

Humus in northern forests: friend or foe?

Cindy E. Prescott^{a,*}, Doug G. Maynard^b, Raija Laiho^c

^a*Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada V6T 1Z4*

^b*Canadian Forest Service, 506 West Burnside Road, Victoria, BC, Canada*

^c*Department of Forest Ecology, University of Helsinki, P.O.B. 24, 00014 Helsinki University, Helsinki, Finland*

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Abstract

Organic matter is of primary importance to the sustainability of long-term site productivity in forest ecosystems. In boreal forests, organic matter accumulates at the surface as mor humus. This may represent a substantial portion of the total nutrient capital of a site, and its decomposition is essential for the short-term availability of nutrients for tree growth and long-term site fertility. However, organic matter accumulation at the soil surface can also effect the forest ecosystem by immobilizing nutrients making them unavailable for plant uptake, and by creating physical and environmental conditions that can impede seedling establishment and survival. Therefore, it is necessary to understand the processes of humus formation and decomposition in order to manage these soils in a manner that will maintain or improve site productivity.

This paper provides an overview of (i) the composition of humus, (ii) the conditions in the boreal forest that result in the surface accumulation of humus, (iii) decomposition processes and (iv) the effects of humus on nutrient (especially nitrogen) availability. Questions relating to the detrimental role of surface organic matter accumulation, the effects of natural disturbances (e.g., fire) and harvesting disturbances on humus loss and accumulation and management practices that can maintain long-term site productivity will also be discussed. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

A notable characteristic of northern forest soils is surface accumulations of organic matter, often referred to as humus. This material consists mostly of plant remains, either in relatively fresh forms or partly decomposed, as well as by-products of decomposition. Although the importance of humus to the nutrition of northern forests has been recognized for at

least a century, management of this resource has been impeded by conflicting ideas about its role in site nutrition. On one hand, humus is a key source of nutrients, and also contributes to moisture retention and soil structure. A substantial proportion of nutrient capital of the site may be located in humus, especially nitrogen. This nutrient reserve is critical to long-term site fertility, and helps to buffer the site against disturbances that might lead to nutrient depletion. Humus may also be viewed as a nutrient sink that essentially competes with trees for this growth-limiting resource. Especially in the case of surface accumulations, the progressive immobilization of nutrients into humus may over time deplete the supply of available nutrients

* Corresponding author. Tel.: +1-604-822-4701;

fax: +1-604-822-9102.

E-mail address: cpres@interchg.ubc.ca (C.E. Prescott)

and reduce site productivity. Surface humus accumulations may also hinder seedling germination and growth. As Romell (1935) pointed out, humus has been regarded both as “the very essence of soil fertility” and “a necessary evil”. This contradiction was largely the result of the term humus being used to describe both incorporated humus (soil organic matter) and surface humus layers (particularly the ‘bothersome mor’ –Romell, 1935).

The first major step towards clarifying the role of humus was the work of P.E. Muller who distinguished the two main types of humus, mull and mor. In mull humus, the organic material has been transformed through soil animal activity and mixed with mineral soil. Mor or ‘raw’ humus forms are surface accumulations in which three fairly distinct layers can be identified, the fresh litter (L), partially decomposed but recognizable Formultningsskiktet (F) and that which has been transformed into relatively homogeneous humus (H). Moders are an intermediate humus form between mors and mulls but are distinctly different because they encompass characteristics of both main humus types (Green et al., 1993). The type of humus formed is a consequence of local ecological conditions (Bernier, 1968), particularly the climate, vegetation and parent material. The type of humus greatly influences site fertility; mull forms provide more nutrients and support greater productivity than mors. Classification of humus forms (e.g., Green et al., 1993) is, therefore, useful in estimating the nutritional status and potential productivity of forest sites. As Romell (1935) stated, the real index of fertility is not the amount of humus, but the type of humus formation. Although the difference between mull and mor is often attributed to faster decomposition in mull humus, it is not the rate but rather the type of decomposition that determines the amount and form of humus (Weetman, 1980). Mor humus forms are the consequence of primarily fungal decomposition, leading to incomplete decomposition (i.e., organic matter is not completely mineralized to CO₂ and nutrients) and nutrient immobilization. Mull humus forms result from passage of organic material through soil animals and consequent bacterial decomposition, leading to more complete decomposition and greater nutrient availability. Although classification of humus forms is useful for predicting site fertility and other ecological conditions, management of the humus resource

requires a more in-depth understanding of the process of humus formation and factors that control the rate of humus accumulation and type of humus formed.

2. What is humus?

Simply put, humus is composed of the recalcitrant products of decomposition. By the time it becomes humus, the material is partly decomposed and chemically stabilized. The process of humus formation is not well understood but is thought to involve microbial modification of lignin and condensation of proteins into humus precursors, followed by their complexing into humus molecules of complex structures. Although individual humus molecules are highly variable, the chemical nature of humus as a whole is fairly consistent. Relative to the original plant material, humus is low in carbohydrates (cellulose, hemicellulose), high in large polyphenolic molecules (usually measured as the acid-insoluble fraction or ‘lignin’ component), and high in N. Most of the N in humus is bound in complex molecules of ‘undetermined’ composition, and so can be considered to be immobilized and essentially unavailable to plants and most microorganisms. Melillo et al. (1989) likened the decay process to a filter, through which litter of highly variable chemistry is transformed into a relatively homogenous material that we call humus.

3. How is humus formed?

The production of humus in an ecosystem is a result of incomplete decomposition. Under less than ideal conditions for decomposition, a portion of the litter entering the forest floor is not completely decomposed, but is modified into humus which may decompose slowly and accumulate. To understand why humus layers develop, we must understand the process of decomposition and the factors that control the rate or completeness of this process. Aber and Melillo (1991) present a general model of the decomposition process from litter to humus in two phases. During the early stage, there is a very rapid loss of solubles and fairly rapid loss of cellulose. There is little loss or possible even a gain of ‘lignin’ (insoluble decay products). During the early phase carbon is relatively

available and nutrients are limiting, and there is immobilization of the limiting nutrient (usually N). Once the litter reaches the second stage, it can be considered as humus, it has stabilized content and slow decay of all components. The onset of the late stage of decay coincides with net loss of lignin and net N mineralization. The critical factor that determines the rate at which humus accumulates on a site is how much of the original litter mass remains at the point at which the material becomes humus and decomposition slows. If most or all of the litter has decomposed by this time, very little humus will be formed. However, if some litter remains, humus will be formed and will accumulate. Berg and Ekbohm (1993) found that the maximum decomposition limit of needle litter varied among species; lodgepole pine had a limit of nearly 100%, while the limit value for Scots pine was about 84% mass loss.

4. What controls the rate of humus formation?

There are three major causes of incomplete decomposition that lead to accumulation of humus

1. climate (temperature and moisture conditions),
2. chemical and physical characteristics of litter (particularly lignin, phenolics) and
3. abundance and composition of soil microbial and faunal communities.

These factors are obviously highly interrelated (Fig. 1). The activity and composition of the soil biota directly influence both the rate and the completeness of decomposition. Their activity and composition is determined by the environmental conditions (particularly temperature and moisture) as well as the quality of their primary food resource (litter).

Climate is generally a good predictor of decomposition rates and good relationships have been found between temperature or actual evapotranspiration and rates of litter decomposition (Meentemeyer and Berg, 1986; Johansson et al., 1995; Aerts, 1997). The influence of temperature and moisture on microbial activity is well established (Bunnell et al., 1976), with suitable conditions of both required for effective decomposition. Climate is considered to be less important than the nature of the organic material in

the later stages of decay. However, there is some evidence that, at least under extreme conditions, temperature and moisture may limit decomposition of humus in boreal forests. Low temperatures are responsible for slow mineralization of organic matter in boreal forests of Alaska (Van Cleve et al., 1981, 1990). Excess moisture and consequent oxygen-deficient and cool conditions are a major cause of organic matter accumulation in boreal peatlands.

The chemical nature of the litter is probably the most significant factor influencing the proportion that becomes humus. The amount of acid insoluble (AIS) material in the litter will obviously influence the proportion of the litter that becomes humus. This fraction is commonly referred to as the 'lignin' or Klason lignin component, and contains cutin, in addition to lignin. These structurally complex materials inhibit decomposition not only through their resistance to enzymatic decomposition but through their contribution to toughness, which limits accessibility of microbes and associated enzymes to potential substrates. Experimental evidence for the importance of the lignin fraction was provided by de Hann (1977), who showed that the initial lignin concentration in organic material determines the amount of humus accumulated over 1 and 10 years. The lignin concentration or the lignin : N of litter is often the best predictor of rates of decomposition (Melillo et al., 1982; Taylor et al., 1989) or N mineralization (Scott and Binkley, 1997). Cutin is among the most recalcitrant of plant materials, and may be a dominant control of late stage decomposition (Gallardo and Merino, 1993; Baldock and Preston, 1995). Other phenolic compounds (phenolic acids, tannins, quinones, humic and fulvic acids) contribute the materials which lead to the complex mixture of aromatic structures which comprise the bulk of soil organic matter (Gallet and Lebreton, 1995). By binding proteins and other organic substrates into insoluble complexes, making them unavailable for further microbial degradation these compounds are particularly important in reducing the supply of inorganic N forms in humus.

The presence of nutrients and carbon in available forms also influences humus decomposition by stimulating microbial activity. Although nutrients may stimulate decomposition in the early stages, N may actually reduce humus decomposition by suppressing lignolytic enzyme systems (Fenn et al., 1981). Avail-

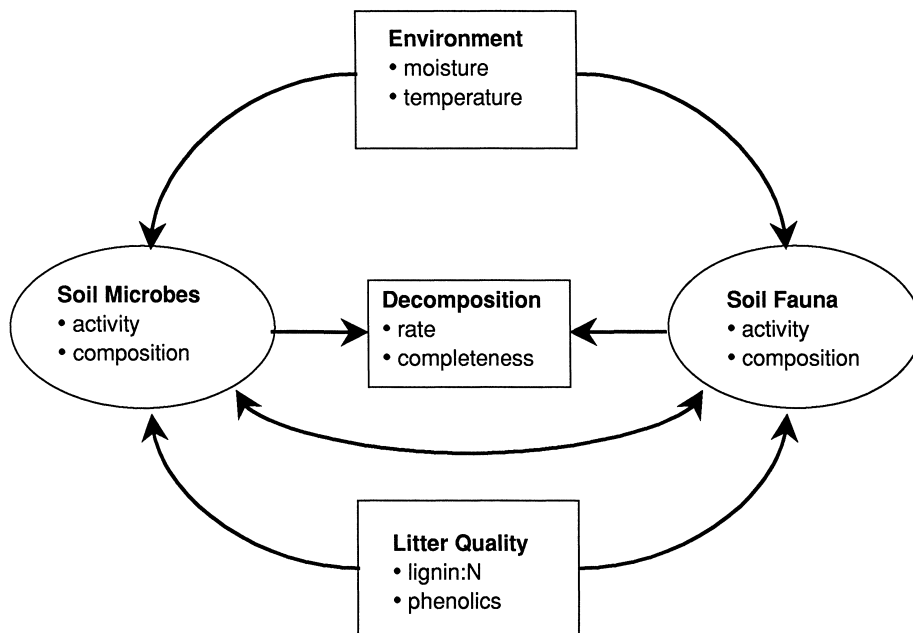


Fig. 1. Interactions among climate, litter quality and soil organisms in controlling litter decomposition.

ability of carbon substrates may be more limiting during later stages of decay, when the readily metabolizable C in litter has been exhausted and C has been transformed into recalcitrant forms. Lignin mineralization depends on the availability of carbon in forms more easily degraded than lignin (Drew and Kadam, 1979). Root exudates provide readily available C which stimulates microbial activity and may promote decomposition of humus (Bradley and Fyles, 1995; Grayston et al., 1996). Applications of fresh residues may also stimulate humus decomposition by providing available C for microbial activity (the 'priming effect', Bingeman et al., 1953).

The composition and activity of the soil biota is critical in determining the type of humus that forms, its rate of decomposition and the resulting accumulation. Soil fauna are known to enhance decomposition by fragmenting or comminuting litter, and also influence the composition of microbial community through selective grazing (Visser, 1985). Sites without soil fauna often have incomplete decomposition, resulting in humus accumulation (Howard and Howard, 1974; Berg et al., 1995). Several microcosm studies have demonstrated increased decomposition, mineralization and respiration in forest soils inoculated with

macrofauna (Anderson et al., 1985; Setälä and Huhta, 1989, 1991). Sites which are too cold, too wet or have litter unsuitable for faunal degradation are therefore prone to incomplete decomposition and humus accumulation. They will also be more likely to have mor type humus (or peat), if there are not macrofauna there to mix the humus with the mineral soil. A diversity of functional guilds of microorganisms is needed for complete decomposition of organic matter. This may be particularly important in later stages of decomposition because relatively few species can degrade the lignin or phenolic complexes that are prevalent in humus. These organisms have specific requirements for readily available C co-substrates and low inorganic N levels, and may be inhibited by the actions of soil invertebrates (Scheu, 1992). At sites where any of these requisite conditions are not met, humus degradation will be impaired and an accumulation of humus will likely result.

5. The role of disturbance

In addition to the rate of organic matter decomposition, the accumulation of humus in forests

depends on the type, frequency and intensity of disturbance. Forest fires are a major disturbance in northern forests (Higgins and Ramsey, 1992) that reduces organic matter. One potential benefit of a fire dominated forest ecosystem is that fire results in a recharge of the short-term nutrient pool by releasing organically bound nutrients from humus. In general, following fire, ash accumulates that increases the surface pH, increases cation concentrations and often results in increased N mineralization (Weber, 1990; Johnson and Elliott, 1998). However, under controlled conditions where fires remain cool, little change in short-term nutrient availability has been measured (Chambers et al., 1986). The variable results reported in the literature are understandable given that the mineralization processes after fire are dependent on so many variables including organic matter quantity and quality (Weber, 1990).

The potential loss of total nutrient capital through volatilization of certain elements and off-site movement of fine particulate ash by wind and water is critical to the potential long-term effects of fire. Nitrogen losses are most often associated with wild fires; however, significant losses of potassium, sulfur and phosphorus can also occur (Raison et al., 1985; Tiedemann, 1987; Dyrness et al., 1989). The amount of organic matter and nutrient loss through fire and the mechanisms of loss depend on: the temperature of the fire, type of fire, tree species, composition of the understory, and climatic conditions following the fire. Fire, either wildfire or prescribed burns, can be beneficial to short-term nutrient availability and long-term site productivity by releasing nutrients tied up in the humus, improving seedbeds and reducing competing vegetation. Under certain conditions, however, the total organic matter and nutrient capital may be reduced, particularly on drier sites. This may affect long-term site productivity by changing the biological and physical properties of the soil as well as the chemical properties (Jurgensen et al., 1990; Johnson and Elliott, 1998; Lynham et al., 1998).

Insect outbreaks may affect the rate of humus decomposition and accumulation directly by altering the quality and quantity of litter fall and indirectly by reducing canopy cover and changing soil moisture and temperature conditions. Insect disturbances would be more conservative in terms of organic matter loss than fire because insect outbreaks relate more to changes in

matter and nutrient distribution than losses often associated with fire (Mattson and Addy, 1975).

It has been suggested that windthrow can stimulate organic matter decomposition in some coastal forests by mixing the soils and improving aeration (Ugolini et al., 1990; Prescott and Weetman, 1994). However, an experimental soil mixing demonstrated either no effects or negative effects on respiration and nutrient mineralization (Keenan et al., 1994).

6. Managing humus

This review of humus formation makes it clear that the amount of humus present on a site is the result of many factors, including the climate, the type of vegetation and the nature of the disturbances. This provides little basis for assuming that the amount of humus on a site is somehow ‘just right’ for the forest presently occupying the site. The management implication is that guidelines for soil conservation or sustainable forestry as they pertain to humus reserves should not be based on measures of present humus accumulation. Rather, they should be based on recognition of the role of humus in site nutrition and the potential for sustaining or improving site productivity through proper manipulation of this resource. Similarly, although the amount of organic matter has been used as an index of sustainability and long-term site productivity (Morris et al., 1997), this may not apply to northern forests. Particularly in boreal forests and some coastal forests, humus accumulations may be excessive in that they limit productivity by immobilizing a substantial portion of the site nutrient capital (Weetman, 1980; Keenan et al., 1993).

Because much of the available nutrient pool in boreal forests is contained in the forest floor, both long and short-term productivity can be affected by activities that alter the rate of input or decay of organic matter. For example, in the short-term, harvesting and site preparation may stimulate mineralization by improving environmental conditions for microbial activities that may improve seedling growth. If, however, excessive amounts of N are mineralized to nitrate, then this could increase leaching losses of nitrate and loss of cations, potentially reducing site nutrient capital and long-term site productivity. Thus, there is the potential to either degrade or improve

productivity by manipulating the humus, and managers should be cognizant of the potential impacts of their activities on this resource.

Management of humus entails two rather divergent considerations

1. conservation of the humus to maintain the organic matter and nutrient capitals of the site to promote long-term site productivity and
2. manipulation of the humus to increase rates of decomposition and nutrient mineralization and to improve seedbeds and reduce competing vegetation to promote short-term productivity (seedling growth).

The critical challenge is to fine-tune practices such that they promote mineralization of humus in ways and at times that will promote uptake of nutrients by the regenerating forest and discourage losses of nutrients from the site. The silviculture practices chosen for a given site will be the best compromise between all management objectives for the site to promote short and long term site fertility. The most appropriate compromise for the single management objective of managing the humus resource will depend on the site and the management objectives, but should be based on an understanding of the ramifications of activities on the humus layer and resulting site nutrition. Following is a review of our understanding of the effects of some of the most common forest management activities on the rates of decomposition and accumulation of humus.

6.1. *Harvesting*

Erosion and mass movement are obvious and extreme examples of harvesting impacts on humus (Powers et al., 1990). Changes in soil physical conditions and the chemical composition of the litter as a result of harvesting will also affect humus decomposition. To some extent, these soil factors will be controlled by the amount of canopy removal (Armson, 1996). Thus, the harvesting system selected may influence the soil conditions that affect humus decomposition processes.

Decomposition of humus have been found to increase in the short-term (<5 year) following clear cut harvesting in many forest ecosystems (Jurgensen

et al., 1997). In northern boreal forests, soil temperature and moisture are generally below optimum for decomposition and changes to soil temperature and moisture as a result of harvesting would increase decomposition and nutrient availability in the short-term (Covington, 1981; Keenan and Kimmins, 1993). Changes to soil moisture, however, may also create conditions that would reduce or inhibit decomposition, depending on site conditions. Loss of trees would reduce evapotranspiration and lead to increased soil moisture, in some cases to point of causing anaerobic conditions within the rooting zone.

Changes in the quantity and quality of litter fall following clear cutting will affect the rates of humus decomposition and accumulation. Reduced organic matter inputs via wood litter fall were predicted for the first several years following clear cutting then increasing at its greatest rate by 10–20 years (Covington, 1981). Reduced organic matter inputs would contribute to reductions in humus following clear cut harvesting. Predicted recovery of forest floor organic matter following clear cutting to preharvest levels have varied from <5 years to 80 years depending on the degree of disturbance and forest type (Aber et al., 1978; Covington, 1981; Vitousek et al., 1992; Crowell and Freedman, 1994; Stone and Eliooff, 1998).

The effects of clear cut harvesting on rates of humus decomposition and accumulation would also depend on the intensity of removal. Whole tree harvesting is known to remove greater amounts of biomass and nutrients than boles only harvesting. In short rotation systems and low fertility stands, whole tree harvesting may result in losses of organic matter and nutrients that may impact long-term productivity (Proe and Dutch, 1994; Worrell and Hampson, 1997). In aspen stands of the Great Lake States, two to three times the nutrients and biomass were removed by whole-tree harvesting (Alban and Perala, 1990). However, the biomass and nutrient levels of the surface organic horizon 4–8 years following whole-tree or conventional harvesting were the same. In a long-term site productivity study of aspen in northern Minnesota, there was no difference in the total C of the forest floor between an undisturbed mature aspen forest and whole-tree harvested plots 5 years after disturbance (Stone and Eliooff, 1998). Similar observations have been made for other forest ecosystems (Worrell and Hampson, 1997).

Johnson and Todd (1998) measured no increase in the amount of C sequestered in soils 15 years after boles only versus whole-tree harvesting. They attributed this to the complete decomposition of the organic matter to CO₂ with boles only harvesting. This study was carried out in the southern US where temperature and moisture were not limiting factors. In northern soils, where the rate and degree of decomposition would be less than optimal, a difference in humus accumulation between boles only and whole tree harvesting might be expected in the long-term.

Changes in the factors affecting the rates of humus decomposition and accumulation following partial cutting or thinning operations would be similar to those mentioned above for clear cut harvesting; soil temperature and moisture, and amounts and quality of litter fall. The degree to which a partial cut system or thinning would affect humus decomposition would be largely dependent upon the amount of canopy removal and the amount of soil disturbance from ground based harvesting. Humus decomposition rates have been shown to increase (Piene and Van Cleve, 1978), decrease (Weetman, 1965) or not change (Will et al., 1983) following thinning. In general, effects would be expected to be less than those observed under a clear cut harvesting system; however, Prescott (1997) found no difference in decomposition and humus during the 2 years following clearcutting and partial cutting in a coastal montane coniferous forest. Armson (1996) indicated a general rule of thumb for determining the appropriate silvicultural system for managing humus. Where a forest floor is retained, even if reduced, then other management considerations will dictate the choice of silvicultural system. Where the forest floor is seasonal or the Ah is the surface horizon, a selection system should be used.

Ground based harvesting systems disturb humus by displacement and mixing of the humus from skid trails and road construction. Compaction is also associated with these disturbances. In extreme examples, these disturbances can account for 20–25% of the harvested area. Redistribution of humus results from the removal (gouging) of material and the deposition of the material in a new location. Thus, increased organic matter is found in the berms and outer tracks of skid trails and lower amounts on inner tracks. Poorer seedling growth has been observed on inner track and was attributed to

compaction and lower organic matter (Smith and Wass, 1994).

6.2. Site preparation

Site preparation is used to create an environment for the regeneration of crop trees (Sutherland and Foreman, 1995). Often one of the objectives of site preparation is a reduction in humus. This may result in successful regeneration in the short-term (10–15 years) but may have detrimental effects in the long-term, possibly not until future rotations. The degree to which site preparation will affect the rates of humus decomposition and accumulation processes will depend on the amount of area disturbed and the severity of the disturbance to the humus (Bulmer et al., 1998). Treatments that are limited to planting areas such as mounding and patch scarification leave a portion of the site intact. In contrast, treatments such as blading would result in a high proportion of the area being disturbed.

The severity of the disturbance to the humus layer is also critical. Loss of biomass and nutrients following harvesting in aspen stands (both pure and mixed wood) were minimal when the surface organic horizon was left largely undisturbed (Crow, 1985; Maynard, 1997; Maynard and MacIsaac, 1998; Stone and Elioff, 1998). At the other extreme, removal of 80% of the forest floor alone or in combination with compaction reduced aspen productivity to about one-third and total biomass to about one-half compared with total tree harvest only (Stone and Elioff, 1998). This occurred despite the fact that in the first 2 years following disturbance the stem densities of aspen in the forest floor removal treatments were 1.5–2 times the harvested only treatment.

In mechanical site preparation, techniques such as mounding, that mix humus material with mineral soil have been reported to accelerate decomposition (Salonius, 1983; Örlander et al., 1990). Embedding needle litter and slash litter in disc trench ridges enhanced mass loss rates and increased nutrient availability compared with needles decomposing on undisturbed forest floor following clear cutting (Lundmark-Thelin and Johansson, 1997). More favorable climatic conditions inside the disc trench ridges as well as the stimulating effect of mixing were suggested as the factors responsible for the increased biological activ-

ity. Soil mixing increased early growth of conifer seedlings in coastal British Columbia after 5 years; however, the effect on available soil nutrients was negative for low productivity site types and negligible for high productivity site types (Messier et al., 1995). The positive growth effects may have been due to the mixing controlling the competing vegetation rather than a change in the decomposition processes. Thus, while it has been hypothesized that mixing increases decomposition there is no clear evidence that this is the case.

6.3. Fertilization

Nitrogen fertilization has been explored as a means of stimulating decomposition and nutrient mineralization from mor humus (Salonius, 1972). However, with the exception of urea that also provides a C source, N fertilizers have not been effective in ‘activating’ mor humus. Increased C storage was reported in N-fertilized pine forest floor, associated with reduced microbial activity (Nohrstedt et al., 1989). Berg (1986) reported reduced rates of decomposition of needle litter in later stages, which was attributed to higher lignin concentrations in fertilized needle litter and suppression of lignin degrading fungi by N. Berg (1986) also pointed out that lignin or humus decomposers require a source of carbohydrates. Species such as birch, which release large amounts of carbohydrates from their roots may therefore promote humus decomposition (Bradley and Fyles, 1995). Applications of C sources to forests have mixed results depending on the type of material applied. Readily available C sources such as glucose or starch (Prescott and McDonald, 1994) will stimulate microbial activity but not the fungi that decompose the more recalcitrant materials in humus, so will have little effect. Woody residues are probably too recalcitrant to stimulate microbial activity and would not provide much readily available C. Likewise, organic wastes such as sewage sludges or composts are unlikely to stimulate mineralization of humus because much of the material has already been processed by microorganisms (Prescott and Brown, 1998). There is some evidence that fresh residues such as straw may promote mineralization of humus by providing C in forms that would stimulate the fungi present in humus (Prescott and Zabek, 1997). The use of mulches for

increasing rates of mineralization of mor humus deserves more attention.

6.4. Liming

Increasing the pH of humus through liming might be expected to increase rates of humus decomposition. Increased respiration and nitrification have been reported after liming, as have reductions in forest floor C (Marschner and Wilczynski, 1991). However, accumulations of humus have also been reported in long-term liming experiments in Finland, which were attributed to reduced rates of lignin decomposition (Smolander et al., 1996).

6.5. Stand conversion

Growing mixtures of species might promote humus decomposition or prevent its accumulation, particularly if hardwoods are interplanted with conifers. In general, broadleaves have higher litter quality and promote greater macrofaunal activity, leading to more humus forms (but see Romell, 1935). Litter decomposition is more rapid under aspen than spruce (Perala and Alban, 1982), thus it may be desirable to maintain some aspen in conifer dominated stands to improve humus decomposition rates (Fons et al., 1998). A mixture effect of conifers has also been observed on heath sites in the UK (McIntosh, 1983), and may be the result of the mycorrhizal associates of some species being better able to access organic forms of N (Ryan and Alexander, 1992). Differential abilities of mycorrhizal fungi to degrade humus complexes have been reported (Abuzinadah and Read, 1986) and deserve further exploration as a potential means of promoting mineralization of humus.

7. Peatlands: a special case

Peatlands, or mires, a common element in boreal landscape, are extreme examples of surface accumulations of organic matter. Boreal and subarctic peatlands have been estimated to contain a total of 455 Pg of deposited C (Gorham, 1991), which comprises ca. 30% of the estimated global soil C pool. There are three principal types of mire formation: paludification of upland forests, terrestrialization of water basins due

to sedimentation of organic matter, and primary mire formation on ‘fresh’ soil after emergence from water or ice. In each case, excessive moisture and consequent oxygen-deficient conditions are the major cause of slow rates of decomposition leading to organic matter accumulation, both directly, hampering microbial activity, and indirectly, through the litter quality of plants adapted to grow in waterlogged conditions, especially *Sphagnum* mosses.

A major part of decomposition in mires takes place in the oxic surface layer, the thickness of which varies with the hydrological conditions; after the remaining plant material gets buried in the permanently anoxic layer some very slow anaerobic decomposition still takes place. The degree of decomposition may vary within the peat profile, depending largely on the time that the material remained in the oxic layer exposed to aerobic decomposition. Typically, peat is a complex composition of varying-degree decay products from rather ‘raw’ plant tissues to humic substances.

Some peatland types are naturally forested and may support commercially exploitable stands. For instance, ca. 18.5 million hectares of Canada’s estimated wetland area of 132 million hectares are forested, and large areas of conifer swamps are being logged for pulpwood, especially in northern Ontario and Quebec (Dahl and Zoltai, 1997). Large peatland areas have also been artificially drained to increase forest growth, mainly in northern and eastern Europe.

Peatland drainage for forestry initiates a secondary succession towards more forest-like communities, unless the site is too poor, or imbalanced, in nutrients to sustain increased forest growth. With improved soil aeration (Boggie, 1977), the amounts of aerobic microbial activity (e.g., Lähde, 1969) and soil mesofauna (Silvan et al., 1999) increase, leading to increased potential for organic matter decomposition on drained sites (e.g., Lieffers, 1988). Consequently, clearly higher CO₂ emissions have been measured from drained peat soils (e.g., Silvola et al., 1985; Glenn et al., 1993; Martikainen et al., 1995). It is not clear, however, the extent to which the increased CO₂ emissions result from increased decomposition of the ‘old’ peat, or from other processes such as root-associated respiration and decomposition of new litter material entering the soil both above- and below-ground. The amount of tree root biomass and root litter increase after drainage (Lieffers and Rothwell,

1987; Laiho and Finér, 1996; Finér and Laine, 1998), and on forested sites about 40% of the increase in C emission may be attributed to increased root and root-associated respiration and decomposition (Glenn et al., 1993; Silvola et al., 1996a). The above-ground litter-fall also increases after drainage (Laiho and Laine, 1996) and its decomposition probably accounts for a part of the remaining increase in the C emission. The net effect of drainage on peatland organic matter accumulation/decomposition largely depends on peatland type. On nutrient-rich sites, where the old peat substrate is of better quality to decomposers, its decomposition is stimulated when efficiently drained leading to a net loss of soil organic matter (Martikainen et al., 1995; Laine et al., 1996; Silvola et al., 1996b; Minkkinen and Laine, 1998a, b). On relatively nutrient-poor, and more acid sites, however, the environmental factors and substrate quality may still be more limiting and peat decomposition may not be stimulated by drainage (cf. e.g., Humphrey and Pluth, 1996). Increased tree litter input may even lead to continuing soil organic matter accumulation on these sites (Minkkinen and Laine, 1998a, b).

The bulk density of the surface peat increases after drainage (e.g., Rothwell et al., 1996; Minkkinen and Laine, 1998a). Other postdrainage changes in the peat substrate include increasing acidity (Laine et al., 1995), and decreasing nutrient concentrations per mass unit, though not necessarily per volume unit due to the compaction of peat (Laiho and Laine, 1994, 1995).

The effects of harvesting and site preparation on decomposition and organic matter quality on peatland sites are still insufficiently known. In the few studies made so far, the C efflux from undrained wetland soils has been found to increase after harvesting, the extent of the change depending on the degree of disturbance (Trettin et al., 1995). On a shallow-peat (5–15 cm) black spruce swamp in the Upper Peninsula of Michigan, summertime whole-tree harvesting led to increased soil temperatures and caused a 47% reduction in soil C during the first 5 years after harvesting (Trettin et al., 1997). Bedding further intensified both phenomena. In contrast, Brown (1976) found no change in soil temperature after strip clear-cutting done in wintertime with ample snow cover, and concluded that any related changes in microbial activity might not be anticipated either. As evapotranspiration

decreases, and soil compaction and rut formation may reduce infiltration, harvesting often leads to increased waterlogging, also on drained peatlands (Heikurainen and Päivänen, 1970; Dubé et al., 1995; Roy et al., 1997). This might in principle also cause a decrease in organic matter decomposition.

Harvesting, especially whole-tree removal, may have serious implications on soil organic matter nutrient status on deep-peat sites, as the tree stand nutrient pools are removed from the cycle limited to the aerobic surface layer, and net leaching also generally takes place some time after harvesting (e.g., Ahtiainen, 1988; Kaunisto and Paavilainen, 1988; Grigal and Brooks, 1997; Laiho, 1997; Teng et al., 1997). Actual long-term changes, however, are not known.

Management objectives for peatland forests are somewhat complicated. Increased decomposition on deep-peat sites would in principle be beneficial for forest growth, but harmful in other respects, such as increased CO₂-emissions. Also, greatly increased nitrogen mineralization may lead to a shortage of other nutrients such as P and K.

8. Summary

Humus refers to both surface accumulations of organic matter and that incorporated into soil organic matter. Humus is a friend of forests in that it is a source of nutrients and if incorporated improves moisture and soil structure. However, humus can also be a problem, particularly surface layers that render a substantial portion of the site nutrient capital unavailable to plants. Humus results from incomplete decomposition, which is the result of imperfect temperature and moisture conditions or poor litter quality. Soil micro-organisms and fauna play a key role in humus formation; any conditions that restrict the activity and diversity of these organisms lead to incomplete decomposition and formation of humus. Many northern forests have surface accumulations of humus that may limit nutrient availability unless activated by natural disturbance or management activities. Humus can be managed to achieve two conflicting objectives

1. conserving humus to maintain the organic matter and nutrient capitals of the site to promote long-term site productivity, and

2. manipulating humus to increase rates of decomposition and nutrient mineralization and to improve seedbeds and reduce competing vegetation to promote short-term productivity.

The critical challenge is to fine-tune practices such that they promote mineralization of humus at times that will promote uptake of nutrients by the regenerating forest and discourage losses of nutrients from the site. Studies on the impacts of forestry practices have shown variable results with respect to humus decomposition and accumulation. Thus, specific forestry practices to manage the humus resource will depend on the site and management objectives. In general, at sites where humus has accumulated at the surface, practices that reduce or ‘activate’ (but not eliminate) humus would be preferred. At sites with an Ah layer or small amounts of humus, practices that minimize disturbance should be considered. Decisions as to how much humus should remain on a site should be based on a sound understanding of the causes of humus accumulation and its role in site nutrition, rather than the assumption that the amount currently present is somehow ‘just right’ for the ecosystem.

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