Biogeochemistry (2010) 101:133–149
DOI 10.1007/s10533-010-9439-0

Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils?

Cindy E. Prescott

Received: 1 November 2009 / Accepted: 23 March 2010 / Published online: 9 April 2010

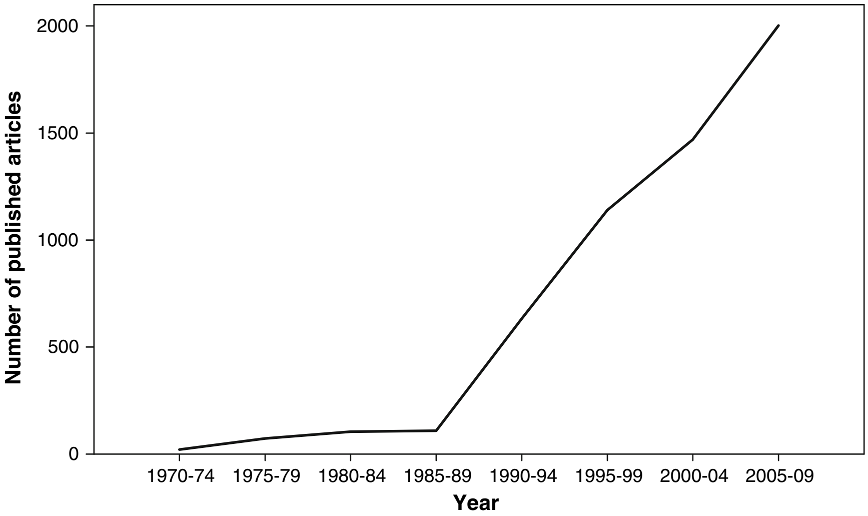
Abstract Key recent developments in litter decomposition research are reviewed. Long-term inter-site experiments indicate that temperature and moisture influence early rates of litter decomposition primarily by determining the plants present, suggesting that climate change effects will be small unless they alter the plant forms present. Thresholds may exist at which single factors control decay rate. Litter decomposes faster where the litter type naturally occurs. Elevated CO_2 concentrations have little effect on litter decomposition rates. Plant tissues are not decay-resistant; it is microbial and biochemical transformations of materials into novel recalcitrant compounds rather than selective preservation of recalcitrant compounds that creates stable organic matter. Altering single characteristics of litter will not substantially alter decomposition rates. Nitrogen addition frequently leads to greater stabilization into humus through a combination of chemical reactions and enzyme inhibition. To sequester more C in soil, we need to consider not how to slow decomposition, but rather how to divert more litter into humus through microbial and chemical reactions rather than allowing it to decompose. The optimal strategy is to have litter transformed into humic substances and then chemically or physically protected in mineral soil. Adding N through fertilization and N-fixing plants is a feasible means of stimulating humification.

Keywords Litter decomposition · Humus · Soil organic matter · Forest management · Litter chemistry · Litter quality · Carbon sequestration · Threshold analysis · Plant functional trait analysis · Humification · Nitrogen fertilization · Tree species effects

Research into the process of decomposition has grown steadily since the development of the litterbag technique in the 1960s, which allowed us to measure mass loss and estimate decomposition rates (through calculation of the decomposition constant or *k* value), and compare rates among sites, litter types and treatments of many kinds. In the 1980s, we measured decomposition rates because we knew it to be an important ecosystem process critical to maintaining available nutrients, because the data were needed for ecosystem models, and because it was interesting—complex but not beyond hope of understanding. It also had several practical applications, such as understanding how N deficiencies develop in northern forests and how ecosystems respond to disturbances, both natural and anthropogenic. By 1990, the intense environmental concern about global warming associated with rising atmospheric carbon dioxide concentrations made the understanding of the decomposition process

C. E. Prescott (✉)
Faculty of Forestry, University of British Columbia,
Vancouver, BC, Canada
e-mail: cindy.prescott@ubc.ca

Fig. 1 Number of published studies on litter decomposition in 5-year periods from 1970 to October 20, 2009, as searched through Web of Science



more urgent, given its central role in the mineralization of organic forms of C and the associated release of carbon dioxide to the atmosphere. Global research intensified in response to the apparently urgent need to predict litter decomposition rates and effects of global change thereon. This heightened demand for knowledge is evident in Fig. 1, which depicts the number of published studies available through Web of Science in 5-year periods from 1970 to today. In contrast to the slow exudation of about 20 papers per year in the 1980s, there is now more than one paper on litter decomposition appearing *each day*. The link between decomposition rates and global C fluxes is prominently mentioned in nearly every published litter decomposition study since 2000, and almost certainly figured prominently in every successful proposal for research on litter decomposition.

What have we learned from this unprecedented effusion of information on litter decomposition? It would be impossible to capture all of the information we have gained in one paper; instead I will attempt to provide an overview of some key developments in our growing understanding of litter decomposition and the factors that control its rate, and suggest how we might harness our collective understanding to improve our ability to sequester additional C in forest soils.

A key development in the last decade has been the completion and publication of the results from a global suite of long-term inter-site decomposition experiments which evaluated the influences of climatic factors and litter “quality” (primarily chemical) characteristics on decomposition rates. Important inter-site studies have been completed across Europe (Berg et al. 1993; McTiernan et al. 2003), Canada (Trofymow et al. 2002), China (Zhou et al. 2008), USA (Harmon et al. 2009), cold biomes (Cornelissen et al. 2007) and the tropics (Powers et al. 2009). An important meta-analysis of published litter decomposition studies was also recently published (Zhang et al. 2008). Each of these studies has determined the relationships among rates of mass loss, climatic factors such as mean temperature and precipitation (or combined indices such as the actual evapotranspiration (AET), potential evapotranspiration (PET) or climate decomposition index (CDI; Adair et al. 2008), and litter quality factors such as C:nutrient ratios, concentrations of acid-unhydrolyzable residue (AUR; formerly referred to as lignin) and AUR:nutrient ratios. It is conceivable that once all ongoing studies are published, we will be able to confidently predict the mass loss rate of any litter anywhere in the world, and model the expected fluxes of C and nutrients, without need for additional data of this nature.

These inter-site experiments have yielded some interesting findings that shed light on the interactions among the factors that influence decomposition rates. This can be illustrated with some of the relationships presented by Zhang et al. (2008). Figure 2a shows the relationship between mean annual temperature of each study site and the average k value for litter decomposition. A linear relationship is significant and fits the data, but another pattern is apparent—below a

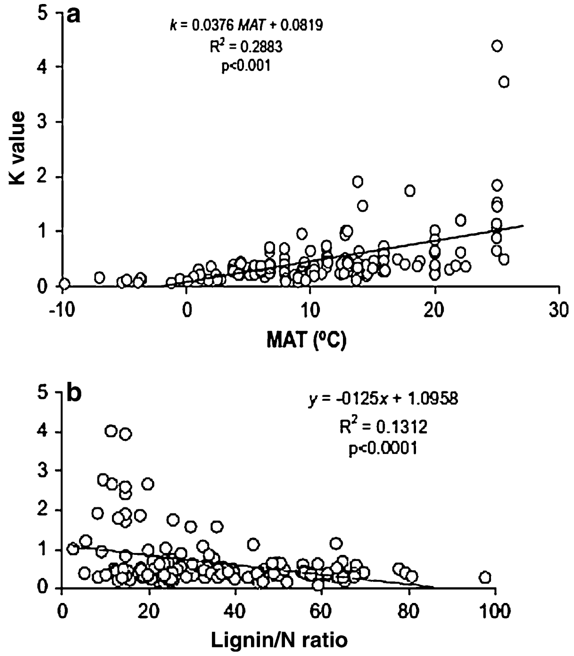


Fig. 2 Relationships between the average *k* value for litter decomposition and then mean annual temperature of each study site (**a**) and average AUR (lignin) :N ratio of each litter type (**b**) from a meta-analysis of 70 published litter decomposition studies (from Zhang et al. 2008)

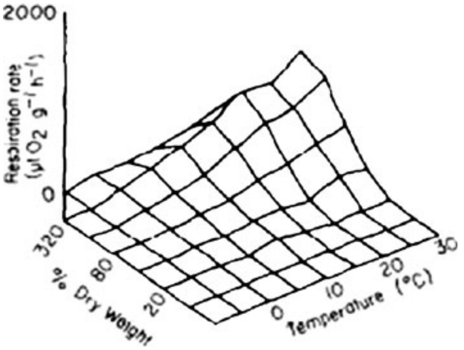


Fig. 3 CO_2 release from decaying aspen leaves under various moisture (% dry weight) and temperature conditions, demonstrating the ability of one factor to constrain decomposition regardless of the other factor (from Bunnell et al. 1977)

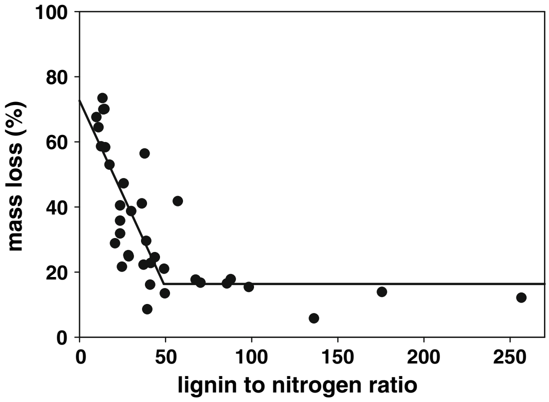


Fig. 4 Relationship between initial ratio of "lignin" (acid-unhydrolyzable residue; AUR) to nitrogen and 3-year mass loss of 14 litter types (including leaves, needles, moss, and fine woody debris) in Rocky Mountain forests, illustrating distinct decay rates of various taxonomic groups (from Taylor et al. 1991)

mean annual temperature (MAT) of 10°C, decomposition is uniformly low, regardless of other factors. Above 10°C, decomposition may be slow or fast, depending on other factors. A similar relationship is visible for AUR:N ratio of the litter—in litters with a AUR:N ratio greater than 40, decomposition is uniformly slow; decomposition of litters with AUR:N ratio below 40 may be slow or fast, depending on other factors (Fig. 2b). This observation—that thresholds exist at which one factor becomes rate-controlling—is often overlooked in favour of the application of the linear relationships which can be derived through correlation and regression analyses. For example, comparing which climatic factor is deemed to be most important for determining litter decomposition rates (based on regression analyses), the Canadian study (perhaps unsurprisingly) determined temperature to be the key factor (Trofymow et al. 2002), while the tropical study (equally unsurprisingly) determined moisture to be more rate-determining (Powers et al. 2009). Thresholds have consistently appeared in the literature—for example in respiration rates of microbes decaying aspen leaves at various temperature and moisture conditions (Bunnell et al. 1977) (Fig. 3) and mass loss of 14 litter types across a spectrum of AUR:N ratios (Taylor et al. 1991; Fig. 4).

A conceptual model for this concept of thresholds for control of decomposition is depicted in Fig. 5. In order for decomposition to be fast and/or complete, conditions must surpass certain thresholds of temperature, moisture, AUR concentrations and nutrient concentrations (similar thresholds for P and polyphenolic compounds probably exist and may control decomposition under certain conditions). Inadequate conditions with respect to any of these can divert litter into the realm of slower decomposition, regardless of the adequacy of other factors. Between these levels,

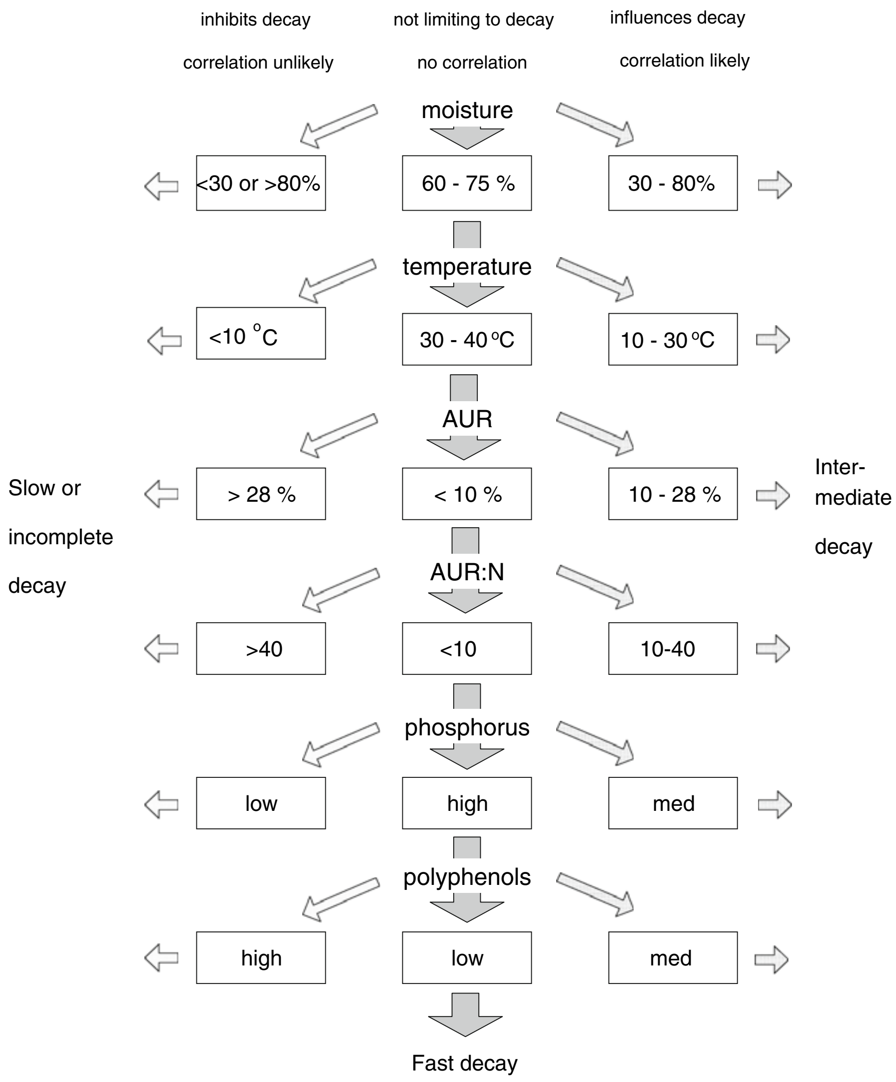


Fig. 5 A conceptual model of thresholds and ranges of influence of factors that influence rate and completeness of decomposition. *Boxes* on the *left* represent suggested thresholds, beyond which decomposition will be constrained regardless of the levels of other factors. *Boxes* in the *center* are suggested ideal (non-limiting) levels for decomposition. *Boxes* on the *right* are the suggested ranges within which the factor is likely to influence decomposition rate. Note that this is the range in which factors will be correlated with decomposition rate; such analyses may not capture the over-riding influence of factors which are beyond the threshold (*left column*)

correlations between the factor and the decomposition rate are likely. Better defining the critical thresholds at which one factor will have an overwhelming influence on decay rate presents an attractive alternative to discussing whether temperature or moisture or litter quality is more important in determining decay rate. Regression tree analysis (Rothwell et al. 2008) appears to be a promising means of identifying thresholds for decomposition effects; MAT of 10°C, moisture contents of 30% and 80% (wet weight basis), and AUR:N of 40 are suggested as tentative effect thresholds.

A strong influence of litter quality—i.e. characteristics of the litter—on decomposition rates has also been a consistent trend in the decomposition literature. A surprising result of a path analysis of the factors that influence mass loss rates litter from 70 published studies (Zhang et al. 2008; Fig. 6) was that the two factors most directly influencing decay rates were both litter quality factors—the C:N ratio and the total nutrient content of the litter (the sum of concentrations of individual nutrients). Temperature and precipitation had small direct effects; instead their influence appeared to be exerted primarily through their influence on the nature of the litter (through their influence on the type of vegetation that exists at a given site). Likewise, in a synthesis of root decomposition data, Silver and Miya (2001) found root chemistry (particularly Ca concentration) to be the factor most strongly related to root decomposition

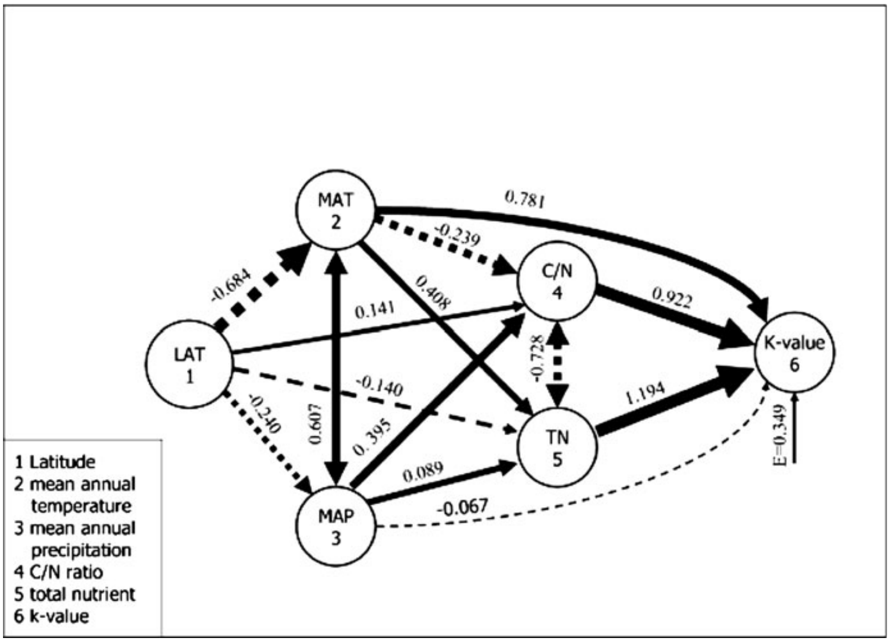


Fig. 6 Path analysis of the factors that influence mass loss rates litter from 70 published litter decomposition studies, demonstrating the direct influence of litter chemistry and indirect influences of moisture and temperature (from Zhang et al. 2008). *Solid lines* represent positive effects and *dotted lines* represent negative effects. The thickness of the *arrow* and the associated value indicate the strength of the effect

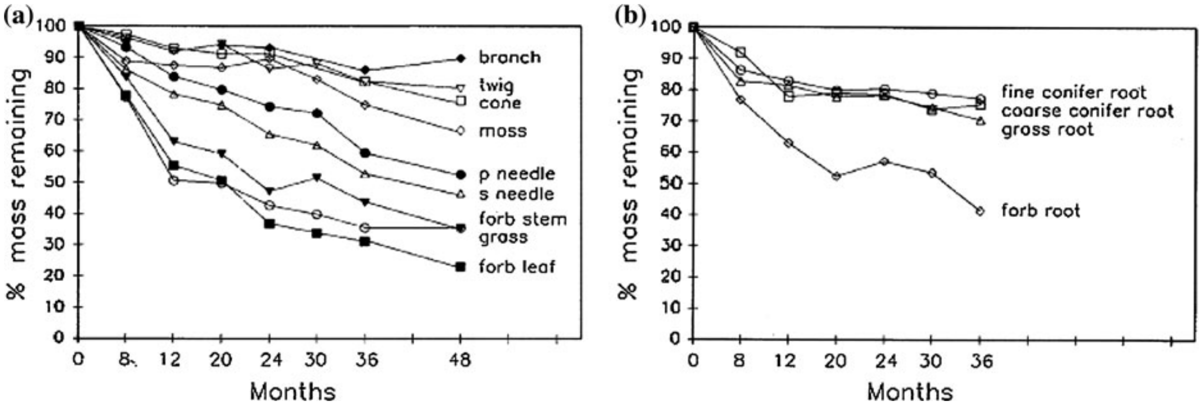


Fig. 7 Mass loss of 14 litter types during the first 4 years of decay in a Rocky Mountain forest (from Taylor et al. (1991)

rates at a global scale. Several individual studies have also suggested that climate-induced changes in rates of litter decomposition and associated feedbacks to soil fertility and productivity are likely to be small unless there is a shift in plant species composition (and thus litter quality), particularly if the composition of plant growth forms in a community is altered (Hobbie 1996; Wardle et al. 2009).

A meta-analysis of experiments comparing mass loss of litters of different types on the same site (818 species at 66 sites on 6 continents; Cornwell et al. 2008), clearly demonstrated the influence of plant functional traits related to phylogenetic groups on mass loss rates. Consistent trends included: faster decay of litter from woody deciduous than woody evergreen species; faster decay of forbs (eudicot herbs) than graminoids, and consistently slow decomposition rates of ferns and bryophytes. Pronounced differences in mass loss rates among widely different litter types have been observed many times in the past (e.g. Taylor et al. 1991; Fig. 7); this meta-analysis confirms these patterns and provides a firm basis from which we can predict relative decay rates based only on tissue type and phylogenetic group. The analysis also confirmed the utility of the various indicators associated with functional traits, which correlate with decay rates and can be used when available to predict mass loss rate, such as %N, %P, % AUR and leaf mass per unit area (LMA; kg/m^2). A recent analysis of litter decomposability in European grasslands (Fortunel et al. 2009) demonstrated how environmental factors (disturbance and climate) affect functional traits of living leaves which inevitably modify litter quality and subsequent litter decomposability. In that study litter decomposability was negatively correlated with community-weighted mean leaf dry-matter content (LDMC; dry mass divided by fresh mass), and positively with community-weighted mean leaf N concentration. The emergence of easily measured indicators of plant structural traits (such as LMA and LDMC) have provided the long-sought convenient measures of physical recalcitrance of litter, and have confirmed the suspected importance of tissue structure and accessibility to decay factors in determining rates of litter decomposition.

Perhaps the greatest contribution of the functional trait approached (Cornelissen 1996; Cornelissen et al. 2004; Kazakou et al. 2006) is causing us to think more holistically about the many characteristics of litter that determine its accessibility and vulnerability to decay, as opposed to single factors such as lignin and nutrient concentrations which are useful indicators of decomposability for predicting mass loss rates but do not, on their own, determine decay rate. Recent explorations of the changes in the three-dimensional architecture and strength of different tissues during decomposition (Lindedam et al. 2009) and the ongoing descriptive work of Ponge and colleagues (Ponge 1991; Mori et al. 2009) will be instructive when we move beyond predicting rates of decomposition and resume our efforts to understand litter decomposition as a biological process. Incorporating the biological activities of soil fauna and their effects on litter decomposition processes and pathways is perhaps the greatest remaining challenge. The recent meta-analysis of the effects of microarthropods on litter decomposition rates (Kampichler and Bruckner 2009) makes clear how poorly we understand this important effect: a slightly positive overall effect on decomposition was reversed when the authors incorporated the estimated side-effects of the unsatisfactory methodological approach of comparing mass loss in fine and coarse-mesh bags as an estimate of faunal influence. The authors also present some interesting evidence for an early publication or submission bias towards publication of data which supported the assumed stimulation of decomposition by soil fauna; more recent studies tend to show negative or neutral effects of fauna (to the extent to which either the coarse-mesh-bag or the naphthalene approach truly reflects faunal influence). Studies of the effects of varying levels of diversity on processes related to decomposition frequently conclude that the effect of diversity depends on the species or types of organisms involved, which underscores the need to better understand the activities of particular species or types of soil fauna, particularly litter transformers, their interactions with other fauna and with soil microbial communities and activities, and their resulting influence on the decay process.

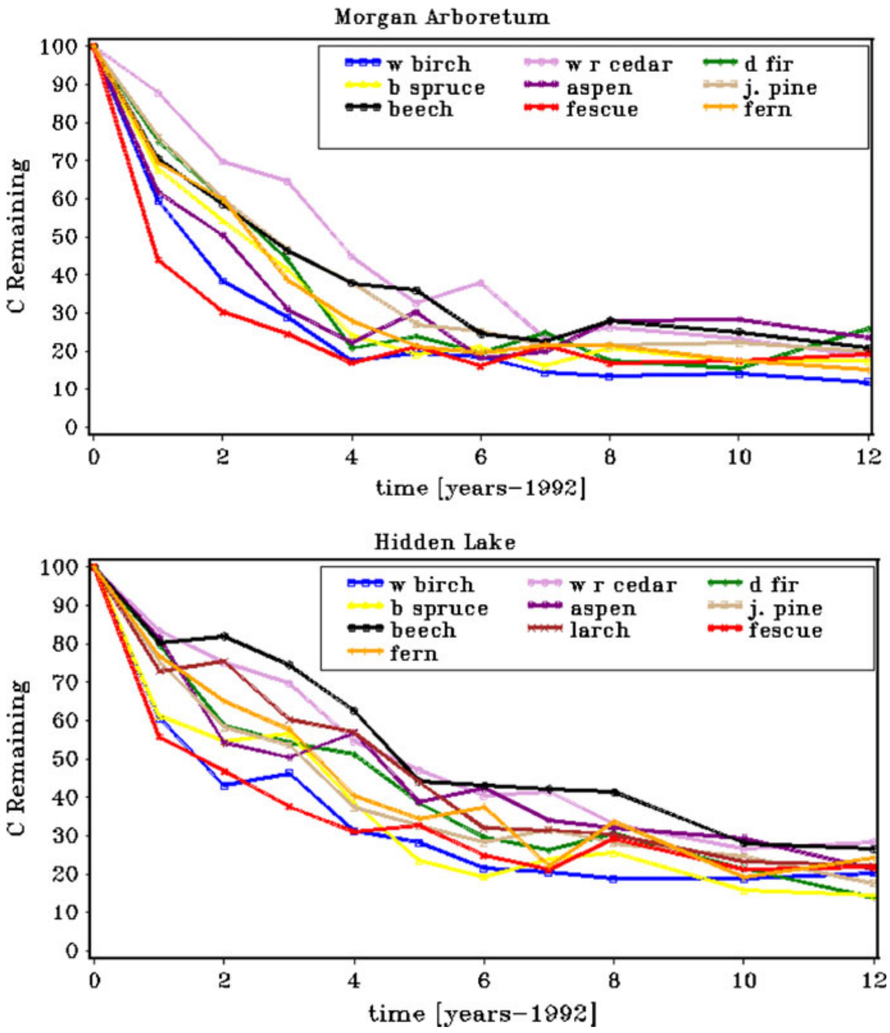
There is now compelling evidence that litter of a given species or type decomposes more rapidly in ecosystems in which that litter type naturally occurs (Wardle 2006; Vivanco and Austin 2008; Ayres et al. 2009; Strickland et al. 2009). This has obvious (but probably minor) implications for inter-site litter decomposition studies—i.e. the home-field advantage effect (Gholz et al. 2000). More intriguingly perhaps, this finding brings to light our woeful understanding of the communities of soil organisms whose activities effect decomposition, how the nature of the litter and environmental factors affect their composition and activities, and how this in turn creates the patterns of decay rates that we have now measured and are able to predict. This lack of understanding can be attributed to the complexity of studying microscopic organisms in a complex environment, although the advent of molecular and biomarker techniques for characterizing microbial communities and their degradation activities in different ecosystems (as well as the roles of specific soil microbes) is beginning to address this knowledge gap (Waldrop and Firestone 2004; Grayston and Prescott 2005). The slow progress in improving our fundamental understanding of soil organisms and activities is also symptomatic of the current nature of research funding, most of which requires that we study grand issues such as global change and biodiversity or topics which directly relate to current policies or practices, which directs our efforts into unsatisfying attempts to predict effects of nebulous changes in environmental conditions on processes that we simply do not understand at a fundamental level. It seems ingenuous to state that a better understanding of the processes and their biological underpinnings would better enable us to predict the effects of factors such as temperature, N deposition or management practices on their rates.

There appears to be resolution of the effects of alterations in the relative abundance of C and N through increased atmospheric CO_2 concentrations or N deposition on litter decomposition. There was concern that increasing CO_2 concentrations would broaden the C:N ratio of litters, thereby reducing their decay rates and leading to declines in nutrient release from litter. However, reviewing the results of numerous studies on the topic, Norby and Cotrufo (1998) concluded that, “most experiments have reported little change in litter chemistry and no significant difference in decomposition rates under different CO_2 concentrations”. Meta-analysis of N-addition studies concluded that N addition stimulates the decomposition of high-quality (i.e. low-lignin) litters, but retards decomposition of high-lignin litters (Knorr et al. 2005). A wealth of evidence now shows that increased availability of mineral N increases the proportion of litter that is humified rather than decomposed, apparently by both biological means (suppressing activity of lignolytic enzymes—Carreiro et al. 2000; Frey et al. 2004 or increasing microbial efficiency—Agren et al. 2001) and chemical reactions that lead to complexing and condensation reactions and humus formation (Berg and Matzner 1997). There is also some intriguing evidence that N also stabilizes organic matter in soil (Neff et al. 2002; Swanston et al. 2004) and interferes with mineralization of old soil C (Hagedorn et al. 2003). Nitrogen addition may well provide a means of impeding decomposition (i.e. not so much slowing decay of litter as forestalling its decay), which may be behind the apparent increase in C storage in forests receiving significant levels of N deposition (Nohrstedt 1992; Adams et al., 2005).

Although our understanding of the processes taking place during late-stage decomposition remains incomplete, we now have data from long-term experiments demonstrating a distinct phase of very slow mass loss, particularly in northern forests. Data from the CIDET experiment across Canada indicate that at most sites, mass loss becomes very slow once 70–80% of the original mass has been lost (Fig. 8). Thus 20–30% of the original litter mass is transformed to humus and decays very slowly thereafter. This phenomenon has also been reported in Scandinavia, and is referred to as the maximum decomposition limit (Berg et al. 1996). Data from the LIDET experiment (Harmon et al. 2009) indicate that this phenomenon may occur only in cold northern forests (or other suboptimal conditions), as it does not appear to occur at warmer locations. Although it was suspected to be an artifact of the litterbag technique, its occurrence in northern forests and its correspondence with rates of humus accumulation in undisturbed northern forests (Berg et al. 2009) indicate that it is a real phenomenon. The long-term mass loss curves presented in Fig. 8 also demonstrate that the differences in initial decomposition rates of different litter types are fleeting. Rates of early decomposition, upon which most estimates of k values have been made, converge for all litter types after a few years of decay. This is a recurring theme in decomposition studies, and suggests that for questions relating to C sequestration, the proportion of the litter that becomes humus may be more important than the time it takes for litter to get to that point.

There have been substantial advances in our understanding of organic chemistry of litters, in particular the nature of the lignin fraction of litter and its relationship to rates of decay. Through NMR analysis of the “lignin” fraction that remains after acid hydrolysis, Preston et al. (1997) found that this acid-unhydrolyzable residue contains many compounds in addition to lignin, including cutin and suberin (the protective layers of shoot and root tissues, respectively), which are highly resistant to decay. Reference to this residue as “lignin”, although appropriate for proximate analysis of wood, is not appropriate for non-woody materials such as most litters, and has misled us as to the importance of lignin in controlling decay rates. Application of techniques such as cupric oxidation and pyrolysis GC–MS to study lignin degradation have indicated that lignin is not as recalcitrant as previously thought, having residence times only in years or decades (Rasse et al. 2005; Heim and Schmidt 2006; Bahri et al. 2008). Even cutin and suberin have been shown to be fairly susceptible to decay (Kogel-Knabner et al. 2002), although these complex molecules will release aromatic humus precursors during their degradation (Wolters 2000). The existing evidence indicates that plant tissues as a whole are not decay-resistant; as von Lutzow et al. (2006) state: “the view that organic matter stabilization is dominated by the selective preservation of recalcitrant organic components that accumulate in proportion to their chemical

Fig. 8 Percent of original C mass remaining of 9 litter types during 12 years of in situ decomposition at two sites in the cross-Canada (CIDET) decomposition study (A. Trofymow, unpublished data)



properties can no longer be accepted". Rather, most stable compounds have been transformed through biological activities and chemical reactions leading to partial breakdown, followed by condensation and other reactions that lead to the production of complex, decay-resistant secondary compounds (Bird et al. 2008; Grandy and Neff 2008). Grandy and Neff (2008) illustrate the tendency for the organic matter in the smallest and most stable fractions to be mostly of microbial origin, demonstrating the importance of microbial transformations and partial decomposition for the production of stable soil C (Fig. 9). Understanding these humification reactions and the conditions under which they occur remains a significant and important challenge. The roles of soil aggregation in physically protecting organic matter from decay, and of adsorption to clay minerals in providing the only sink of truly stable soil C has also been demonstrated (Sollins et al. 1996, Grandy and Neff 2008), although there is some evidence that the protective effects of aggregation has been overgeneralized (Goebel et al. 2009). von Lutzow et al. (2006) concisely review the existing evidence for C stabilization through selective preservation of recalcitrant materials, spatial inaccessibility and interactions with mineral surfaces and metal ions, and the timelines associated with each potential pool of C (Table 1), and urge continued research focused on the molecular composition and stability of organic matter in specific soil fractions.

There has also been some welcome *imagining* of decomposition (as opposed to measuring decomposition), which has the potential to improve our thinking about the *process* of decomposition and in fact, the

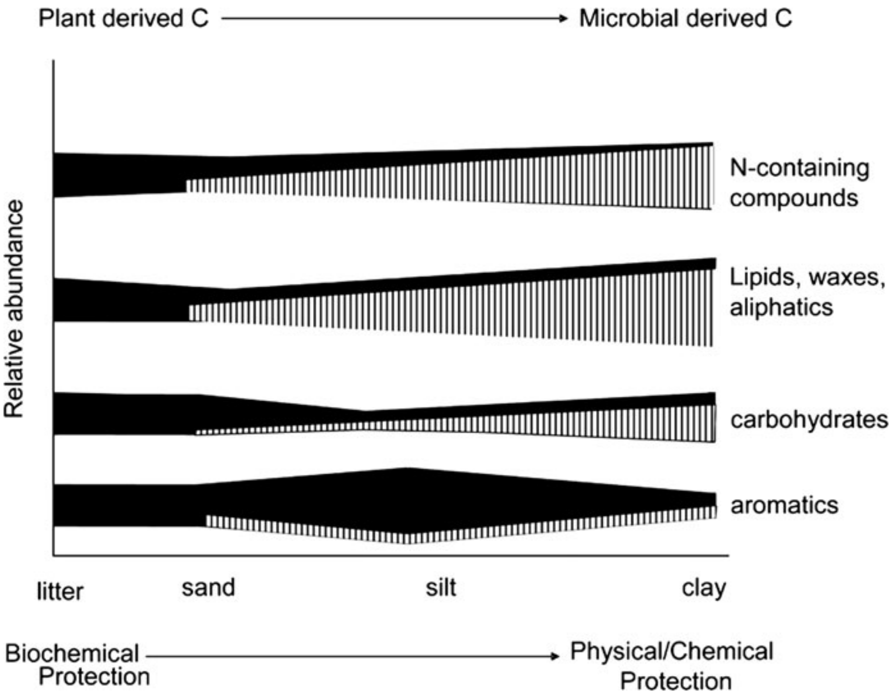


Fig. 9 Carbon compounds associated with different soil size classes, illustrating the tendency for the organic matter in the smallest and most stable fractions to be mostly of microbial origin. The black regions indicate plant-derived compounds and the shaded regions indicate microbiologically-derived compounds (from Grandy and Neff 2008)

likelihood of decomposition. It has been useful to be reminded by Schimel and Bennett (2004) and Ekschmitt et al. (2005), that decomposition occurs as a result of what may be thought of as the "hopeful act" of secretion of extracellular enzymes by micro-organisms, and so is reliant on the successful diffusion of enzymes to appropriate organic matter, and successful diffusion of decay products back to a micro-organism (who is unlikely to be the same one who secreted the enzyme). For decomposition to occur, there must be adequate temperature, a water film, aeration, suitable pH, enzymes, diffusion conditions, and an accessible and susceptible substrate—in the same place at the same time. This imagining allows us to realize how unlikely it is that organic matter will be completely decomposed and the factors that determine this likelihood, and may assist us in envisioning ways in which we might adjust the proportion that is decomposed.

It becomes apparent from reviewing our current knowledge about litter decomposition in forests that applying this knowledge to management of C stocks requires a shift in our thinking—concerning ourselves not so much with predicting and changing *rates* of litter decomposition but rather thinking about how we could *divert* litter into humus or soil organic matter rather than decomposition and thereby forestall its decay. To use a railroad analogy (Fig. 10)—rather than trying to adjust the speed at which decomposition moves the litter towards CO_2, we should be trying to divert more of the litter onto sidings (as humus or soil organic matter) where they will remain for some time before eventually arriving at CO_2.

How can we divert more litter into humus and soil organic matter and thus forestall its decay? Following from the above discussion, the following approaches present themselves:

1. make conditions less suitable for microbial activity, enzyme production and diffusion
2. make organic matter less vulnerable to enzymatic degradation
3. promote microbial transformations that lead to the creation of recalcitrant products
4. promote the chemical reactions that lead to humus formation
5. encourage physical protection of organic matter in soil aggregates
6. encourage chemical protection of organic matter in soil

The recent evidence that most stable soil organic matter has been microbiologically transformed suggests that approaches 1 and 2 will not be as effective as the other approaches which cause it to be

Table 1 Time-scales of stabilization mechanisms for organic matter and their relevance in soils and soil horizons with differing texture and mineralogy (from von Lutzow et al. 2006)

Mechanisms	Relevant in soil types or soil horizons	Time-scale/year
(1) Selective preservation due to recalcitrance		
Recalcitrance of plant litter and rhizodeposits	Forest floor, A-horizons	1–10
Recalcitrance of microbial products	Forest floor, A-Horizons	1–10
Recalcitrance of humic polymers	All soils? Little evidence	>100
Recalcitrance due to production of charcoal	Soils under vegetation fires	>100
(2) Stabilization by spatial inaccessibility of OM for microorganisms and enzymes		
Occlusion of OM by aggregation (macroaggregates >250 µm)	Loamy and clayey topsoils	1–10
Occlusion of OM by aggregation (microaggregates 20–250 µm)	Loamy and clayey soils	10–100
Occlusion of OM by aggregation (clay microstructures <20 µm)	Loamy and clayey soils	>100
Intercalation within phyllosilicates	Acid soils, little evidence	>100
Hydrophobicity	Acid soils, topsoil, forest floor	1–10 (<100)
Encapsulation in organic macromolecules	More likely in topsoils	>100
(3) Stabilization by interaction with surfaces and metal ions		
Ligand exchange	Acid soils, soils rich in oxides, more relevant in subsoils?	>100
Polyvalent cation bridges	Soils with exchange complex dominated by Ca^{2+} or Al^{3+}	>100
Weak interactions	All soils? Clear evidence is missing	>100
Interaction of metal ions with organic substances (complexation)	Acid soils, calcareous soils, heavy metals contaminated soils	>100

transformed into more complex humic substances and/or protected in soil aggregates or adsorbed to clay minerals. Approaches 3 and 4 raise the question of whether surface humus accumulations create a long-term sink for organic matter. Surface organic matter is significant C pool in northern forests (Berg et al. 2009), and the slow rate of humus decay and evidence of large surface of accumulations of humus in undisturbed areas (Wardle et al. 1997) indicate considerable potential to store C in humus layers, at least for decades (Jandl et al. 2007). The likelihood of intense wildfires and resulting combustion of surface organic matter would need to be factored into decisions about where this strategy would be most effective. The optimal strategy would be to have litter microbiologically transformed into complex and recalcitrant humic substances and then chemically or physically protected in the mineral soil. We should also be considering how to invest our efforts strategically, for example, focusing our efforts on sites with soils that have excess capacity to retain organic matter as a consequence of their depth, texture and mineralogy. Deep, clay-rich, calcareous soils may represent the greatest opportunities for sequestering C in soil.

Operational management activities are crude for this purpose, and will have side-effects in addition to their effects on decomposition and C sequestration, which need to be carefully assessed. Nevertheless, three approaches appear from the preceding discussion to warrant further consideration.

- add N
- promote species whose litter is more likely to be mixed into soil
- focus on roots rather than aboveground litter

Convincing evidence now exists that additions of N to forests, through fertilization, N-fixing plants or

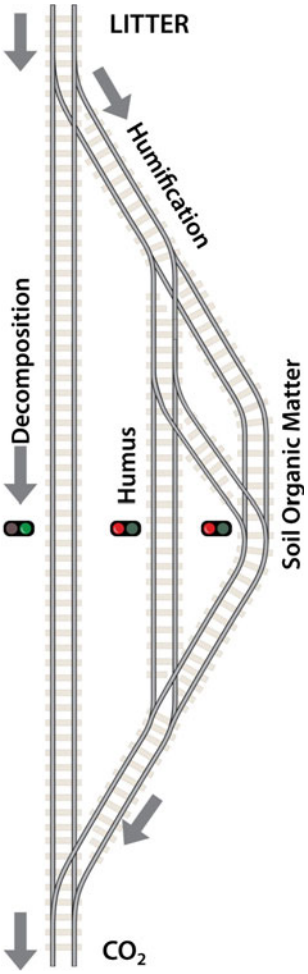


Fig. 10 Representation of refocusing our thinking from changing *rates* of litter decomposition to how we could *divert* litter into humus or soil organic matter and thereby forestall its decay

atmospheric deposition, lead to greater accumulations of humified organic matter (Malkonen and Kukkola 1991; Nohrstedt 1992; Olsson et al. 2005). A plethora of recent studies (mentioned earlier) have convincingly demonstrated the effect and identified the mechanisms involved (suppression of lignolytic enzymes, complexing into humic substances). Johnson and Curtis (2001) determined through meta-analysis of existing studies that N addition was the only forest management practice that had a clear positive effect on the soil C pool. The need now is to determine the site conditions under which N fertilization would be most effective for sequestering C and the net gain when greenhouse gas emissions related to fertilizer production, transportation and application are factored in. Incorporation of N-fixing plants presents an alternative means of adding N to forest soils. Contrary to expectations based on their higher N concentrations, leaf litter from N-fixing species does not decompose significantly faster than that of non-N-fixers (Prescott et al. 2000; Cornwell et al. 2008, Sanborn and Brockley 2009). Leaf litter from N-fixing species may have lower decomposition limits (i.e. a greater proportion will be humified; Berg et al. 2001) by virtue of having greater N concentration and in some cases such as *Alnus*, high AUR concentrations (Taylor et al. 1991). Greater accumulations of soil C are consistently associated with N-fixing plants (Johnson 1992; Resh et al. 2002; Nave et al. 2009). Resh et al. (2002) determined that this resulted from both greater accretion of new soil organic C and greater retention of old soil organic C, which is in keeping with the finding of Hagedorn et al. (2003) that N interferes with mineralization of old SOM. Although the mechanisms are not clear, incorporation of N-fixing plants appears to be a promising means of increasing C sequestration in forest soils.

The much longer residence times for organic matter that becomes physically or chemically protected in soil suggest that the residence time of C could be greatly lengthened if more of it was to become associated with mineral soil. Mixing of litter and mineral soil could be enhanced by promoting activity of soil macrofauna by incorporating broadleaf species into forest from which they are absent. This suggestion seems counter-intuitive, as broadleaf litter generally has faster rates of mass loss than needle litter (Cornwell et al. 2008), and so also would not appear to be an effective means of sequestering C in forest soils. However, many of the broadleaf species in northern forests do not decay significantly faster than needles (Fig. 11), and if they do this difference is only evident for the first 1–3 years, after which time a similar or (in some cases) greater proportion of the original mass of broadleaf litter may remain compared with needle litter. The belief that broadleaf litters decompose faster than needle litters has also been fueled by studies that report much smaller surface accumulations of litter and humus under broadleaf species than under conifers, without considering the underlying mineral soil. Studies that also report C contents of the mineral soil have

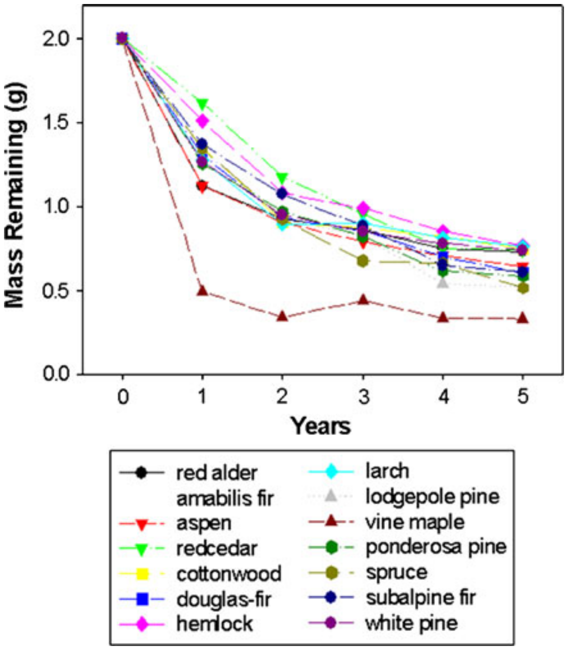


Fig. 11 Mass remaining of leaf litter of 14 tree species during a 4-year experiment in British Columbia, illustrating the small and fleeting differences between decay of common broadleaf litters (aspen, alder and birch) and needle litters (from Prescott et al. 2004). Note: vine maple is a broadleaf woody shrub

demonstrated similar amounts of C in the combined humus and mineral soil layers in broadleaf forests or under broadleaf species as in coniferous forests (Turk et al. 2008; Vesterdal et al. 2008). Incorporation of litter into mineral soil occurs through the activities of geophagic macrofauna such as earthworms, which tend to be more numerous and active in broadleaf than needle litter layers. Earthworm activities may enhance conversion of litter into more stable organo-mineral aggregates, although this effect must be weighed against evidence that earthworm activities also accelerate the degradation of resistant soil C (Wolters 2000; Fox et al. 2006). Litter transformers such as millipedes may also retard litter decomposition rates through consumption, gut passage and egestion in faeces. Millipedes can consume substantial amounts of leaf litter in forests, and about 90% of the litter mass consumed by millipedes is released in faecal pellets (Cárcamo et al. 2000). Prior to earlier assumptions of faster decomposition of this material based on its lower C:N ratio than litter and high rates of CO_2 evolution, recent experiments have demonstrated that microbial activity on faecal material of millipedes is low (following a short-lived flush) (Rawlins et al. 2007), and the material is chemically recalcitrant (Rawlins et al. 2006). The durability of faunal faecal material is supported by earlier studies and by observations of the large volumes of it present in many ecosystems (c.f. Wolters 2000; Osler and Sommerkorn 2007; Galvana et al. 2008). The persistence of faunal faecal material, and the factors which influence it, warrants urgent investigation. The benefits of broadleaf incorporation into stands depend on the net effects of faunal activities that both stabilize and destabilize soil organic matter, which is difficult to predict with our current understanding.

Finally, there are several reasons to give more consideration of the importance of roots in the creation of stable organic matter. Roots are already primarily in the mineral soil, and so do not have to be incorporated to afford the opportunity for them to become associated with aggregates or clay minerals. Second, the roots themselves, the mycorrhizal fungal hyphae associated with them, and the exudates that they produce are all means by which soil aggregates can be formed. Root litter usually decomposes more slowly than leaf litter of the same species (Lauenroth and Gill 2003; Cusack et al. 2009), and root C has a longer residence time in soil than does shoot C (Rasse et al. 2005). Crow et al. (2009) concluded that increased belowground productivity was the mechanism most likely to increase formation of stable soil C in the forest types which they studied. Rasse et al. (2005) describe the key mechanisms that lead to stabilization of root C in soil: chemical recalcitrance of roots due in part to the presence of the recalcitrant compound suberin, physical protection in aggregates, and physico-chemical protection of lignin and reactive C compounds in exudates and mucilages by association with clay minerals (Fig. 12). In acid forest soils, binding of Al and Fe ions to roots may further reduce their susceptibility to decomposition. However, the possibility that labile C exuded from roots stimulates the decomposition of recalcitrant soil organic matter (i.e. the priming effect; Kuzyakov et al. 2000; Dijkstra and Cheng 2007; Fontaine et al. 2007), may counteract the otherwise positive effects of roots for soil C sequestration, and warrants urgent investigation.

The three potential means of increasing C sequestration in forest soils suggested here are intended to stimulate and focus research to determine if and under what conditions these interventions may be

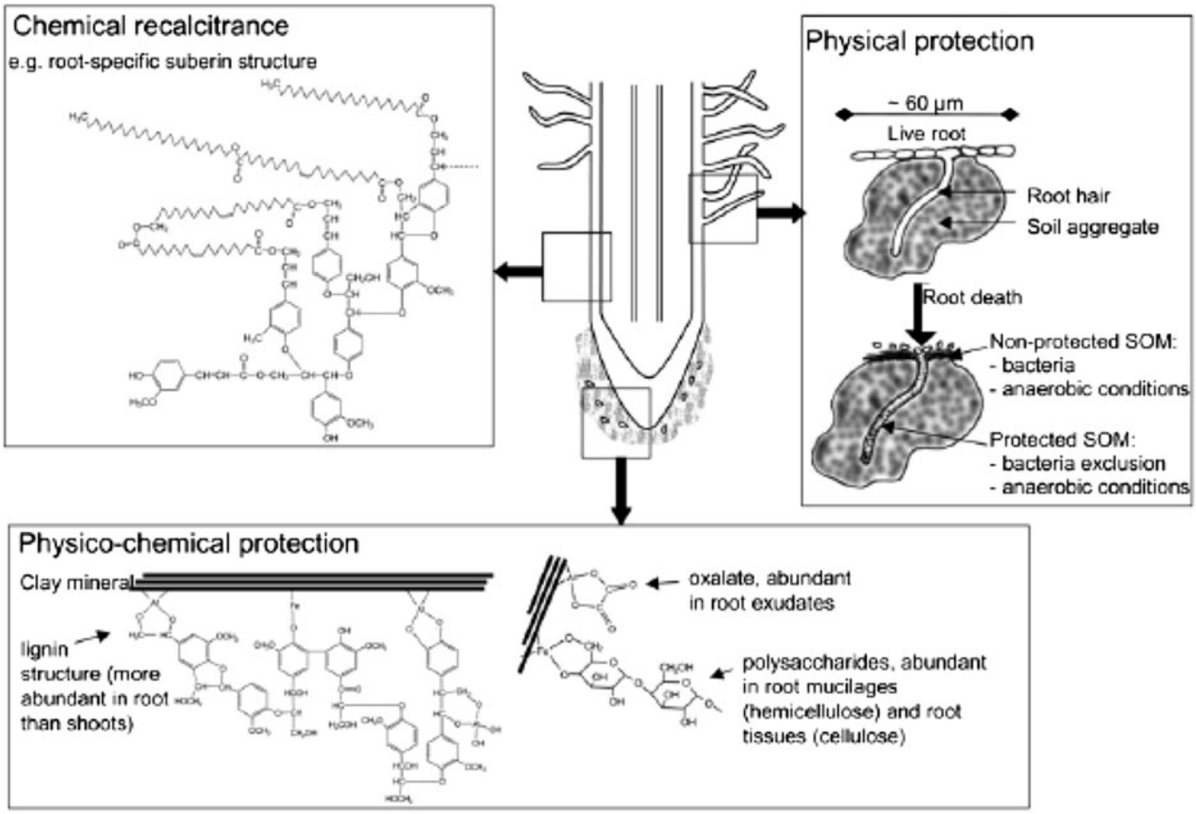


Fig. 12 Schematic representation of the main processes resulting in the protection of root carbon in soils, including chemical recalcitrance of the complex suberin molecule (*left panel*), the process leading to physical protection of dead roots in soil aggregates (*right panel*), and physic-chemical protection resulting from adsorption of various compounds from root exudates or sloughing onto clay minerals (*bottom panel*). From Rasse et al. (2005)

successful, if the effects will be substantial enough to warrant the intervention, and to identify unintended ecological consequences on the recipient ecosystem. Our understanding of decomposition processes is expanding but remains incomplete, and fundamental research that improves our understanding of this complex process will bolster our attempts to harness this knowledge to deal with global change.

Conclusions

Some things we now know about decomposition:

- We can predict early rates mass loss from measures of climate and litter chemistry
- Litter chemistry has the most direct influence on decay rates; AUR:N is the most consistent predictor of decay rate (AUR being the residue formerly known as lignin)
- Plant functional traits related to phylogenetic groups are reliable indicators of litter decomposability; leaf dry matter content and specific leaf area are useful predictors of mass loss rates
- There appear to be thresholds at which individual factors have an overriding influence on decomposition
- Changing a single characteristic of the litter (such as N or AUR concentration) is unlikely to substantially alter decomposition rates
- Plant tissues are not decay-resistant—even lignin, cutin and suberin have residence times in years or decades
- A substantial portion of litter may be humified under suboptimal conditions (cold temperatures or excessive moisture)

- Nitrogen addition promotes humification rather than decay

Can we alter decomposition such that we can sequester more C in forest soils?

- We need to determine not how to *slow* decomposition, but rather how to *divert* more C into humus and SOM pools rather than allowing it to decompose.
- The optimal strategy is to have litter transformed into complex and recalcitrant humic substances and then chemically or physically protected in the mineral soil.
- Addition of nitrogen is a promising and feasible means of stimulating humification.
- Incorporation of N-fixing plants appears to increase sequestration of soil C and may be preferable to fertilizer additions when associated greenhouse gas emissions are factored in.
- Incorporation of broadleaves and associated stimulation of soil macrofaunal activity shows promise, but the conditions under which this would sequester more C need to be determined.
- Treatments that stimulate root production could lead to more C sequestration in soil, but this strategy must be balanced against evidence that labile root exudates stimulate mineralization of stabilized soil C.

Acknowledgements I thank Mike Starr and the other organizers of BIOGEOMON 2009 for inviting this review, Bob Edmonds and Dan Binkley for thoughtful reviews and insightful comments on the manuscript, and Dale Johnson for ably serving as Editor of this special issue. This paper is dedicated to the memory of Dennis Parkinson, PhD, FRSC (1927–2009), whose enthusiasm for soil ecology and passion for science inspired many of us to embark on this fascinating life-long journey.

References

Adair EC, Parton WJ, Del Grosso SJ, Silver WL, Harmon ME, Hall SA, Burke IC, Hart SC (2008) Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. Glob Chang Biol 14:2636–2660

Adams AB, Harrison RB, Sletten RS, Strahm BD, Turnblom EC, Jensen CM (2005) Nitrogen-fertilization impacts on carbon sequestration and flux in managed coastal Douglas-fir stands of the Pacific Northwest. For Ecol Manag 220:313–325

Agren GI, Bosatta E, Magill AH (2001) Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia 128:94–98

Ayres E, Steltzer H, Berg S, Wall DH (2009) Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. J Ecol 97:901–912

Bahri H, Rasseb DP, Rumpela C, Dignaca M-F, Bardouxa G, Mariotti A (2008) Lignin degradation during a laboratory incubation followed by ^{13}C isotope analysis. Soil Biol Biochem 40:1916–1922

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ Rev 5:1–25

Berg B, Berg MP, Bottner P, Box E, Breymeyer A, Calvo de Anta R, Coûteaux MM, Gallardo A, Escudero A, Kratz W, Madeira M, Mälkönen E, Meentemeyer V, Munoz F, Piussi P, Remacle J, Virzo De Santo A (1993) Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry 20:127–159

Berg B, Ekbohm G, Johansson MB, McClaugherty C, Rutigliano F, DeSanto AV (1996) Maximum decomposition limits of forest litter types: a synthesis. Can J Bot 74:659–672

Berg B, McClaugherty C, De Santo AV, Johnson D (2001) Humus buildup in boreal forests: effects of litter fall and its N concentration. Can J For Res 31:988–998

Berg B, Johansson M-B, Nilsson A, Gundersen P, Norell L (2009) Sequestration of carbon in the humus layer of Swedish forests—direct measurements. Can J For Res 39:962–975

Bird JA, Kleber M, Torn MS (2008) ^{13}C and ^{15N} stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. Org Geochem 39:465–477

Bunnell FL, Tait DEN, Flanagan PW, Van Cleve K (1977) Microbial respiration and substrate weight loss 1. A general model of the influences of abiotic variables. Soil Biol Biochem 9:33–40

Cárcamo HA, Abe TA, Prescott CE, Holl B, Chanway CP (2000) Influence of millipedes on litter decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. Can J For Res 30:817–826

Carreiro MM, Sinsabaugh RL, Repert DA, Parkhurst DF (2000) Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81:2359–2365

Cornelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J Ecol 84:573–582

Cornelissen JHC, Quested HM, Gwynn-Jones D, Van Logtestijn RSP, De Beus MAH, Kondratchuk A, Callaghan TV, Aerts R (2004) Leaf digestibility and litter decomposability are related in a wired range of subarctic plant species and types. Funct Ecol 18:779–786

Cornelissen JHC, van Bodegom PM, Aerts R, Callaghan TV, van Logtestijn RSP, Alatalo J, Chapin FS, Gerdol R, Gudmundsson J, Gwynn-Jones D, Hartley AE, Hik DS, Hofgaard A, Jónsdóttir IS, Karlsson S, Klein JA, Laundre J, Magnusson B, Michelsen A, Molau U, Onipchenko VG, Quested HM, Sandvik SM, Schmidt IK, Shaver GR, Solheim B, Soudzilovskaia NA, Stenström A, Tolvanen A, Totland Ø, Wada N, Welker JM, Zhao X, Team MOL (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecol Lett 10:619–627

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, van Bodegom P, Brovkin V, Chatain A, Callaghan TV, Díaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB, Soudzilovskaia NA, Vaieretti MV, Westoby M (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol Lett 11:1065–1071

Crow SE, Lajtha K, Filley TR, Swanston CW, Bowden RD, Caldwell BA (2009) Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. Glob Chang Biol 15:2003–2019

Cusack DF, Chou WW, Yang WH, Harmon ME, Silver WL, The LIDET Team (2009) Controls on long-term root and leaf litter decomposition in neotropical forests. Glob Chang Biol 15:1339–1355

Dijkstra FA, Cheng WX (2007) Interactions between soil and tree roots accelerate long-term soil carbon decomposition. Ecol Lett 10:1046–1053

Ekschmitt K, Liu M, Vetter S, Fox O, Wolters V (2005) Strategies used by soil biota to overcome soil organic matter stability—why is dead organic matter left over in the soil? Geoderma 128:167–176

Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–280

Fortunel C, Garnier E, Joffre R, Kazakou E, Quested H, Grigulis K, Lavorel S, Ansquer P, Castro H, Cruz P, Doležal J, Eriksson O, Freitas H, Golodets C, Jouany C, Kigel J, Kleyer M, Lehsten V, Lepš J, Meier T, Pakeman R, Papadimitriou M, Papanastasis VP, Quétier F, Robson M, Sternberg M, Theau J-P, Thébault A, Zarovali M (2009) Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. Ecology 90:598–611

Fox O, Vetter S, Ekschmitt K, Wolters V (2006) Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. Soil Biol Biochem 38:1353–1363

Frey SD, Knorr M, Parrent JL, Simpson RT (2004) Chronic nitrogen enrichment affects the structure and function of the soil microbial community in temperate hardwood and pine forests. For Ecol Manag 196:159–171

Galvana P, Ponge J-F, Chersicha S, Zanellad A (2008) Humus components and soil biogenic structures in Norway spruce ecosystems. Soil Sci Soc Am J 72:548–557

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Glob Chang Biol 6:751–765

Goebel M-O, Woche SK, Bachmann J (2009) Do soil aggregates really protect encapsulated organic matter against microbial decomposition? Biologia 64:443–448

Grandy AS, Neff JC (2008) Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. Sci Total Environ 404:297–307

Grayston SJ, Prescott CE (2005) Microbial communities in forest floors under four tree species in coastal British Columbia. Soil Biol Biochem 37:1157–1167

Hagedorn F, Spinnler D, Siegwolf R (2003) Increased N deposition retards mineralization of old soil organic matter. Soil Biol Biochem 35:1683–1692

Harmon ME, Silver WL, Fasth B, Chen H, Burke IC, Parton WJ, Hart SC, Currie WS, LIDET (2009) Long-term patterns of mass loss during decomposition of leaf and fine root litter: an intersite comparison. Glob Chang Biol 15:1320–1338

Heim A, Schmidt MWI (2006) Lignin turnover in arable soil and grassland analysed with two different labelling approaches. Eur J Soil Sci 58:599–608

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol Monogr 66:503–522

Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137:253–268

Johnson DW (1992) Effects of forest management on soil carbon storage. Water Air Soil Pollut 64:83–120

Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. For Ecol Manag 140:227–238

Kampichler C, Bruckner A (2009) The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. Biol Rev 84:375–389

Kazakou E, Vile D, Shipley B, Gallet C, Garnier E (2006) Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. Funct Ecol 20:21–30

Knorr M, Frey SD, Curtio PS (2005) Nitrogen additions and litter decomposition: a meta analysis. Ecology 86: 3252–3253

Kogel-Knabner I (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biol Biochem 34:139–162

Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. Soil Biol Biochem 32:1485–1498

Lauenroth WK, Gill R 2003 Turnover of root systems. In: de Kroon H, Visser EJW (eds) Root ecology. Ecological studies 168. Springer, Berlin, pp 61–89

Lindedam J, Magid J, Poulsen P, Luxhøi J (2009) Tissue architecture and soil fertility controls on decomposer communities and decomposition of roots. Soil Biol Biochem 41:1040–1049

Malkonen E, Kukkola M (1991) Effect of long-term fertilization on the biomass production and nutrient status of Scots pine stands. Fertil Res 27:113–127

McTiernan KB, Coûteaux M-M, Berg B, Berg MP, Calvo de Anta R, Gallardo A, Kratz W, Piussi P, Remacle J, Virzo De Santo A (2003) Changes in chemical composition of *Pinus sylvestris* needle litter during decomposition along a

European coniferous forest climatic transect. Soil Biol Biochem 35:801–812

Mori K, Bernier N, Kosakic T, Ponge J-F (2009) Tree influence on soil biological activity: what can be inferred from the optical examination of humus profiles? Eur J Soil Biol 45:290–300

Nave LE, Vance ED, Swanston CW, Curtis PS (2009) Impacts of elevated N inputs on north temperate forest soil C storage, C/N, and net N-mineralization. Geoderma 153:231–240

Neff JC, Townsend R, Glexner G, Lehmann SJ, Turnbull J, Bowman WD (2002) Variable effect of nitrogen additions on stability and turnover of soil carbon. Nature 419: 915–917

Nohrstedt H-O (1992) Soil chemistry in a *Pinus sylvestris* stand after repeated treatment with two types of ammonium nitrate fertilizer. Scand J For Res 7:457–462

Norby RJ, Cotrufo MF (1998) A question of litter quality. Nature 396:17–18

Olsson P, Linder S, Giesler R, Hogberg P (2005) Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. Glob Chang Biol 11:1745–1753

Osler GHR, Sommerkorn M (2007) Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 88: 1611–1621

Ponge J-F (1991) Succession of fungi and fauna during decomposition of needles in a small area of Scots pine litter. Plant Soil 138:99–113

Powers JS, Montgomery RA, Adair EC, Brearley FQ, DeWalt SJ, Castanho CT, Chave J, Deinert E, Ganzhorn JU, Gilbert ME, González-Iturbe JA, Bunyavejchewin S, Grau HR, Harms KE, Hiremath A, Iriarte-Vivar S, Manzane E, de Oliveira AA, Poorter L, Ramanamanjato J-B, Salk C, Varela A, Weiblen GD, Lerdau MT (2009) Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. J Ecol 97:801–811

Prescott CE, Zabek LM, Staley CL, Kabzems R (2000) Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type and litter mixtures. Can J For Res 30:1742–1750

Prescott CE, Vesterdal L, Simard SW, Preston CM (2004) Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Can J For Res 34:1714–1729

Preston CM, Trofymow JA, Sayer BG, Niu J (1997) ^{13}C nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning investigation of the proximate analysis fractions used to assess litter quality in decomposition studies. Can J Bot 75:1601–1613

Rasse DP, Rumpel C, Dignac M-F (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilization. Plant Soil 269:341–356

Rawlins AJ, Bull ID, Poirier N, Ineson P, Evershad RP (2006) The biochemical transformation of oak (*Quercus robur*) leaf litter consumed by the pill millipede (*Glomeris marginata*). Soil Biol Biochem 38:1063–1076

Rawlins AJ, Bull ID, Ineson P, Evershad RP (2007) Stabilisation of soil organic matter in invertebrate fæcal pellets through leaf litter grazing. Soil Biol Biochem 39: 1202–1205

Resh SC, Binkley D, Parrotta JA (2002) Greater soil carbon sequestration under nitrogen-fixing trees compared with Eucalyptus species. Ecosystems 5:217–231

Rothwell JJ, Futter MN, Dise NB (2008) A classification and regression tree model of controls on dissolved inorganic nitrogen leaching from European forests. Environ Pollut 156:544–552

Sanborn PT, Brockley RP (2009) Decomposition of pure and mixed foliage litter in a young lodgepole pine—Sitka alder stand in the central interior of British Columbia. Can J For Res 39:2257–2262

Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. Ecology 85:591–602

Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129:407–419

Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74:65–105

Strickland MS, Osburn E, Lauber C, Fierer N, Bradford MA (2009) Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculums characteristics. Funct Ecol 23:627–636

Swanston C, Homann PS, Caldwell BA, Myrold DD, Ganio L, Sollins P (2004) Long-term effects of elevated nitrogen on forest soil organic matter stability. Biogeochemistry 70: 227–250

Taylor BR, Prescott CE, Parsons WFJ, Parkinson D (1991) Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Can J Bot 69:2242–2250

Trofymow JA, Moore TR, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, Camiré C, Duschene L, Kozak L, Kranabetter M, Visser S (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can J For Res 32: 789–804

Turk TD, Schmidt MG, Roberts NJ (2008) The influence of bigleaf maple on forest floor and mineral soil properties in a coniferous forest in coastal British Columbia. For Ecol Manag 255:1874–1882

Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P (2008) Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For Ecol Manag 255:35–48

Vivanco L, Austin AT (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. J Ecol 96:727–736

von Lutzow M, Kogel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner B, Flessa H (2006) Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions—a review. Eur J Soil Sci 57:426–445

Waldrop MP, Firestone MK (2004) Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions. Biogeochemistry 67:235–248

Wardle DA (2006) The influence of biotic interactions on soil biodiversity. Ecol Lett 9:870–886

Wardle DA, Zackrisson O, Hörnberg G, Gallet C (1997) The influence of island area on ecosystem properties. Science 277:1296–1299

Wardle DA, Bardgett RD, Walker LR, Bonner KI (2009) Among- and within-species variation in litter decomposition in contrasting long-term chronosequences. Funct Ecol 23:442–453

Wolters V (2000) Invertebrate control of soil organic matter stability. Biol Fertil Soils 31:1–19

Zhang D, Hui D, Luo Y, Zhou G (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J Plant Ecol 1:1–9

Zhou G, Guan L, Wei X, Tang X, Liu S, Liu J, Zhang D, Yan J (2008) Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. Plant Soil 311:61–72