with an average of 180 kg ha⁻¹ yr⁻¹ (Fig. 7), as based on the stable-residue concept. The annual C sequestration for the whole country was estimated to $4.8 \cdot 10^6$

tons.

The climate gradient shows decreasing C sequestration rates from the south-western to the northern part of the country. In the southernmost part and on the west coast the C sequestration rates exceed

300 kg ha⁻¹ yr⁻¹, in mid-Sweden the rates range mainly between 150 and 200 kg ha⁻¹ yr⁻¹ and in the northern parts the sequestration rate is lower than 100 kg ha⁻¹ yr⁻¹ with a minimum of 40 kg ha⁻¹ yr⁻¹ at and north of the Arctic Circle. The main patterns of AET distribution and C sequestration rates are similar (Fig. 7ab). The AET spans from 375 mm in the northern part of Sweden to 540 mm in the south-western part with higher temperature and more precipitation. The more scattered picture in Fig. 7b is due to more detailed information about tree species and forest types.

Different tree species have an effect on C sequestration. According to litter-fall measurements, foliar litter fall was higher in spruce than in pine forests (Berg and Meentemeyer, 2001). A higher litter fall results in a higher annual mean C sequestration in spruce than in pine forests; 200 kg ha⁻¹ compared to 150 kg ha⁻¹. The mean C sequestration rate in birch forests is the same as for pine, but the gradient over Sweden is more emphasized in pine forests (Fig. 7b) with a wider range (60 to 260 kg C ha⁻¹ yr⁻¹) than for birch (150 to 260 kg C ha⁻¹ yr⁻¹).

The litter group for 'other deciduous trees' is limited to the southernmost part of the country. That litter class has the greatest stable fraction, 0.36 (Table 4), which leads to a higher C sequestration rate, (about 400 kg ha⁻¹ yr⁻¹) than for litters of spruce, pine, and birch with a stable fraction of 0.22. In that part of Sweden forests of common beech and common oak make up a significant fraction of the forested area, namely c. 22% of the standing volume (Anonymous, 2003).

9.2. Direct measurements of humus depths

An overview to the direct measurement study. Berg et al. (2009), made their calculations in three steps using data on humus depth collected over 41 years. Humus depth had been recorded annually and primarily they used c. 450,000 of more than 800,000 single measurements in 82,513 tracts. For the treatment of data the forested land of Sweden was divided into grid cells of 25*25 km, which became the basic unit in their calculations (Fig. 8). They also divided the country into three main climatic regions called High, Medium, and Low, based on temperature sum (degree days; 5 °C; Fig. 9; Odin et al., 1983). These regions to some extent also reflect the distribution of the two main tree species, namely Norway spruce and Scots pine, the latter dominant in region Low and the former in region High.

In a first step they calculated the increase rate in humus depth for each 25*25 km grid cell. This was done separately for stands dominated by (i) Scots pine, (ii) Norway spruce and (iii) for all kinds of combinations of species (Table 5). In a second step they used humus density (Fig. 9b, see below) and calculated the density of C in the humus layer (amount of C per mm humus layer and hectare) for each of the 25*25 km grid cells. Finally they used the C analysis values for each grid cell and calculated the annual increase in sequestered C (Fig. 9c).

There are linear relationships between the thickness of the humus layer and time. Linear relationships between time and humus depth were calculated for each 25*25 km grid cell. In practice, all of the linear relationships for humus-layer growth showed a significant increase rate ($p < 0.05$; Table 5). For the forest types without species dominance ('all species') 550 of the 557 relationships were positive and 7 were negative *viz.* had a decrease. For the spruce-dominated forest types 449 out of the 457 relationships were positive and 8 negative. For the pine-dominated forest types all 507 relationships were positive. The reasons to a lack of significant relationships may vary on a very local basis.

Using a new concept, namely humus density, Berg et al. (2009) converted the increases in humus depth to C sequestration rates. For C density, they used the unit kg C mm⁻¹ ha⁻¹ and found that it varies over the country with a factor of c. 2. Considering all species, the highest density class was found in the south-western part of the country with more than 431 kg C mm⁻¹ ha⁻¹ in an area with both a high rainfall and a generally high N deposition. The least dense humus was found in the northern half of the country with less than 280 kg C mm⁻¹ ha⁻¹.

Fig. 8. The figure gives an illustration of the use of the national Swedish coordinate system. We have used intersections at a distance of 25 km and each such intersection becomes the centre of a circle with a radius of 55 km. All sampling plots that were located within such a given circular area were used for calculating the humus depth at the intersection, namely the centre of the circle. Sampling plots clustered together in tracts are shown as black spots at uniform distances. Lakes and the Baltic are shown as grey areas. Figure from Berg et al. (2009).

There were some general patterns for humus-layer growth rates. Using data for all tree species Berg et al. (2009) found a general tendency for the average humus-layer thickness to increase with time. In the studied 41-yr period its growth rate ranged from c. 0.1 mm yr⁻¹ to > 1.2 mm yr⁻¹. Although these values were significantly different and gave a general tendency, the increasing thickness was better distinguished when comparing data for the three separate regions, namely Low, Medium, and High (Fig. 9a). By using these regions they showed that the humus layers were thicker in the southern third of the country, namely in region High with 7.19 cm and in region Medium with 6.40 cm as compared to region Low with 5.27 cm already before the measurements started. The initial thickness in humus layers was thus significantly different among the three regions (Fig. 10).

After 41 years the humus layers had increased to an average of 11.39 cm in region High, which was significantly higher than in the first inventory. In region Medium the increase to 9.00 cm was significant as it was in region Low with an increase to 7.56 cm (Fig. 10).

The measurements include the residues of all produced litter as well as treatments of the organic layers, including management practices, such as clear-cuts, site preparation, and ditching. Further, this approach with direct measurements of the humus-layer thickness is not based on the concept 'stable residue' but allows a determination of a net increase, including possible decomposition also for undisturbed systems.

Humus depth recalculated to carbon sequestration rates. After recalculation, direct measurements of humus depth over time give rates for the actual C sequestration. The annual C sequestration for all the forested land was c. 6.7 * 10⁶ tons.

Using changes in humus depth and C density in the humus layer, Berg et al. (2009) converted the increase rate of the humus layer to annual increase in bound C using each one of the 25*25 km grid cells as a unit for the calculations. Using linear relationships they obtained C sequestration rates ($p < 0.05$) ranging mainly between 140 and

Fig. 9. Stepwise calculation of amount of sequestered C in the forested land of Sweden. Data for the 41-year period between 1961 and 2002. A) Annual increase rate in the humus layer, B) Amount of C per mm humus layer and hectare as calculated from bulk density and carbon concentration, C) Annual rate of C sequestration in the humus layer in Swedish forests over 41 years. A climate index, namely temperature sum was used to subdivide the country into three regions, namely Low, Medium, and High. Region with temperature sum > 1249 degree days was called region High, the one with a temperature sum between 850 and 1249 degree days was called region Medium. Region Low was defined as those areas with a temperature sum of < 850 degree days. From Berg et al. (2009).

Fig. 9. (continued)

420 kg C ha⁻¹ yr⁻¹ and with the average rate of 251 kg C ha⁻¹ yr⁻¹.

The growth rate of the sequestered C did not show any clear pattern over the country. Thus, in the northern parts they found areas with both low (less than 140 kg C ha⁻¹ yr⁻¹) and relatively high (above 281 kg C ha⁻¹ yr⁻¹) increase rates for sequestered C (Fig. 9c).

The rates differed among the forest types and were on the average 239 kg C ha⁻¹ yr⁻¹ for spruce-dominated forests, 283 kg C ha⁻¹ yr⁻¹ for those dominated by pine and 251 kg C ha⁻¹ yr⁻¹ for those encompassing all species.

Climate and tree species influence carbon sequestration rate. There was a highly significant positive relationship between temperature sum (Tsum, 5°) and C sequestration rate. Using all grid cells with both Scots pine and Norway spruce Berg et al. (2009) found a positive linear relationship between stored C and the temperature sum ($R^2 = 0.29$, $n = 548$, $p < 0.0001$).

The C sequestration rates were higher in humus layers (mor layers)

in Scots pine forest soils than in those of Norway spruce. Using all data for the forested land, Berg et al. (2009) found that Scots pine stands on the average sequestered 283 kg C ha⁻¹ yr⁻¹ and Norway spruce 239 kg C ha⁻¹ yr⁻¹. Using only those 25*25 km grids cells that had both Scots pine and Norway spruce stands (348 ones) and the same climate, resulted in a highly significant difference of 71 kg ha⁻¹ yr⁻¹ ($p < 0.0001$).

10. A validation – comparison of two regional approaches

10.1. Validation

The two approaches we compare are both regional and we may compare them using regional aspects such as (i) total annual sequestration, (ii) response to the gradient in AET and Tsum (MAT) along Sweden. Further, as there are measurements for single stands from both

Table 5

Number of linear relationships for humus depth vs time for forests dominated by Scots pine and Norway spruce (basal area) plus forests encompassing all combinations of tree species. The average C sequestration rate for each type is given. Table from Berg et al. (2009).

Tree species	Number of crossing points (proportion within brackets)			C sequestration (kg ha ⁻¹ yr ⁻¹)			
		Significant	Not significant	Mean	SD	Min	Max
All species	557 (100%)	402 (72%)	155 (28%)	197	102	-25	696
positive relationship	550	402	148				
negative relationship	7	0	7				
Spruce-dominated (> 70% spruce of basal area)	457 (100%)	244 (53%)	213 (47%)	188	111	-39	841
positive relationship	449	244	205				
negative relationship	8	0	8				
Pine-dominated (> 70% pine of basal area)	507 (100%)	429 (85%)	78 (15%)	271	125	5	750
positive relationship	507	429	78				
negative relationship	0	0	0

Fig. 10. Humus depth vs time is shown as linear relationships using non-parallel lines. Average values for humus depth are shown for each region as calculated on an annual basis, with each value being an average of 62 to 3626 recorded mean values. For region High the slope coefficients is 1.05 mm (O —), for region Medium is 0.65 mm (● —), and for region low 0.57 mm (Δ —) (cf. Fig. 9). From Berg et al. (2009).

northern and southern Sweden we may use them, too for a limited validation.

In a first step we may compare annual totals. The annual C sequestration rates over the whole region for both approaches were similar. With an annual sequestration rate of $4.8 \cdot 10^6$ tons of C for the stable-residue approach as compared to $6.7 \cdot 10^6$ tons of C for the approach with direct measurements we may consider the amounts to be rather close – considering the differences in approach. Both were made using the same forested land. The difference of $1.9 \cdot 10^6$ tons means that the stable-residue approach gave c. 30% lower annual sequestration than the one for humus growth. This may in part be due to the fact that the stable-residue approach was based on foliar litter fall only, considered to be c. 70% of total litter fall from trees. Further, the humus depth measurements gave a net result for all litter inflows from all plants. A difference of 30% may thus be explained at least in part. Still, some closer views may be rewarding.

A similar behaviour in a climate gradient. There is a gradient in AET, MAT, and Tsum along the country with values for all three parameters decreasing from the south to the north. In Scandinavia temperature is limiting for the processes we discuss, namely litter fall and decomposition (V. Meentemeyer, pers. comm.) and thus our focus on a comparison of temperature is correct.

The stable-residue approach for C sequestration showed mainly a gradient with decreasing C sequestration rates from the southwestern to the northern part of the country, which spanned from 40 to $420 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fig. 7a,b). This approach was based on the linear relationships between AET and litter fall (Table 1). That there was a positive relationship between sequestered C and AET is thus a direct consequence. The measured humus-depth approach showed the same trend and there was a positive and highly significant relationship between Tsum and sequestered C ($R^2 = 0.29$; $n = 548$; $p < 0.0001$).

We may validate using measured data from the literature. We may use literature data for C sequestration for (i) single stands in southern Sweden with high rates, (ii) from some stands in the north with low rates and compare to the regional approach. The high C sequestration rates for southern Sweden may be supported by the direct measurements of Vesterdal and Raulund-Rasmussen (1998). For seven sites they

found C accumulation rates that ranged from c. 170 to c. $530 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The climate in Denmark is very similar to that in southernmost Sweden and the data are therefore comparable from that point of view. In the southernmost province (Sweden) the measured rates ranged from 141 to $420 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ (cf. Fig. 9c). Using the stable-residue approach they were estimated to range from 250 to $420 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ (Fig. 7b). For northern stands, Wardle et al. (1997) have given C sequestration rates of a magnitude of 65 to $83 \text{ kg C ha}^{-1} \text{ yr}^{-1}$, for a mixed forest in Swedish Lapland. Also that range fits to both approaches (Figs. 9c, 7b).

11. Some long-term trends

The historical SOM layer build-up in the boreal forests of Sweden has probably followed a cycle with accumulation of a SOM layer, normally ending with a forest fire, resulting in high loss of C to the atmosphere and a ‘resetting’ of the system (Sverdrup and Stjernquist, 2002). With regular intervals forest fires have removed at least part of the SOM layer but since the 1950ies more efficient prevention of wild-fires has mainly removed fire as an agent decreasing SOM layers. The present situation, almost without wild-fires but with clearcutting, also has an effect on SOM-layer buildup. Clear-cutting is normally conducted with intervals of 60 to 140 years on almost the entire area of the productive forest in Sweden.

Without disturbance and wild-fires the SOM-layer buildup can continue for millennia. Thus, in an investigation in a boreal forest, Wardle et al. (1997) found that under growing trees, SOM mor layers had built up for almost 3000 years to an amount of c. 50 kg SOM per meter square. Other evidence for the production of recalcitrant organic matter comes from radio-dated soils. Thus, ^{14}C -dating indicates that SOM could be 1000 to 10,000 years old (Paul, 1984; Stevenson, 1982). Chronosequence studies support the idea that, in the absence of disturbance, organic-matter layers continue to increase for millennia (e.g. Wardle et al., 1997; Berg et al., 2001). Such long-term increase was hypothesized already by Jenny (1980).

Several measurements of organic layers (e.g. LFH) in chronosequences and repeated samplings in growing stands indicate a linear increase with time for periods up to less than 100 years (e.g. Ovington, 1957, 1959). Data presented by Wardle et al. (1997) and by Berg et al. (2001) gave a statistically significant linear relationship between accumulated C and time for a period between 120 and 2984 years, suggesting that the C sequestration rate was rather constant. This also means that no steady state was indicated below 3000 years and below a total C accumulation of $250,000 \text{ kg C ha}^{-1}$ in the organic layer, further supporting stability. These observations were made in undisturbed forest stands.

12. Comments on some uncertainties and a possible development

The stable-residue (limit-value) concept implies a method that allows us to calculate C sequestration rates in SOM in forest soils using a limited input of data. The calculations simply combine litter-fall information and a stable litter fraction to give a SOM build-up. This study also has shown that the method using AET and litter fall for scaling up was relatively easy to perform.

Different kinds of uncertainties can be identified in this study; the variation around the linear relationship between litter fall and AET (quantified by standard errors). For the stable-residue concept Akselsson et al. (2005) used a constant fraction instead of a variable one. The AET modelling was based on temperature and precipitation data with high accuracy for 95 sites from Swedish Meteorological and Hydro-logical Institute. Still, the scaling-up process was based on 95 sites with calculated AET – the uncertainties connected with the scaling up of AET from 95 sites to 17,000 grids using the $5 \cdot 5 \text{ km}$ grid-cell system require further attention.

The linear relationship between litter fall and AET as well as the

stable-residue concept have been discussed and validated in several studies (Meentemeyer et al., 1982; Berg and Meentemeyer, 2001). Input data for forest type was based on a satellite-based forest classification with a total accuracy of 71% (Mahlander et al., 2004).

The stable-residue concept as applied onto C sequestration has been validated for the boreal and the temperate zones, but may have a wider validity. Thus, it has been possible to calculate limit values from litter decomposition data gathered under a subtropical climate (e.g. Berg et al., 2003; Faituri, 2003). Still, we cannot conclude a general validity. We have not yet seen comparable studies from the tropical zone and cannot predict a general validity there. However, as a consequence of climate change and N deposition – and thus a changing litter chemical composition – both the size of the stable fraction and the productivity of the forest and thus the corresponding litter fall will be influenced.

Information on litter fall and its relationship to climate, e.g. to the indices AET and MAT, is dependent on tree species (e.g. Liu et al., 2004) and such relationships need to be established for each studied region.

Only foliar litter has been included in the calculations. Woody litter has different decomposition kinetics, which at present makes it difficult to estimate its long-term contribution to C sequestration, which possibly is small (Berg and McLaugherty, 2003) and for the different root and rhizome litter types we still miss basic information from decomposition studies and know too little to apply the stable-residue concept (Berg and McLaugherty, 2003).

13. Conclusions and suggested future research

In the near future there could be less focus on ‘decomposition rate’ and more on the size of a readily available fraction and a recalcitrant residue as well as factors re-gulating their relative size and stability. So far N and Mn have been suggested as important substrate factors for decomposition pattern and possibly Ca will be important for specific litter genera. Also some elements in the group ‘heavy metals’ may be important.

The clear trend to an increasing stable residue with increasing MAT via litter N and Mn concentrations will help us to predict sequestration of C and humus. Also the effects of climate change and of litter species may be predicted. The calculable stable residue may have a certain decomposition rate, reflecting its stability and factors that may influence that stability need to be investigated. To investigate effects of climate on decomposition patterns it may be worth considering climate gradients within the extension of a given ecosystem type such as a temperature gradient of a given tree species.

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