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OPINION

Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept

MICHAEL J. CASTELLANO[1], KEVIN E. MUELLER[2], DANIEL C. OLK[3], JOHN E. SAWYER[1] and JOHAN SIX[4]

[1]*Department of Agronomy, Iowa State University, Ames, IA 50011, USA,* [2]*United States Department of Agriculture, Agricultural Research Service, Rangeland Resources Research Unit, Ft. Collins, CO 80526, USA,* [3]*United States Department of Agriculture, Agricultural Research Service, National Laboratory for Agriculture and the Environment, Ames, IA 50011, USA,* [4]*Department of Environmental Systems Science, Swiss Federal Institute of Technology, ETH-Zurich, Zurich CH 8092, Switzerland*

Abstract

Labile, 'high-quality', plant litters are hypothesized to promote soil organic matter (SOM) stabilization in mineral soil fractions that are physicochemically protected from rapid mineralization. However, the effect of litter quality on SOM stabilization is inconsistent. High-quality litters, characterized by high N concentrations, low C/N ratios, and low phenol/lignin concentrations, are not consistently stabilized in SOM with greater efficiency than 'low-quality' litters characterized by low N concentrations, high C/N ratios, and high phenol/lignin concentrations. Here, we attempt to resolve these inconsistent results by developing a new conceptual model that links litter quality to the soil C saturation concept. Our model builds on the Microbial Efficiency-Matrix Stabilization framework (Cotrufo *et al.*, 2013) by suggesting the effect of litter quality on SOM stabilization is modulated by the extent of soil C saturation such that high-quality litters are not always stabilized in SOM with greater efficiency than low-quality litters.

Keywords: decomposition, litter, mineralization, nitrogen, residue

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Introduction

Soils are the largest global pool of actively cycling organic C and N. Maintaining and increasing soil organic matter (SOM) is a prominent strategy for mitigating atmospheric CO_2 and adapting agriculture to climate change (Walthall *et al.*, 2012). As a result, effective climate change mitigation and adaptation strategies will be based in part on processes that promote SOM stabilization.

Plant litter is the primary source of all SOM. However, the processes of litter decomposition and SOM stabilization are often considered separate (Sollins *et al.*, 2007). Litter decomposition research has focused on the effects of litter quality on short-term mineralization and nutrient release (Parton *et al.*, 2007), whereas SOM stabilization research has focused on organomineral interactions that slow SOM turnover relative to total SOM due to physicochemical protection by mineral association and microaggregate occlusion (Six *et al.*, 2002; von Lützow *et al.*, 2008; Stewart *et al.*, 2008a).

To understand, model, and manage the response of SOM to global environmental change, litter decomposition must be linked to SOM stabilization (Prescott, 2010; Dungait *et al.*, 2012). However, recent attempts to link these processes may have reinforced their separation by suggesting that (1) low-quality litters (i.e., litters characterized by low substrate quality due to the molecular structure or elemental composition of its components) are not selectively preserved in physicochemically stabilized SOM; (2) most physicochemically stabilized SOM is derived from microbial residues; and (3) litter quantity rather than quality is the main determinant of the amount of physicochemically stabilized SOM (Grandy & Neff, 2008; Gentile *et al.*, 2011; Carrington *et al.*, 2012; Dungait *et al.*, 2012). Coupled with evidence that abiotic condensation reactions are minor contributors to SOM stabilization (Kleber & Johnson, 2010), these findings have led to the view that environmental and biological controls operating within the mineral soil matrix dominate SOM stabilization rather than the quality (i.e., molecular structure or elemental composition) of litter or microbial residues (Kogel-Knabner, 2002).

Nevertheless, it remains widely accepted that litter quality can affect SOM stabilization. For example, in contemporary ecosystem models, litter quality is an important control on the mean residence time of SOM (Wieder *et al.*, 2014a). Yet, there is uncertainty about when, where, and how litter quality affects SOM stabilization. The role of litter quality may vary across stable

Correspondence: Michael J. Castellano,
tel. 515-294-3963, fax 515-294-3163,
e-mail: castellanomichaelj@gmail.com

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SOM pools that differ by the source of organic matter (plant vs. microbial residues) and the mechanism of stabilization (physical, chemical, and biochemical protection; Six *et al.*, 2002).

To link litter decomposition with SOM stabilization in the mineral soil matrix, Cotrufo *et al.* (2013) developed the Microbial Efficiency-Matrix Stabilization (MEMS) framework. The framework is based on the principles that (1) mineral association is the most effective means of SOM stabilization (Six *et al.*, 2002; von Lützow *et al.*, 2006) and (2) most mineral-stabilized SOM is of microbial origin and thus suggests plant litter quality can affect the rate of SOM stabilization by affecting microbial biomass and substrate use. Plant litters that produce more microbial residues result in more organic matter that can be physicochemically stabilized (i.e., more SOM stabilization opportunities). When microbial substrate use is high (high-quality litters), the microbial anabolism: catabolism ratio is high. As a result, more microbial residues and less CO_2 are produced per amount of plant litter metabolized and stable SOM stocks are predicted to be relatively large. In contrast, when substrate use is low (low-quality litters), microbial biomass is relatively low and fewer microbial residues are produced per amount of plant litter metabolized. As a result, stable SOM stocks are predicted to be relatively small.

Consistent with this conceptualization of plant litter effects on SOM stabilization, mineral nutrient additions including N fertilizer can also enhance microbial biomass and microbial use efficiency of plant litter, thereby increasing the transfer of plant litter to total SOM and physicochemically stabilized SOM (Ågren *et al.*, 2001; Schimel & Weintraub, 2003; Moran *et al.*, 2005; Thiet *et al.*, 2006; Kirkby *et al.*, 2013). Mineral nutrient additions can alter litter quality after plant uptake (Brown *et al.*, 2014) or can be directly accessed by microbes during decomposition (Kirkby *et al.*, 2013). Presumably, both of these effects of mineral nutrient additions increase litter transformation to SOM by better matching microbe and substrate stoichiometries (Kirkby *et al.*, 2013).

Within the MEMS framework, the amount of microbial residue stabilization is ultimately determined by physicochemical protection mechanisms operating within the mineral soil matrix. Thus, litter quality should have no effect on the stable SOM stocks or the rate of SOM stabilization when a soil has no additional capacity for SOM stabilization (i.e., when soil is C-saturated). Indeed, some studies report an effect of litter quality on total and/or physicochemically stabilized SOC pool size or the litter-C to SOM-C conversion rate, while others do not (Table 1).

Here, we describe an easily testable conceptual model that can resolve the inconsistent effects of litter quality on mineral-stabilized SOM by linking MEMS to the soil C saturation concept (Hassink & Whitmore, 1997; Six *et al.*, 2002). Our model expands the matrix stabilization component of MEMS by separating the chemically stabilized mineral-associated SOM pool that is dominated by microbial residues from particulate SOM pools that are dominated by plant residues and either physically stabilized by microaggregate occlusion or nonprotected (i.e., not physicochemically stabilized within the mineral soil matrix; Six *et al.*, 2002). We suggest that the effect of litter quality on mineral-associated SOM is a function of the unsatisfied C storage potential (i.e., the C saturation deficit) such that (1) litter quality should affect mineral-associated SOM stocks only when there is a saturation deficit (i.e., litter quality should not affect mineral-associated SOM in C-saturated soils) and (2) the capacity to store additional mineral-associated SOM in soils receiving high-quality litters will saturate at a lower litter input rate than soils receiving low-quality litters. This second feature is important because it allows for situations when comparative studies could measure greater stabilization of low- vs. high-quality litters.

Our model focuses on SOM that is stabilized by mineral association because, in most soils and particularly arable land soils, this pool comprises the majority of SOM and is dominated by microbial residues (e.g., Kirchmann *et al.*, 2004; Miltner *et al.*, 2012; Plaza *et al.*, 2013). However, we explicitly explore situations when plant residues could account for a substantial portion of SOM pools. In particular, we relate our model to nonprotected and microaggregate-stabilized particulate SOM as well as situations when plant residues are proportionally large contributors to mineral-associated SOM.

With the concepts developed herein, we intend to provoke new experimentation and discussion rather than provide an accurate numerical framework for predicting SOM stabilization based on litter quality. To this end, we suggest future approaches to test our concepts and we explore potential limitations of a framework based on microbial substrate use and stabilization of microbial residues via organomineral interactions.

The soil carbon saturation concept

A growing body of evidence from a diverse array of ecosystems indicates that soils have a finite capacity to store C within relatively stable pools in the mineral soil matrix. Further, the unsatisfied capacity for stable C storage affects the ability of soils to retain new litter inputs in stable SOC (Hassink, 1997; Huggins *et al.*,

Table 1 Summary of literature that has examined the effect of litter quality (or other biological compounds) on soil organic carbon (SOC) in mineral (i.e., nonorganic) soils. Only reports that added similar amounts of different quality litters are included; we define 'similar' as <10% difference in mass addition across litter qualities. Reports that compared litter quality effects across treatments with great differences in the amount of litter inputs and then scaled change in SOC to litter input (ΔSOC/litter-C input) are not included because differences in litter amount affect environmental controls on litter decomposition and SOC stabilization (e.g., temperature and moisture). Only reports that measured a significant change in SOC or transfer of isotopically labeled litter to SOC are included to avoid reports that lacked statistical power

Study	Method*	Setting	Effect of litter quality on total SOC?	Range of C addition converted to total SOC (%)	Effect of litter quality on mineral-associated SOC?	Range of C addition converted to mineral-associated SOC (%)	Effect of litter quality on aggregate-occluded SOC?	Range of C addition converted to aggregate-occluded SOC (%)	Study duration (years)
Beyaert & Voroney (2011)†	1	Field	No	5.9–7.1	N/A	N/A	N/A	N/A	15
Bird *et al.* (2008)‡	1	Field	No	18–18	N/A	N/A	N/A	N/A	1.6
Bradford *et al.* (2013)	2	Field	Yes	10–25	Yes	6–18	N/A	N/A	0.54
Gentile *et al.* (2011)	1	Laboratory	No	18–21	Yes	0.85–1.3	Yes	4.7–6.5	1.5
Gentile *et al.* (2011)	3	Field	No	N/A	No	N/A	No	N/A	3.0
Helfrich *et al.* (2008)	1	Laboratory	No	N/A	No	4–9	No	8–13	0.23
Kirchmann *et al.* (2004)	3	Field	Yes	16–28	Yes	16–26	N/A	N/A	42
Rubino *et al.* (2007)	1	Laboratory	No	0–22	N/A	N/A	N/A	N/A	0.66
Throckmorton *et al.* (2012, 2015)§	2	Field	No	20–30	No	N/A	No	N/A	3.1
Throckmorton *et al.* (2012, 2015)§	2	Field	Yes	3–12	No	N/A	No	N/A	2.4
Vityakon *et al.* (2000)§	3	Field	No	10–16	N/A	N/A	N/A	N/A	1.0
Vityakon *et al.* (2000)§	3	Field	Yes	8–33	N/A	N/A	N/A	N/A	1.0
Puttaso *et al.* (2013)	4	Field	Yes	N/A	Yes	N/A	Yes	N/A	13
Voroney *et al.* (1989)	1,2	Field	Yes	14–16	No	N/A	N/A	N/A	7
Wuest & Gollany (2012)	4	Field	Yes	N/A	N/A	N/A	N/A	N/A	8.0

*(1) Isotopically labeled litter traced into SOC. (2) Isotopically labeled biocompounds traced into SOC. (3) Difference in rate of SOC change across litter quality treatments. (4) Difference in total SOC across litter quality treatments after litter additions (ranges of litter-C addition converted to SOC are not available with method 4).

†Soybean and wheat litters in conventional tillage were compared due to similar inputs (142 vs. 149 g C m^{-2}). Other litters were excluded due to large differences in input (15–400%).

‡Litter quality had a significant effect on the alkaline-extracted humic fraction.

§These experiments added different quality litters to two different soils and found an effect of litter quality on SOC in one soil, but not another.

N/A = not available.

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1998; Six *et al.*, 2002; Stewart *et al.*, 2007, 2008a; Chung *et al.*, 2008; Heitkamp *et al.*, 2012). When SOC pools that are physicochemically stabilized in mineral matrices can no longer increase in size, soils are considered 'C-saturated'. At this point, an increase in steady-state C input rate does not increase steady-state physicochemically stabilized SOC. Alternatively, when an increase in steady-state C input rate does increase steady-state physicochemically stabilized SOC, soils have an unsatisfied capacity to store C that is referred to as the '*saturation deficit*' (Hassink, 1997; Stewart *et al.*, 2007). A soil with no physicochemically stabilized SOC has a saturation deficit of 100%, while a soil that is C-saturated has a saturation deficit of zero. New C inputs can be stored in physicochemically stabilized SOC only when there is a saturation deficit.

Importantly, the C saturation concept is independent from management and climate – C saturation is the theoretical maximum C stabilization potential under optimum conditions. However, an 'effective' soil C saturation can be observed at lower levels of SOC due to limitations on SOC stabilization imposed by management and climate (Stewart *et al.*, 2007). In fact, soils that are considered to be severely depleted in SOC can be 'effectively' C-saturated (Stewart *et al.*, 2007). For example, annually cultivated soil can be effectively C-saturated if an increase in steady-state C inputs does not produce a concomitant increase in steady-state physicochemically stabilized SOC without a change in management or climate (Chung *et al.*, 2008; Gulde *et al.*, 2008; Brown *et al.*, 2014). Thus, '*effective C saturation*' represents the capacity for physicochemical SOC stabilization under a particular set of management and climate circumstances that do not maximize potential physicochemical SOC stabilization.

Effective C saturation can be empirically identified by experiments that increase C inputs to a soil that has been previously observed to have unchanged physicochemically stabilized SOC contents over a time period with similar C inputs and management: If an increase in C inputs does not increase physicochemically stabilized SOC over time, the soil is considered to be effectively C-saturated under that specific management and climate. Effective C saturation can also be inferred from experimental gradients of C inputs to identically managed soils (Chung *et al.*, 2008; Gulde *et al.*, 2008): If instantaneous measures of physicochemically stabilized SOC across the input gradient reveal a lack of difference in physicochemically stabilized SOC stocks, the soil may be effectively C-saturated (although it is also possible that SOC could be increasing or decreasing at similar rates despite different C inputs).

Evidence is strong for effective C saturation of relatively stable, slow-turnover SOC pools that are physicochemically protected from mineralization (Chung *et al.*, 2008; Gulde *et al.*, 2008; Stewart *et al.*, 2008b; Brown *et al.*, 2014). These stable pools are protected from mineralization through chemical association with fine mineral particles and physical occlusion in microaggregates (Jastrow *et al.*, 1996; Mueller & Koegel-Knabner, 2009). In contrast to physicochemically stabilized SOC pools, evidence for saturation of nonprotected SOC pools is weak (Gulde *et al.*, 2008; Brown *et al.*, 2014). Nonprotected SOC, commonly measured as 'light fraction' and 'free particulate organic matter', is not physicochemically protected within the mineral soil matrix and has mean residence times that are typically lower than physicochemically stabilized SOC (Six *et al.*, 2002).

Evidence for saturation of physicochemically stabilized SOC pools, but not relatively labile nonprotected SOC pools, led to the development of a two-pool model for C saturation that includes a stable slow-turnover SOC pool that exhibits saturation behavior and a relatively labile fast-turnover SOC pool that does not exhibit saturation behavior (Stewart *et al.*, 2007; Fig. 1). This model can be operationally defined such that plant litter is decomposed to the point that it is <2 mm and thus enters the labile nonprotected SOC pool, which is dominated by plant residues that are not physicochemically stabilized (i.e., nonprotected SOC). Decomposition products from the labile nonprotected SOC pool are then transferred to the physicochemically stabilized SOC or mineralized. As C inputs increase, SOC in the physicochemically stabilized pool asymptotically increases to a maximum (i.e., saturation; Fig. 1). Saturation of the physicochemically stabilized pool with increasing steady-state litter-C inputs is conceptually fit by the equation

$$y = a(1 - e^{-bx}) \tag{1}$$

where y = physicochemically stabilized soil C stock; a = maximum C storage; b = rate constant for litter-C to physicochemically stabilized SOC conversion (i.e., storage efficiency of inputs); and x = C inputs. A consequence of this relationship, which has been empirically demonstrated, is that the saturation deficit directly affects the kinetics of SOM stabilization (Stewart *et al.*, 2008a; Castellano *et al.*, 2012). The stabilization efficiency of new litter inputs from nonprotected SOC declines in proportion to the amount of physicochemically stabilized SOC already present such that the proportion of new litter inputs transferred to the physicochemically stabilized SOC pool declines exponentially as the physicochemically stabilized SOC pool approaches C saturation. New litter inputs not transferred to the physicochemically stabilized SOC pool accumulate in the nonprotected SOC pool or are mineralized. Because the nonprotected SOC pool is

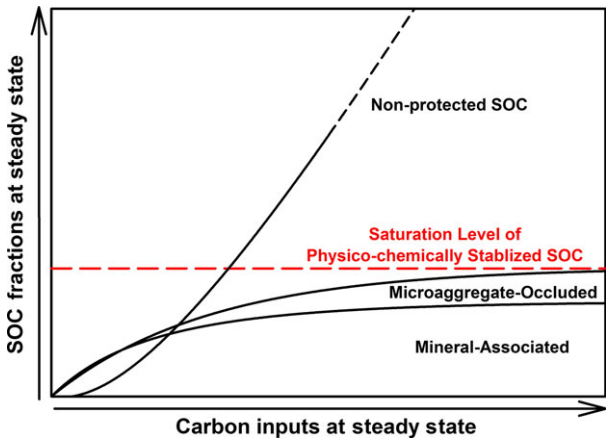

Fig. 1 Theoretical steady-state relationships between carbon (C) inputs, physicochemically stabilized soil organic carbon (SOC) fractions, and the nonprotected SOC fraction (adapted from Stewart *et al.*, 2007). In our conceptualization, stable SOC fractions are subdivided into two pools that are both known to exhibit saturation behavior: mineral associated and microaggregate occluded (including free microaggregates and microaggregates within macroaggregates). Consistent with hierarchical C saturation theory (Kool *et al.*, 2007), the mineral-associated fraction is larger and saturates before the microaggregate-occluded fraction. In this model, the nonprotected SOC fraction includes nonprotected particulate organic C fractions that are not occluded within microaggregates and are recognized as plant litter but operationally defined as SOC because they are <2 mm. This fraction includes free particulate organic C and particulate organic C within macroaggregates, but not particulate organic C within microaggregates. Evidence for saturation of mineral-associated and microaggregate-occluded C fractions is strong (Gulde *et al.*, 2008; Brown *et al.*, 2014). In contrast, evidence shows that the nonprotected SOC fraction (<2 mm) linearly increases with C inputs (Gulde *et al.*, 2008; Brown *et al.*, 2014). Nevertheless, there is evidence that nonprotected SOC fractions can saturate at high C inputs exceeding potential net primary production (e.g., >45 Mg C ha^{-1} y^{-1}; Campbell *et al.*, 1991; Janzen *et al.*, 1992); thus, we have extrapolated the nonprotected SOC pool as a dashed line.

dominated by plant residues, we conceptualize the nonprotected pool as litter rather than SOC. This conceptualization is consistent with our focus on relationships between plant litter quality, plant litter input rate, and the amount of physicochemically stabilized SOC in the mineral soil matrix.

Linking litter quality and carbon saturation

Model development

As litter quality can affect SOM stabilization by affecting the production of microbial residues, so should any environmental or physicochemical process that affects the stabilization of microbial residues in SOM. For example, litter quality should not affect physicochemically stabilized SOM in C-saturated or effectively C-saturated soils because the physicochemical process of C saturation limits SOM stabilization. However, the two-pool model of C saturation suggests a much more dynamic relationship among litter quality and SOM stabilization because litter quality affects the production of microbial residues that are available for stabilization, while saturation deficit affects the kinetics of and capacity for microbial residue stabilization.

We propose that the effect of litter quality on mineral-associated SOM stabilization is a function of the saturation deficit in stable mineral-associated SOM pools. We describe this relationship through a conceptual model that explicitly considers the effects of litter quality and C saturation deficit on mineral-associated SOM. In our conceptual model shown in Fig. 2 and described below, we refer to the effect of litter quality on mineral-associated SOC stocks at equilibrium (i.e., steady state).

At equal rates of high- and low-quality litter inputs, a soil receiving high-quality litter will always have a greater mineral-associated SOC stock and smaller saturation deficit (lower SOC stabilization potential). As a result, high-quality litters will not necessarily have a greater litter-C to mineral-associated SOC conversion rate because the conversion of high-quality litter to mineral-associated SOC is more limited by C saturation deficit than the conversion of low-quality litter to mineral-associated SOC.

Figure 2 displays mineral-associated SOC as function of litter inputs for high- and low-quality litters. In this figure, initial litter-C to mineral-associated SOC conversion rate for high-quality litter is 100% greater than that of low-quality litter. However, with an increase in mineral-associated SOC due to an increase in litter inputs, the difference in litter-C to mineral-associated SOC conversion rates between litter qualities decreases until they are equal (Fig. 2b). At this point, the difference in mineral-associated SOC stock between litter qualities is maximized (Fig. 2a). Beyond this point, the litter-C to mineral-associated SOC conversion rate of low-quality litters is greater than the litter-C to mineral-associated SOC conversion rate of high-quality litters (Fig. 2b) because mineral-associated SOC in the soil receiving high-quality litters is closer to saturation despite equal litter inputs (Fig. 2a). In other words, the soil receiving low-quality litter has a greater saturation deficit and thus a greater litter-C to mineral-associated SOC conversion rate beyond this point.

In summary, at extremely large saturation deficits (low total SOM), the effect of litter quality on steady-state mineral-associated SOM is small because the

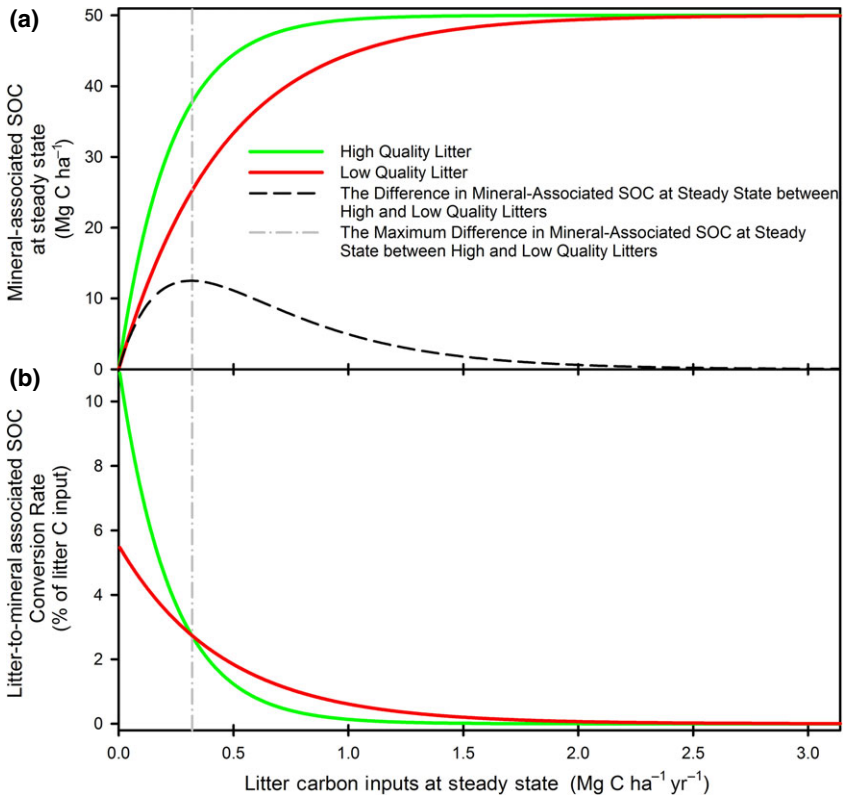

Fig. 2 (a) Hypothetical relationships between carbon (C) input level and mineral-associated soil organic carbon (SOC) stocks at steady state for two litters that differ in quality. (b) The proportion of litter C that is converted to mineral-associated SOC pools. The maximum difference in steady-state mineral-associated SOC stocks is coincident with the point at which litter-C to mineral-associated SOC conversion rates are equal for the two litter qualities.

conversion of litter-C to mineral-associated SOC is high – independent of litter quality. As litter-C input and mineral-associated SOC increase, however, the effect of litter quality on steady-state mineral-associated SOC grows until the soil receiving high-quality litter reaches saturation at a lower rate of litter input than an identical soil receiving the same input of low-quality litter (Fig. 2a). Thus, with increasing litter input, there is a greater decrease in the capacity for (Fig. 2a) and kinetics of (Fig. 2b) SOM stabilization in the soil receiving high-quality litter. As a result, the litter-C to mineral-associated SOC conversion rate of high-quality litters becomes lower than the litter-C to mineral-associated SOC conversion rate of low-quality litters as the rate of litter input increases and soils approach C saturation. However, at all times before saturation, soils receiving high-quality litters have greater mineral-associated SOC pools (Fig. 2a).

Model evaluation

This link between C saturation and MEMS (Fig. 2) suggests three testable hypotheses: (1) Litter quality should affect mineral-associated SOM stocks only when there is a saturation deficit; (2) the effect of litter quality on mineral-associated SOM stocks should be most easily observed at moderate saturation deficits; and (3) the relative difference in litter-C to mineral-associated SOM-C conversion rates between different quality litters is a function of saturation deficit and will not always be greater for high-quality litters (Fig. 2).

The first prediction can be indirectly evaluated with published literature. In some soils, an increase in C inputs does not increase total and/or physicochemically stabilized SOC stocks, indicating that the soils are near or at C saturation (e.g., Huggins *et al.*, 1998; Reicosky *et al.*, 2002; Gulde *et al.*, 2008). In these situations, our model predicts that litter quality should have no effect on SOM stocks. Coincident with this prediction, some studies that compare total SOC or physicochemically stabilized SOC across treatments receiving identical input rates of different quality litters find no effect of litter quality on SOC stock or litter-C to SOM-C conversion rates (Table 1).

We hypothesize that some of these soils are C-saturated. For example, Vityakon *et al.* (2000) found a

significant effect of litter quality on total SOC stock in an upland ultisol, but not a lowland ultisol. Both soils received identical litter qualities at identical input rates, but the lowland ultisol had ~25% more SOC at initial conditions. Although this study did not separate physicochemically stabilized SOM, it is possible that nonprotected SOC in the lowland ultisol was also saturated (Fig. 1). In a field study with identical litter input rates but different litter qualities, Gentile *et al.* (2011) found no effect of N fertilizer, litter quality, or their interaction on physicochemically stabilized SOM pools. Similarly, across a 13-year N fertilizer input gradient where the C/N ratio of litter inputs decreased by >20% from zero N to the highest N fertilizer input, Brown *et al.* (2014) found no differences in physicochemically stabilized SOC pools. Although differences in litter-C input prohibited inclusion of this report in Table 1, litter-C inputs increased as litter C/N ratio decreased and all litter was incorporated in mineral soil via intensive tillage.

Nevertheless, more research is required because the lack of litter quality effects on total and/or physicochemically stabilized SOC stock could be due to (1) a true lack of litter quality effect on the size of physicochemically stabilized SOC stocks; (2) a lack of statistical power to detect an effect of litter quality on physicochemically stabilized SOC stocks (Kravchenko & Robertson, 2011); or (3) C saturation dynamics (Fig. 2). Moreover, few field experiments have explicitly investigated the effect of litter quality on physicochemically stabilized SOM pools (Table 1).

Robust tests of all three model predictions require a fully factorial experiment that modulates litter quality, litter amount, and C saturation deficit. This experimental framework could use two approaches. First, a direct approach can be used where physicochemically stabilized SOM is compared across a soil that is treated with the same mass of different quality litter inputs (i.e., identical masses of litter C that differ only in quality are applied to replicated plots). Preferably, the change in physicochemically stabilized SOM is measured over time within plots to test for steady-state assumptions. Second, an indirect approach can be used where the change in physicochemically stabilized SOM storage is compared between different crop systems that vary in quantity and quality of litter inputs (e.g., wheat vs. corn or maple vs. oak; Drinkwater *et al.*, 1998). In this case, litter-C to SOM-C conversion rates are compared among treatments to control for differences in mass of C inputs (i.e., ΔSOC/mass litter-C input is compared). The first approach is highly preferable because differences in plant structure/physiognomy and mass of litter-C inputs can have a greater effect on SOM stabilization than litter quality by altering other factors that influence SOM stabilization such as water availability and temperature (Manzoni *et al.*, 2012; Wieder *et al.*, 2014b). Existing organic matter input gradients could be used to provide a saturation deficit gradient.

The role of plant residues and microaggregate occlusion

Current evidence suggests microbial residues in mineral-associated SOM account for the majority of SOM in most soils (e.g., Kirchmann *et al.*, 2004; Miltner *et al.*, 2012; Plaza *et al.*, 2013). However, plant residues can directly contribute to stable mineral-associated and microaggregate-occluded SOM pools as well as SOM pools that are not physicochemically stabilized (i.e., nonprotected particulate SOM that may or may not be biochemically recalcitrant). Our model and MEMS, which are based on the assumption that most SOM is comprised of microbial residues stabilized in the mineral soil matrix, may or may not be effective in these different situations.

In nutrient-poor soils, mineral-associated SOM pools can contain large amounts of plant-derived aromatic, polyphenolic, and aliphatic compounds (Gillespie *et al.*, 2013; Sanderman *et al.*, 2014). In these situations, depolymerized plant compounds appear to be stabilized on or near mineral surfaces. If depolymerization and retention of these relatively low-quality biopolymers is proportional with their concentration in litter, high-quality litters could result in lower stabilization of plant compounds via mineral surfaces as compared to low-quality litters. However, if depolymerization of plant biopolymers proceeds more rapidly or completely when concentrations of litter nutrients or cell solubles are higher (Klozbucher *et al.*, 2011; Talbot *et al.*, 2012), then high-quality litters could result in similar or greater release of plant compounds and retention near mineral surfaces, despite lower concentrations of these plant biopolymers. In these situations, effective C saturation levels are likely to be far lower than absolute C saturation levels because nutrient availability limits SOM stock (Six *et al.*, 2002).

In contrast to mineral-associated SOM which is considered as dominated by microbial residues in most soils, microaggregate-occluded SOM is dominated by plant residues and microaggregate-occluded SOM pools can have mean residence times exceeding mineral-associated SOM (Jastrow *et al.*, 1996; Mueller & Koegel-Knabner, 2009). However, controls on the pool size of microaggregate-occluded SOM are complex. It is hypothesized that the pool size of microaggregate-occluded SOM is the result of a Gaussian function of aggregate turnover rate (Plante & Mcgill, 2002). At moderate turnover rates, the microaggregate-occluded SOM pool is maximized. Thus, changes in aggregate

turnover may increase or decrease the pool of microaggregate-occluded SOM, thereby altering the C saturation deficit (Plante & Mcgill, 2002). Recent evidence suggests high-quality litters hasten short-term aggregate turnover (Chivenge *et al.*, 2011a,b; Puttaso *et al.*, 2013). However, longer duration studies find that litter quality has little effect on microaggregate-occluded SOM pools (Chivenge *et al.*, 2011a,b; Puttaso *et al.*, 2013). In the future, it will be important to separate short-term litter quality effects on aggregate turnover from relatively long-term effects of litter quality on pools of microaggregate-occluded SOM. Nevertheless, high-quality litters increase microbial biomass, and microbial residues are widely considered to be an important contributor to the amount of microaggregate-occluded SOM (Guggenberger *et al.*, 1999; Ludwig *et al.*, 2015). If high-quality litters, through their effect on microbial residue production, enhance microaggregate abundance and stability, our model should apply to the pool of microaggregate-occluded SOM despite the dominance of plant residues in this SOM pool.

In some ecosystems, plant residues that are not stabilized by microaggregate occlusion or mineral association (i.e., nonprotected SOM) can account for a significant proportion of total SOM. When plant residues in nonprotected SOM are proportionally large contributors to total SOM, high-quality litters may not lead to greater SOM. In some sandy soils, nonprotected SOM fractions can account for >50% of total SOC (e.g., Liao *et al.*, 2006; Zeller & Dambrine, 2011). In these soils, shifts toward plant communities that produce more phenolic lignin residues or cutin- and suberin-derived plant compounds can significantly increase total SOM, apparently through enhanced biochemical recalcitrance (Filley *et al.*, 2008; Gaiser *et al.*, 2011; Carrington *et al.*, 2012; Creamer *et al.*, 2012). Across C saturation gradients, the contribution of these compounds to nonprotected SOM fractions has been shown to increase as a proportion of the fraction and in total mass (Carrington *et al.*, 2012). These results are consistent with the concepts that biochemical recalcitrance can be an important mechanism of SOM stabilization and nonprotected SOM pools dominated by plant residues may not saturate (Fig. 1).

Methodological challenges

Further evaluation of the linkages between litter quality and SOM stabilization requires a more accurate and complete characterization of the direct contributions of microbial- and plant-derived compounds to mineral-associated SOM and other relatively stable SOM pools. There are significant challenges to the characterization of SOM, including the inefficiency of extraction procedures and the accurate assignment of individual biomolecules to plant or microbial origins. Currently, the relative abundances of plant- and microbial-derived residues are often estimated through soil extraction and chromatographic analyses for specific monomers of carbohydrates, fatty acids, and phenols. The hemicellulosic carbohydrates, arabinose and xylose, are presumed to be largely of plant origin and galactose and mannose of largely microbial origin, so their ratios have been used to assess the balance of microbial- and plant-derived carbohydrates. Specific longer-chained fatty acids represent plant residues, while specific short-chained fatty acids are considered markers for microbial residues (Frostegard *et al.*, 1993; Jandl *et al.*, 2005; Mendez-Millan *et al.*, 2010). Syringyl, vanillyl, and cinnamic acid phenols measured by the standard CuO oxidation technique are widely considered to be derived from plant lignin (Kogel-Knabner, 2002).

Yet, evidence suggests incomplete extraction of all these compounds from soil, which could cause miscalculation of plant or microbial residue abundance. Hernes *et al.* (2013) could not extract >50% of mineral-associated lignin phenols from soil using the CuO technique. Fatty acid concentrations are normally considered as minor proportions of SOM when based on extraction/chromatography (Stevenson, 1994), but ^{13}C nuclear magnetic resonance spectroscopy has typically found about 25% of soil C to be aliphatic (Mahieu *et al.*, 1999). This aliphatic signal is conventionally assigned to fatty acids and other alkyl compounds, which are often presumed to be derived at least in part from plant lipids including cutans and cutins (Kogel-Knabner, 2002). Similarly, Song *et al.* (2008) and Simpson *et al.* (2007) described about half of all soil C that was found to be a mixture of plant and microbial components, including plant cutans and cutins. Accurate characterization of the source of stable SOM is required for accurate prediction of litter quality effects on stable SOM.

Conclusions

The interaction between litter quality and C saturation has significant potential to affect soil processes in managed and unmanaged ecosystems where the combination of climate change and ecological disturbances could lead to shifts in both litter quality and C saturation deficits. However, the incorporation of litter quality and C saturation concepts in numerical models requires a greater understanding of the relative importance of the many additional factors that regulate SOM stabilization. For example, plants that differ in litter quality frequently differ in litter production as well. And, as our concept model suggests (Equation 1 and Fig. 2), litter quantity likely has a larger effect on

steady-state stable SOM, particularly when C saturation deficits are large. Nevertheless, our concept model may be immediately useful for managing SOM stocks in agroecosystems because these ecosystems are more likely to contain SOM stocks dominated by mineral-associated SOM due to tillage and comprised of microbial residues due to high nutrient inputs and generally the high quality of agricultural crop residues. Moreover, agroecosystems account for a large fraction of land area that is relatively easily managed for litter quality and nutrient inputs.

To expand the role of the mineral soil matrix in the MEMS framework (Cotrufo *et al.*, 2013), our model unifies three key observations from recent literature related to SOM dynamics: (1) high-quality litters enhance microbial biomass, (2) microbial residues dominate relatively stable mineral-associated SOM, and (3) C saturation status affects the kinetics of SOM stabilization. Links among these observations lead to three testable hypotheses that can help to reconcile the effect of litter quality on stable SOC: (1) Litter quality should affect stable SOC storage only when there is a saturation deficit; (2) the effect of litter quality on stable SOC is most easily observed at moderate saturation deficits; and (3) the difference in litter-C to stable SOC conversion rates between litter qualities is a function of saturation deficit and not necessarily greater for high-quality litters. Future tests of our model within the MEMS framework may evaluate these hypotheses in the light of potential feedbacks between SOM, litter quality, and microbial communities. Ecosystem process models that include microbial dynamics have potential to predict SOC change and such models may be improved through tests of the concepts developed herein.

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