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Review

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

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ABSTRACT

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 – 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=hT9MHlWAAgE

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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 belowground 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 kg C ha^{-1} yr^{-1} to be compared to a directly measured value of 251 kg C ha^{-1} 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 × 5 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 × 25 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).

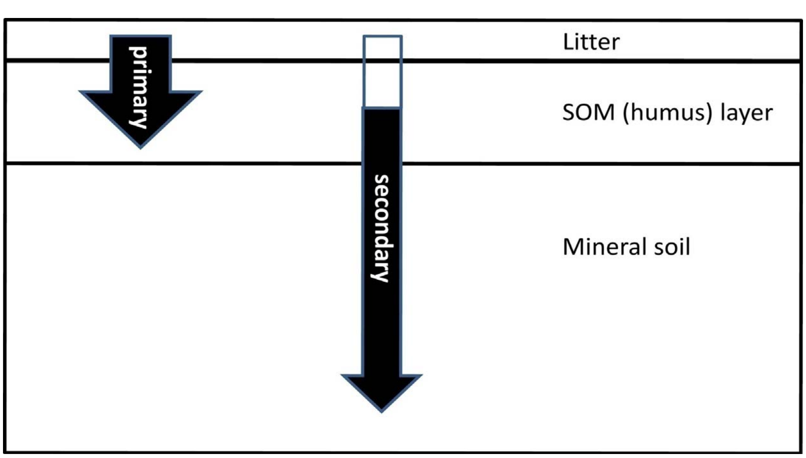

Fig. 1. A rough definition of the concepts 'primary' and 'secondary' C sequestration in humus and mineral soil. The arrow labelled 'primary' indicates transport of partly decomposed litter to the stable organic layers, thus into a sink for long-term stable material, for example a mor layer. The arrow 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).