



2016

Role of soil texture, clay mineralogy, location, and temperature in coarse wood decomposition—a mesocosm experiment

Cinzia Fissore
cfissore@whittier.edu

Martin F. Jurgensen

James Pickens

Chris Miller

Deborah Page-Dumroese

See next page for additional authors

Follow this and additional works at: <https://poetcommons.whittier.edu/envsc>



Recommended Citation

Fissore, C., Jurgensen, M. F., Pickens, J., Miller, C., Page-Dumroese, D., & Giardina, C. P. (2016). Role of soil texture, clay mineralogy, location, and temperature in coarse wood decomposition—a mesocosm experiment. *Ecosphere*, 7(11), 1-13. <https://doi.org/10.1002/ecs2.1605>

This Article is brought to you for free and open access by the Faculty Publications & Research at Poet Commons. It has been accepted for inclusion in Environmental Science by an authorized administrator of Poet Commons. For more information, please contact library@whittier.edu.

Authors

Cinzia Fissore, Martin F. Jurgensen, James Pickens, Chris Miller, Deborah Page-Dumroese, and Christian P. Giardina

Role of soil texture, clay mineralogy, location, and temperature in coarse wood decomposition—a mesocosm experiment

CINZIA FISSORE,^{1,†} MARTIN F. JURGENSEN,² JAMES PICKENS,² CHRIS MILLER,²
DEBORAH PAGE-DUMROESE,³ AND CHRISTIAN P. GIARDINA⁴

¹Department of Biology and Environmental Science, Whittier College, Whittier, California 90608 USA

²School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan 49931 USA

³USDA Forest Service, Rocky Mountain Research Station, Moscow, Idaho 83843 USA

⁴USDA Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, Hilo, Hawaii 96720 USA

Citation: Fissore, C., M. F. Jurgensen, J. Pickens, C. Miller, D. Page-Dumroese, and C. P. Giardina. 2016. Role of soil texture, clay mineralogy, location, and temperature in coarse wood decomposition—a mesocosm experiment. *Ecosphere* 7(11):e01605. 10.1002/ecs2.1605

Abstract. Of all the major pools of terrestrial carbon (C), the dynamics of coarse woody debris (CWD) are the least understood. In contrast to soils and living vegetation, the study of CWD has rarely relied on ex situ methods for elaborating controls on decomposition rates. In this study, we report on a mesocosm incubation experiment examining how clay amount (8%, 16%, and 24% clay), clay type (soil reconstructed with kaolinite vs. montmorillonite), wood placement (on litter layer surface, at the litter layer–soil interface, buried in the mineral soil), and laboratory incubation temperature (10°, 20°, or 30°C) control decomposition rates of highly standardized stakes and blocks of coarse aspen wood. Clay type effect was pronounced, with wood decomposing more quickly in kaolinite- than in montmorillonite-amended soils, perhaps due to a combined effect of moisture and microbial access to the substrate. Clay amount had only very limited effect on wood decomposition, which was a function of contact with the mineral soil (*Surface* < *Interface* < *Mineral*), perhaps due to greater contact with the decomposer community. Temperature effects were significant and dependent on interactions with clay type and wood placement. Effects of temperature on wood decomposition declined as the effects of soil variables increased, suggesting a hierarchy of controls on wood decomposition rates. Both water content and temperature had a strong effect on wood decomposition. Our results highlight that multiple interacting factors likely regulate wood decomposition processes. Multifactorial field experiments are needed to examine the physical, chemical, and biological factors controlling wood decomposition.

Key words: aspen wood stakes; clay mineral assemblages; kaolinite; mesocosm incubation; montmorillonite; wood decomposition.

Received 17 June 2016; revised 13 October 2016; accepted 24 October 2016. Corresponding Editor: Kristofer D. Johnson.

Copyright: © 2016 Fissore et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** cfissore@whittier.edu

INTRODUCTION

Dead wood material, often described as coarse woody debris (CWD), can comprise 20% or more of total forest biomass (Harmon et al. 1986, Heath et al. 2003). Wood is considered an important terrestrial carbon (C) sink due to its relatively slow decomposition rate (Woodall et al.

2008, Hagemann et al. 2010), and it represents a substantial, yet poorly quantified component of the terrestrial CO₂ flux to the atmosphere (Harmon and Hua 1991, Weedon et al. 2009). A better understanding of the factors that control early stages of wood decomposition would assist with efforts to identify relevant CO₂ offset opportunities.

Enormous attention has been devoted to understanding the effects of biotic and abiotic factors on the decomposition of leaf litter (e.g., Hobbie 1996, Harmon et al. 2009), roots (e.g., Merckx et al. 1985, Silver and Miya 2001, Harmon et al. 2009), and soil organic C (SOC) in mineral soil (e.g., Winkler et al. 1996, Townsend et al. 1997, Giardina and Ryan 2000, Fissore et al. 2008). In comparison with fine litter, fine roots, and SOC, there have been relatively few studies on the factors, especially with respect to soil characteristics, that control decomposition of CWD (Chambers et al. 2000, Mackensen et al. 2003, Jurgensen et al. 2006).

Plant material decomposition and the stabilization of organic matter (OM) in organic and mineral horizons represent a complex set of processes involving the processing and decomposition of OM by diverse communities of soil fauna and microorganisms, as well as chemical–physical interactions with mineral soil particles (e.g., Six et al. 2002, Giardina et al. 2014). While decomposition of CWD is likely to be sensitive to the same factors and underlying processes that control C decomposition and storage in other compartments of terrestrial ecosystems, the large size of CWD (>2 cm in diameter) and high variation in wood chemistry across species suggest that CWD decomposition may be distinct from that of fine litter or SOC (Garrett et al. 2007). To date, studies have shown that wood decomposition is driven primarily by climatic conditions, wood chemistry, and soil biota (e.g., Chambers et al. 2000, Stokland 2001, Beets et al. 2008, Gonzales et al. 2008, Hermann and Prescott 2008, Freschet et al. 2012, Bradford et al. 2014).

Soil texture, and especially the amount of clay and related surface properties, has been extensively described as a driver of litter and SOC decomposition and subsequent stabilization (Sørensen 1981, Jastrow et al. 2007, Berhe and Kleber 2013), which can contribute to offsetting atmospheric CO₂ concentrations and future climate warming. Concentrations of SOC generally increase as soil particle sizes decrease (e.g., Adisa and Nortcliff 2011), as do water retention and nutrient exchange properties (e.g., Elliot et al. 1980, Stotzky and Rem 2002)—conditions that affect soil microbial–substrate interactions (e.g., Frey et al. 1999). Increased SOC concentration with increasing clay content also leads to greater

stabilization of microbially produced metabolites, which are less available for further decomposition (e.g., Merckx et al. 1985, Amato and Ladd 1992, Saggar et al. 1996, Scott et al. 1996).

It is unclear whether a greater amount of clay-sized particles results in an increase in OM decomposition by increasing water-holding capacity and nutrient exchange sites, but increasing clay content could also reduce soil O₂ levels and increase protection of OM, by reducing substrate accessibility, both of which would reduce OM decomposition rates (Umar 2010). Using global databases, Silver and Miya (2001) indicated that the decomposition of conifer, broadleaf, and graminoid roots was greater in clay loam soils than in either four coarser-textured soil classes or finer-textured clay soils, suggesting a decomposition sweet spot of the above factors. Saggar et al. (1996) found a more rapid decomposition of fresh rye grass in two silt loam soils (20% clay) than in finer-textured soils (58% clay). Mtambanengwe et al. (2003) reported, for a mesocosm experiment, a linear decline in soil CO₂-C respiration as clay content increased from 5.6% to 56%. In contrast to these studies, Scott et al. (1996) found no effect of soil texture on the decomposition of wheat straw in sand, sandy loam, or loam soils. Similarly, one of the few studies trying to relate soil texture and soil horizon development to wood decomposition failed to find significant effects (Fahey and Arthur 1994). Such uncertainty may relate to the need to investigate not only soil texture, and by default clay amount, but also specific characteristics of the mineral phase (surface area, cation exchange capacity, etc.) and the potential role of clay type in affecting wood decomposition.

Clay types, because of their specific characteristics, can have a strong influence on OM decomposition. Clay minerals with a 2:1 interlayer lattice structure, such as montmorillonite, are characterized by high interlayer surface area and charge, which increases water retention, cation exchange capacity (CEC), aggregate formation, and protection of microbial metabolites from decomposers (Dixon 1981, Saggar et al. 1996, Miltner and Zech 1998). Clays with a 1:1 lattice structure, such as kaolinite, have lower surface area, hold less water, and would be less protective of C metabolites released during the decomposition process (Torn et al. 1997). In a 30-day laboratory incubation study, D'Acqui et al. (1998) found that tree leaf

litter decomposed more rapidly in soil mixed with montmorillonite clay than with kaolinite. Similar results for other organic substrates were reported by Stotzky (1986), Holland and Coleman (1987), and Saggar et al. (1996).

Most wood decomposition studies have been conducted on wood located on the surface or incorporated into the litter layer, but much less is known on factors controlling decomposition of wood located within the mineral soil (Smyth et al. 2016). In moving from the litter surface to mineral soils, wood is exposed to different soil physical, chemical, and microbial regimes (Jurgensen et al. 2006, Osono et al. 2006, Fujii and Takeda 2010, Smyth et al. 2016), which affect decomposition rates and subsequent incorporation and stabilization of wood-derived C in the soil matrix (Holland and Coleman 1987, Remsburg and Turner 2006, Van der Wal et al. 2007).

Because of the paucity of studies on CWD decomposition in relation to clay type and clay amount, either at the soil surface or in the mineral soil, we established a highly controlled, long-term (420-d) mesocosm experiment to understand controls on early stages of coarse wood decomposition. This experiment included treatments of clay type and amount (three levels of montmorillonite and kaolinite clay added to a sand soil), wood placement (on the surface of a litter layer—*Surface Block*, the litter layer–mineral soil interface—*Interface Block*, and embedded in the mineral soil—*Mineral Stake*), with three replicates of all combinations of the above treatments run at each of three laboratory incubation temperatures (LITs). We hypothesized that (1) increased amounts of each clay type would decrease wood decomposition rates as higher clay content may physically protect wood from the decomposer community; (2) wood would decompose more quickly when associated with soils containing 2:1 lattice-structure montmorillonite clay, due to a higher water-holding capacity, than with soils containing 1:1 kaolinite clay; (3) *Mineral Stake* decomposition would be fastest, while *Surface Block* decomposition would be slowest because contact with mineral soil exposes wood directly to decomposers and other resources required by the decomposer community; and (4) as the incubation temperature increases, wood decomposition rates would also increase. We anticipated that the complexity of

the design would also allow us to explore diverse interactions between factors; for example, how temperature effects might vary with wood position or clay amount.

MATERIALS AND METHODS

Soil and clays

We collected approximately 200 kg of a sand soil (Typic Haplargids: 91% sand, 6.4% silt, 2.5% clay) from the Sevilleta National Wildlife Refuge, New Mexico, USA. We selected this soil because it contains low levels of organic C (0.5%) and N (0.02%). Vegetation cover where soils were sampled was predominantly black grama (*Bouteloua eripoda* Torr.). Soils from 0 to 10 cm depth were excavated after vegetation was removed by clipping and scalping. The soils were sent to the USDA Forest Service laboratory in Houghton, Michigan, USA, in sealed ~40-L plastic buckets, where they were immediately processed by passing soils through a 5-mm mesh screen to remove rocks and plant material (roots, stems). Soils were then repeatedly mixed to homogenize them, and sieved through a 2-mm mesh. Soils were placed back into sealed buckets and stored for up to 2 months until mesocosm construction.

In preparation for mesocosm construction, Sevilleta soil was mixed with varying amounts of Ca-montmorillonite or kaolinite to yield three texture groups: 8%, 16%, and 24% clay. We also examine how three levels of incubation temperature would affect wood decomposition under both clay type and clay amount treatments (3 clay amounts \times 2 clay types \times 3 incubation temperatures = 18 possible combinations of treatments). We replicated each combination three times, yielding a total of 54 mesocosms. Prior to mixing, the mineralogy of each clay was confirmed through X-ray diffraction analysis (Scintag Inc., Cupertino, California, USA), and the C and N contents were determined: montmorillonite 0.5% C, below detection N; kaolinite 0.07% C, 0.02% N.

Mesocosms

Construction.—We constructed 54 mesocosms (volume = 5.3 L) using 30 cm long, 15 cm diameter PVC pipe, which were sealed at the bottom with a PVC tube stopper. To allow for drainage, a 1 cm diameter hole was drilled in the stopper,

and then fitted with a removable cap. A 2-mm plastic mesh was placed at the bottom of each cylinder to keep the drainage hole open and avoid soil loss. The open end of the cylinder was fitted with a 15 cm diameter PVC tube stopper, which was fitted with a 1 cm diameter rubber septum. Silicon-based high-vacuum grease was placed on each septum and cylinder rim to stop gas loss when the stoppers were in place. Gas leakage tests were run prior to the start of the experiment to confirm airtightness.

Each cylinder was filled with one of the six types of soil–clay mixture, and packed to give a soil bulk density of $\sim 1.30 \text{ g}\cdot\text{cm}^{-3}$. During the filling operation, a 20 cm \times 2.5 cm \times 2.5 cm aspen wood stake (*Mineral Stake*) of known weight was placed in each cylinder so the top of the stake was at the soil surface. A 2.5 cm \times 2.5 cm \times 2.5 cm aspen wood block (*Interface Block*) of known weight was placed on top of the mineral soil. The soil and the *Interface Block* were then covered with 5.46 g of loose, freshly fallen aspen leaf litter collected from an aspen forest near Houghton, Michigan. This aspen litter amount is 150% of estimated annual litterfall for young aspen forests in the region (Talhelm et al. 2012). A second 2.5 cm \times 2.5 cm \times 2.5 cm aspen wood block (*Surface Block*) of known weight was placed on top of the leaf litter. Control wood sections 3 cm long were cut from each mineral stake prior to mesocosms assemblage and stored for future C and N calculations.

Each mesocosm was top-watered to 70% water-holding capacity (WHC). 100% WHC was determined for each combination of clay type and amount at a bulk density of $1.3 \text{ Mg}\cdot\text{m}^{-3}$. A known amount of air-dry soil (0% WHC) was saturated, allowed to drain freely for about 6 h, and weighed. The difference between the weight of air-dry soil and freely drained soil was taken as 100% WHC.

In order to help establish naturally occurring microbial communities in the soil–clay mixtures, a soil extract was obtained by shaking a solution of 250 mL of DI water and 100 g of subsurface mineral soil (collected from the same aspen forest where leaf litter was collected) for 24 h, filtered through a 47- μm cloth mesh, and mixed with water during the first wetting cycle. Fertilizer (Scott Miracle-gro 30-10-10) was also added to each mesocosm at this time (0.51 mg N, 0.17 mg

P, and 0.17 mg K) to avoid soil N and P levels limiting microbial activity.

Incubation.—Eighteen mesocosms were incubated for 420 days at one of three controlled temperatures (LITs): 10°, 20°, and 30°C. The 10° and 30°C mesocosms were placed in Precision 815 low-temperature incubators (Winchester, Virginia, USA), while the 20°C mesocosms were incubated in the USDA Forest Service soil laboratory, which was maintained at controlled $20^\circ \pm 2^\circ\text{C}$ throughout the experiment. Four drying and rewetting cycles of approximately 100 days each were applied to each mesocosm. At the beginning of each cycle, water was added to bring the soil moisture content back to 70% WHC.

At the end of the incubation, we removed all *Surface Blocks*, handpicked leaf litter from the soil surface, and removed all *Interface Blocks* and *Mineral Stakes*. All wood and leaf litter samples were weighed, placed in a drying oven at 105°C, and weighed again to determine moisture content and percentage weight loss. Changes in C and N contents of *Mineral Stakes* in the different clay mesocosms were determined by comparing the *Mineral Stake* C and N contents to C and N levels in the corresponding control section (set aside at the time of mesocosms assemblage). All stakes and control sections were passed through a Wiley Mill (0.40-mm screen), a subsample was ground in a ball mill, and C and N concentrations were measured on a Costech ECS 4010 at the Soil Analytical Laboratory, School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan.

Calculations and statistical analysis

The decomposition rate constants k (yr^{-1}) for the *Surface* and *Interface Blocks* and *Mineral Stakes* were calculated according to Eq. (1) following Olson (1963)

$$k = \ln(DW_0/DW_t)/t, \quad (1)$$

where DW_0 is the initial dry mass prior to the incubation and DW_t is the dry mass at the end of the period t (1.15 yr).

This factorial experiment of a completely randomized design investigated four factors in the wood stake and wood block weight loss model. The factors considered were wood location (three levels: *Surface*, *Interface*, and *Mineral*), clay amount (three levels: 8%, 16%, and 24%), clay

type (two levels: montmorillonite and kaolinite), and LIT (three levels: 10°, 20°, and 30°C). The response variable was wood weight loss as a proportion of original weight. The arcsine square root transformation was applied to the response variable to homogenize the error term (Steele and Torrie 1980).

Initial analyses were conducted using the traditional effects model, where each factor and all possible interactions were included in the ANOVA model. When significant interactions were identified, we used the means model (Milliken and Johnson 1984), which includes each combination of the factors involved in the interaction as a separate treatment level, to better assess the significant interaction terms. Analysis of significant interaction terms testing certain hypotheses regarding interaction effects was conducted through the development of contrasts as described in Petersen (1985). Except for sample location, we used a similar approach for leaf litter decomposition. Leaf litter weights were transformed using the arcsine square root. Separate ANOVAs were conducted for wood moisture levels and C and N contents. In all analyses, we assessed significance at an $\alpha = 0.05$, and all tests were conducted using SAS version 9.2.

RESULTS

Our incubation mesocosm study yielded results that only partly supported our hypotheses. The

complexity of the design highlighted various interactions among study variables, which were a much more important driver of wood decomposition than anticipated—often overshadowing main treatment effects. Contrary to our expectations, aspen wood stakes and blocks clearly decomposed more rapidly in kaolinite vs. montmorillonite soils (Table 1, Fig. 1), with significant interactions with wood position in the mesocosm (Table 1, Fig. 1). As expected, incubation temperature (LIT) exerted a significant overall effect on wood decomposition, and significantly interacted with other study variables (Table 1).

We observed a significant interaction among clay amount, LIT, and wood position (Table 1). For example, contrasts analysis indicated that *Mineral Stakes* placed in soil with 24% montmorillonite that were incubated at 20°C had significantly lower mass loss than those incubated in soil with 16% clay (Fig. 2). Similarly, contrast analysis showed significant differences in wood decomposition between *Mineral Stakes* incubated in 8% montmorillonite vs. 24% clay, at LIT 10°C. Increasing LIT resulted in increased *Mineral Stakes* decomposition in both clay types only from 10° to 20°C for the 8% and 16% clay content. For 24% clay, each LIT step increase resulted in significantly greater decomposition, but only for montmorillonite-amended soil (Fig. 2).

As we expected, the overall water content of *Mineral Stakes* in montmorillonite-amended soils was higher than in soil with kaolinite clay

Table 1. Summary of ANOVA for main and interaction effects on wood stakes and blocks decomposition.

Source	SS	df	MS	F	P
Clay type	0.5847	1	0.5847	71.95	<0.0001
Clay amount	0.0221	2	0.0111	1.36	0.261
LIT	0.8878	2	0.4439	54.62	<0.0001
Position	3.0178	2	1.5089	185.66	<0.0001
Clay type × Clay amount	0.0371	2	0.0186	2.28	0.1069
Clay type × LIT	0.0295	2	0.0147	1.81	0.1681
Clay amount × LIT	0.0532	4	0.0133	1.64	0.1708
Clay type × Position	0.1359	2	0.0679	8.36	0.0004
Clay amount × Position	0.0288	4	0.0072	0.89	0.4756
LIT × Position	0.1087	4	0.0272	3.34	0.0127
Clay type × Clay amount × LIT	0.0506	4	0.0126	1.56	0.1917
Clay type × Clay amount × Position	0.0337	4	0.0084	1.04	0.3913
Clay type × LIT × Position	0.0664	4	0.0166	2.04	0.0938
Clay amount × LIT × Position	0.1828	8	0.0229	2.81	0.0072
Clay type × Clay amount × LIT × Position	0.0667	8	0.0083	1.03	0.4218

Notes: Bold values indicate significance at $\alpha = 0.05$. LIT, laboratory incubation temperature.

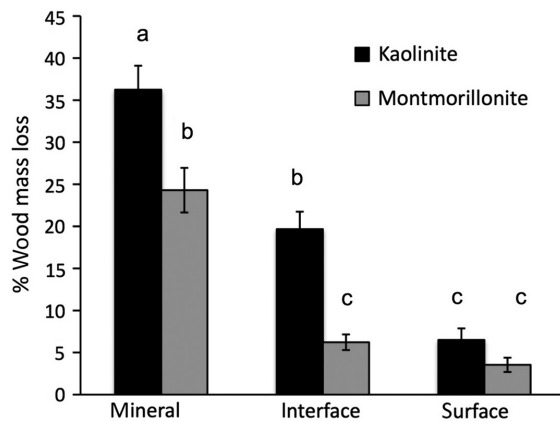


Fig. 1. Effect of clay type and degree of contact with soil on wood stakes and blocks decomposition expressed as percentage mass loss. Bars are average \pm SE. Different letters indicate significant difference at $\alpha = 0.05$.

(significantly higher only at LIT 10°C), and decreased significantly with increasing LIT at all clay levels (Table 2). However, contrary to our expectations, higher *Mineral Stakes* water contents were associated with lower wood decomposition in montmorillonite-amended mesocosms, which was likely related to significant wood water–LIT interaction at these temperatures (wood water % \times LIT: $P = 0.015$).

Similar to *Mineral Stakes*, wood decomposition for *Interface Blocks* increased from 10° to 20°C in both clay types, but not from 20° to 30°C, and was significantly greater with kaolinite clay than with montmorillonite at all LITs (Fig. 3). *Interface Blocks* incubated at LIT 10°C had significantly higher moisture contents than at 20° and 30°C, while moisture content was not significantly different between LITs 20° and 30°C (Table 3).

Surface Blocks decomposition increased with increasing LIT in kaolinite-amended soils, but mass loss was significantly different between LITs 10° and 30°C (Fig. 3). Conversely, wood mass loss was not significantly different across LITs in montmorillonite-amended soils (Fig. 3). Water content in *Surface Blocks* was significantly lower than in *Interface Blocks* only at LIT 10°C, whereas there was no significant difference at 20° and 30°C (Table 3). There was a correspondence between *Surface Blocks* decomposition and aspen leaf litter decomposition, as both *Surface*

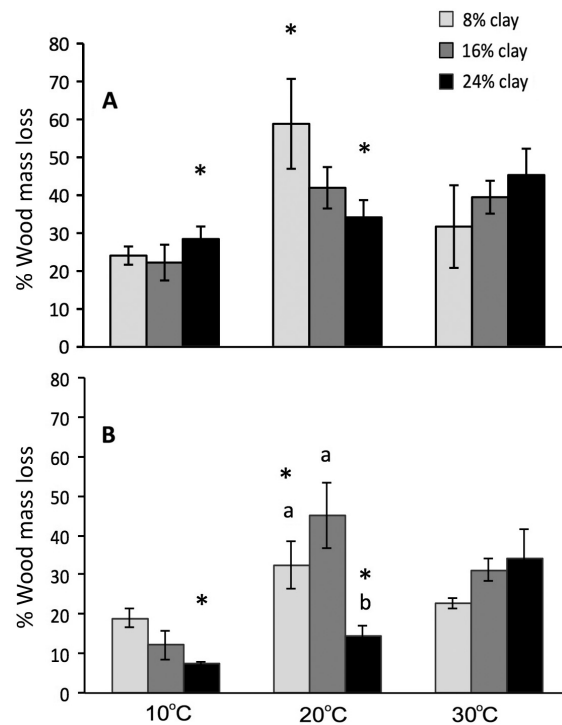


Fig. 2. Effect of clay type, clay amount, and incubation temperature (LIT) on mass loss and water content of *Mineral Stakes* at the end of a 420-day incubation†. Values are means \pm SE. (A) Kaolinite-amended soils. (B) Montmorillonite-amended soils. †Values denoted with an asterisk are significantly different ($\alpha = 0.05$) between clay type at the same LIT and clay %. Bars with different letters indicate significant difference within clay type and LIT.

Blocks and leaf litter decomposition were not affected by clay type or clay amount, but positively responded to increasing temperature. Aspen leaf litter that was placed on top on the mineral soil–clay mixtures increased with LIT as follows: 17.6% at 10°C, 34.2% at 20°C, and 53.4% at 30°C.

Decomposition rate constants (k) of *Mineral Stakes* over the study period reflect the mass loss patterns between the two clay types, averaging 0.420 (± 0.190) for kaolinite and 0.259 (± 0.155) for montmorillonite clay across the three incubation temperatures and clay amounts ($P = 0.008$; Table 4). Average k rates of aspen *Interface Blocks* were also significantly higher ($P = 0.0001$) with kaolinite clay (0.172 ± 0.08) than with montmorillonite (0.066 ± 0.032). Kaolinite-amended soils

Table 2. *Mineral Stakes* mass loss and water content across clay types and LITs.

Clay type	LIT	Average	
		Mass loss (%)	Water (%)
Kaolinite	10°C	24.9 ^{A*}	36.7*
	20°C	45.0 ^{B*}	41.5
	30°C	38.8 ^{AB}	30.4
Montmorillonite	10°C	12.9 ^{A*}	90.5 ^{X*}
	20°C	30.7 ^{B*}	53.8 ^Y
	30°C	29.3 ^B	30.3 ^Z

Notes: Average mass loss and water values with uppercase letters are significantly different among LITs within the same clay type. All values denoted with an asterisk are significantly different between clay types at the same LIT. LIT, laboratory incubation temperature.

resulted in marginally higher *k* than montmorillonite-amended soils in the case of *Surface Blocks* (0.066 ± 0.063 vs. 0.052 ± 0.025), but the difference was not significant.

Carbon concentrations in *Mineral Stakes* showed little change at the end of the incubation, and C loss was strongly correlated with mass loss ($r^2 = 0.99$, $P < 0.001$, results not shown). In contrast to C, wood N concentrations increased in both clay types as wood decomposition increased in response to differences in LIT and clay amount (Table 5; $r^2 = 0.80$). These higher N concentrations were caused by the immobilization of initial wood N by decay fungi, and inputs of N from external sources (% N gain) during the decomposition process. However, the amounts of N accumulated during decomposition of the high C:N *Mineral Stakes* did not affect wood mass loss in both clay types (kaolinite: $P = 0.84$, montmorillonite: $P = 0.55$), but generally reflect increased wood decomposition with higher incubation temperatures ($P = 0.015$).

DISCUSSION

Our study indicates that interactive effects among factors affect wood decomposition to a greater degree than initially anticipated. The results from our 420-day incubation study showed that, opposite to our expectations, aspen wood decayed much faster in a sand soil amended with kaolinite clay than in sand soil amended with montmorillonite clay. We initially speculated that the greater surface area and higher cation exchange capacity (CEC) of a 2:1

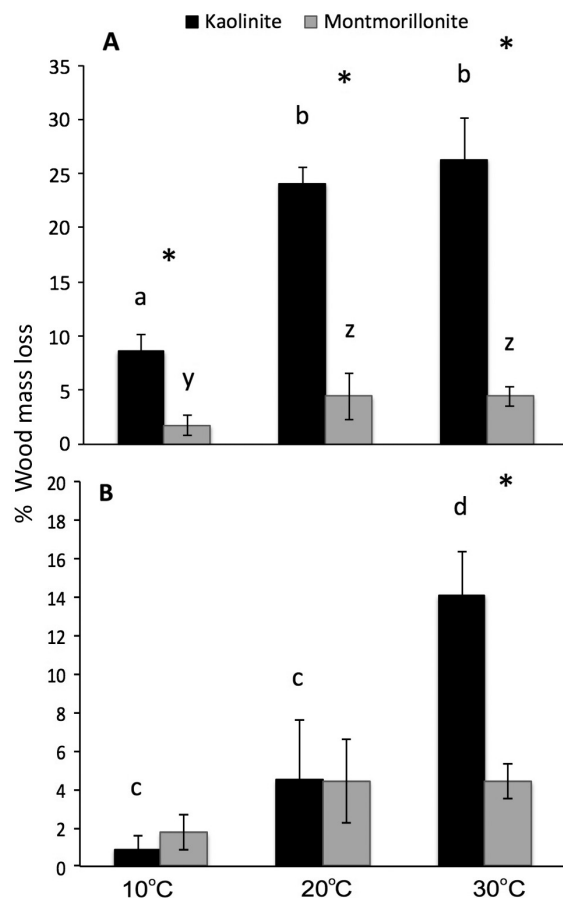


Fig. 3. Effect of clay type and incubation temperature on wood mass loss for (A) *Interface* and (B) *Surface Blocks* at the end of the 420-day incubation†. Values are means \pm SE. †Bars denoted with an asterisk are significantly different ($\alpha = 0.05$) between clay type at the same LIT. Bars with different letters indicate significant difference across LITs within same clay type. Clay % in both clay–soil mixtures had no significant effect on *Surface* and *Interface Blocks* mass loss.

Table 3. Average moisture content % of *Surface* and *Interface Blocks* at the end of the 420-day incubation.†

LIT	Wood position	
	Surface	Interface
Water content (%)		
10°C	13.9*	17.9*
20°C	11.2	12.4
30°C	10.9	12.7

Note: LIT, laboratory incubation temperature.
† Values with * are significantly different between *Surface* and *Interface Blocks* at $\alpha = 0.05$ for the same LIT.

Table 4. Aspen wood decomposition rates (k) across incubation temperatures and clay types and amounts at the end of the 420-day incubation.

Clay type	Wood position	Clay amount (%)	LIT			Average k
			10°C	20°C k values	30°C	
Kaolinite	Surface	8	0.014 ± 0.003	0.046 ± 0.061	0.060 ± 0.021	0.066 ± 0.063
		16	0.023 ± 0.009	0.072 ± 0.080	0.180 ± 0.031	
		24	0.008 ± 0.001	0.033 ± 0.012	0.161 ± 0.064	
	Interface	8	0.069 ± 0.033	0.164 ± 0.101	0.234 ± 0.067	0.172 ± 0.080 *
		16	0.076 ± 0.017	0.149 ± 0.100	0.238 ± 0.084	
		24	0.103 ± 0.049	0.220 ± 0.035	0.299 ± 0.240	
	Mineral	8	0.240 ± 0.047	0.841 ± 0.424	0.353 ± 0.261	0.420 ± 0.190 *
		16	0.222 ± 0.090	0.481 ± 0.141	0.441 ± 0.109	
		24	0.293 ± 0.071	0.368 ± 0.108	0.538 ± 0.182	
Montmorillonite	Surface	8	0.073 ± 0.062	0.050 ± 0.038	0.061 ± 0.028	0.052 ± 0.025
		16	0.029 ± 0.034	0.065 ± 0.060	0.087 ± 0.058	
		24	0.019 ± 0.000	0.067 ± 0.084	0.017 ± 0.012	
	Interface	8	0.020 ± 0.022	0.066 ± 0.023	0.078 ± 0.019	0.066 ± 0.032 *
		16	0.058 ± 0.006	0.107 ± 0.058	0.084 ± 0.041	
		24	0.013 ± 0.000	0.101 ± 0.041	0.069 ± 0.048	
	Mineral	8	0.184 ± 0.043	0.349 ± 0.139	0.224 ± 0.025	0.259 ± 0.155 *
		16	0.114 ± 0.063	0.554 ± 0.284	0.327 ± 0.062	
		24	0.067 ± 0.006	0.139 ± 0.046	0.374 ± 0.170	

Notes: Values are means ± SD. Asterisks indicate significant difference for average k between clay types with similar wood position.

clay, such as montmorillonite, would retain more moisture during the extended decomposition process than those of a 1:1 clay, thereby favoring greater microbial activity in the mesocosms. D'Acqui et al. (1998) reported more rapid

decomposition of chestnut and beech leaf litter in a 30-day laboratory study when mixed with pure montmorillonite clay than with kaolinite. Nelson et al. (1997) reported greater mineralization of pea straw in soil amended with 15% illite-kaolinite

Table 5. Effect of clay type and clay amount on N concentrations and N gains during the decomposition of *Mineral Stakes*.†

Clay type and LIT	Clay amount					
	8%		16%		24%	
	N (%)	N gain (%)	N (%)	N gain (%)	N (%)	N gain (%)
Kaolinite						
10°C	0.145	133	0.115	81	0.132	76.2*
20°C	0.501	276	0.221	139	0.176	118.5*
30°C	0.237	190	0.233	187	0.241	132.4
Montmorillonite						
10°C	0.174	179	0.106	84	0.060	8.3*
20°C	0.268	255	0.360	182	0.059	−0.9*
30°C	0.137	117	0.175	132	0.194	135.9

† Values with * are significantly different between clay type with the same clay % and same LIT.

clay than with 15% smectite, which they attributed to greater OM protection from microbial attack by the 2:1 lattice clay. Brais and Drouin (2012) speculated that wood decomposition would be slower in a soil with low CEC, although they did not mention potential effects of specific clay types. Additionally, it has been shown that soil with higher CEC can reduce OM decomposition by immobilizing the substrate or enzymes on exchange sites or in soil aggregates (Chivenge et al. 2011). However, in our study, most fungal wood decay occurred within large stakes or blocks rather than in OM well mixed with soil particles, suggesting that few fungal metabolites and enzymes would be held on montmorillonite exchange sites. If this were the case, greater CEC in our montmorillonite-amended soil would not be sufficient to explain the greater mass loss and wood decay rate in our kaolinite-amended soils.

We were surprised by the overall small impact that clay amount had on wood decomposition in our study. In part, the non-significant main effect can be explained by the significant high-level, interactive effects involving clay amount, especially in montmorillonite-amended soils. Other studies incorporated ^{14}C -labeled or unlabeled plant materials into soils with varying textures and clay amounts, and measured decomposition as CO_2 efflux or C retention (e.g., Saggar et al. 1996, Mtambanengwe et al. 2003), findings that seem to point to a significant effect of clay amount on substrate decomposition. However, the OM used in these studies was well mixed with mineral soil, and these results may reflect the rapid decomposition of OM mixed with the mineral soil and the incorporation into soil C pools, but also secondary decomposition of microbial biomass and metabolites active in the initial decay process. Others have observed greater plant substrate decomposition in coarser- rather than in finer-textured soil (e.g., Strong et al. 2004); however, some have argued that moisture may exert substantial effects on substrate decomposition (Manning et al. 2008, Smyth et al. 2016). Similarly, Chivenge et al. (2011) suggest that maize residues in clay soils, as compared to sand soils, resulted in relative greater C stabilization in soils due to a combination of soil moisture and soil texture effects.

Yatskov et al. (2003) argued that temperature affects wood decomposition more than moisture.

While high water content can inhibit wood decomposition (Smyth et al. 2016), low water levels have less impact (Hicks 2000, Hicks et al. 2003). In our study, *Mineral Stakes* incubated in montmorillonite-amended soil had higher water contents than *Mineral Stakes* incubated in kaolinite, as observed at the end of the study. However, wood in mesocosms of either clay type was unlikely to be wet enough for extended periods during the four wet-dry cycles to severely limit oxygen availability to wood-decay fungi, especially at the higher incubation temperatures. Therefore, the lower *Mineral Stakes* decomposition observed in our montmorillonite-amended soil was likely not caused by oxygen limitations deriving from high wood water content. Additionally, wood decomposition was greater with kaolinite at 10° and 20°C and in soil with 24% clay, and there was no significant difference in wood water content among clay amounts in both clay types.

Temperature had a significant effect on our *Surface* and *Interface Blocks* and *Mineral Stakes*, in particular for temperature changes from 10° to 20°C. Decomposition studies across various ecosystems have reported a two- to threefold increase in fungal activity per 10°C temperature step increase, followed by a rapid decline when temperature exceeds microbial optimum at approximately 40°C (Hicks 2000). Our study highlighted several interactive effects of laboratory incubation temperature with other factors, such as wood placement. This is in line with the observation by Mackensen et al. (2003), who observed that for wood placed on top of the forest floor, temperature was the main driver of wood decomposition. Similarly, Smyth et al. (2016), in a field experiment, noted that wood blocks placed on the litter surface tend to dry due to the effect of temperature and have slower decomposition than similar blocks buried in the soil. It is often difficult to separate the combined effect of increasing temperature from decreased substrate water content.

Mineral Stakes in both montmorillonite- and kaolinite-amended soils accumulated external N during decomposition, as also observed in the field by Smyth et al. (2016). The accumulated N derives from fungal transport of N from the mineral soil into wood during the decomposition process (Tlalka et al. 2008), and from the activity of N_2 -fixing bacteria in the wood (Hendrickson

1991). The N content of aspen wood is typically low (C:N = 300–400), and adding N before or during decomposition could increase the wood decay rate, as observed for recalcitrant plant substrate by Chivenge et al. (2011). However, N availability did not seem to be an important factor in our study, as the amounts of N accumulated during wood decomposition were poorly correlated with stake decomposition in both clay types and were more likely reflective of the wood water content–LIT effect on wood decomposition, especially in the montmorillonite-amended soils.

Wood decomposition differences between *Surface Blocks*, *Interface Blocks*, and *Mineral Stakes* demonstrate the importance of wood contact with the mineral soil matrix in the wood decomposition process, as also observed for logs and branches in a 13-year field study by Ganjegunte et al. (2004) and in wood blocks in a Canadian forest by Smyth et al. (2016). Such location effect is likely caused by increased moisture and greater colonization by wood-decay fungi (Orchard and Cook 1983). In our study, we measured the mass loss of aspen wood stakes and blocks placed at three soil locations. Consequently, the impact of clay type and clay amount on wood decomposition would primarily occur at contact points of the wood surface with the mineral soil and litter particles, or indirectly by affecting the amount of soil water diffusing into the wood, and the levels of soil N available to wood-decay fungi (Hicks et al. 2003, Osono et al. 2006, Van der Wal et al. 2007). Van der Wal et al. (2007) linked location-specific microbial communities to different decomposition rates for wood fragments incubated for up to 40 weeks in or on top of two mineral soils with a similar coarse sand textural class. Temperature differences at different soil locations or depths can affect wood decomposition (Hagemann et al. 2010), but would not have been a factor in our controlled temperature mesocosms.

Looking back at our study design, we speculate that more frequent wood harvest during the four wet–dry cycles, rather than just at the end of the study, would have perhaps clarified some of the still remaining uncertainties concerning drivers of wood mass loss. Specifically, more frequent wood stake and block samplings could be useful to better characterize the temperature–

wood water content relationships between the two clays, and possibly explain why clay amount had such limited effect on wood decomposition. We note that we were not able to also vary moisture as a treatment, but we strongly suspect that clay type by moisture-level interactions could exert a strong influence on the processes examined here and could be valuable to better compare future laboratory work to field conditions.

Improved understanding of the effect of soil–clay type on early stages of wood decomposition will further elucidate the role of clay minerals in terrestrial C cycling and may help incorporating clay–wood relationships into existing C decomposition models. The mixed results concerning the effects of texture on early wood decomposition, the lack of information concerning wood decomposition across textural gradients and for specific clay types, and the lack of controlled studies all point at the need for further investigations.

CONCLUSIONS

There have been many studies on decay and fungal succession of woody material located on top of the litter layer or on the mineral soil surface after clear-cut harvesting or fire (e.g., Laiho and Prescott 2004, Remsburg and Turner 2006, Olsson et al. 2011), but there is paucity of literature that compares wood decomposition in soils with different clay types, clay amounts, or position in the soil profile. The results of our long-term controlled mesocosm incubation showed strong effects of clay mineralogy on wood decomposition, which in part could be due to the effect of clays on soil porosity, moisture content, cation exchange capacity, and organo-mineral bonding. Clay type (kaolinite vs. montmorillonite) more than clay amount affected wood stakes and blocks decomposition. The study also highlights the important interactions that are possible with other variables, such as soil and wood moisture content, temperature, and level of contact with the soil matrix. While wood decomposition was often enhanced by increasing incubation temperature, results suggest that overall decomposition is contingent upon microbe accessibility to the substrate as conditioned by the soil environment and by the level of protection exerted by clay minerals, processes

that have been extensively investigated elsewhere and whose investigation was beyond the scope of this study. Our results point to the interpretation that clay type can influence temperature-driven rates of wood decomposition rates in forest ecosystems in a changing climate.

ACKNOWLEDGMENTS

This work was supported by the Northern, Rocky Mountain and Pacific Southwest Research Stations of the USDA Forest Service and by a grant from the Clay Mineral Society. We thank Jennifer Eikenberry, Melissa Porter, and Christa Luokkala for help with the GC analyses and laboratory incubations. The authors have no conflict of interest to declare. CF, MJ, and CG conceived and designed the study; JP and CM conducted statistical tests; and all authors contributed to performing the research, analyzing the data, and writing the manuscript.

LITERATURE CITED

- Adisa, S. J., and S. Nortcliff. 2011. Carbon fractions associated with silt-size particles in surface and subsurface soil horizons. *Soil Science Society of America Journal* 75:79–91.
- Amato, M., and J. N. Ladd. 1992. Decomposition of ¹⁴C-labelled glucose and legume material in soils: properties influencing the accumulation of organic residue C and microbial biomass C. *Soil Biology & Biochemistry* 24:455–464.
- Beets, P. N., I. A. Hood, M. O. Kimberley, G. R. Oliver, S. H. Pearce, and J. F. Gardner. 2008. Coarse woody debris decay rates for seven indigenous tree species in the central North Island of New Zealand. *Forest Ecology and Management* 256:548–557.
- Berhe, A. A., and M. Kleber. 2013. Erosion, deposition, and the persistence of soil organic matter: mechanistic considerations and problems with terminology. *Earth Surface Processes and Landforms* 38:908–912.
- Bradford, M. A., R. J. Warren, P. Baldrian, T. W. Crowther, D. S. Maynard, E. E. Oldfield, W. R. Wieder, S. A. Wood, and J. R. King. 2014. Climate fails to predict wood decomposition at regional scales. *Nature Climate Change* 4:625–630.
- Brais, S., and P. Drouin. 2012. Interactions between deadwood and soil characteristics in a natural boreal trembling aspen – jack pine stand. *Canadian Journal of Forest Research* 42:1456–1466.
- Chambers, J. Q., N. Higuchi, J. P. Schimel, L. V. Ferreira, and J. M. Melak. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Pecologia* 122:380–388.
- Chivenge, P., B. Vanlauwe, R. Gentile, and J. Six. 2011. Comparison of organic versus mineral resource effects on short-term aggregate carbon and nitrogen dynamics in a sandy soil versus a fine textured soil. *Agriculture, Ecosystems and Environment* 140:361–371.
- D'Acqui, L. P., E. Daniele, F. Fornasier, L. Radaelli, and G. G. Ristori. 1998. Interaction between clay microstructure, decomposition of plant residues and humification. *European Journal of Soil Science* 49:579–587.
- Dixon, J. B. 1981. Roles of clays in soils. *Applied Clay Science* 5:489–503.
- Elliot, E. T., R. V. Anderson, D. C. Coleman, and C. V. Cole. 1980. Habitable pore space and microbial trophic interactions. *Oikos* 35:327–335.
- Fahey, T. J., and M. A. Arthur. 1994. Further studies of root decomposition following harvest of a northern hardwoods forest. *Forest Science* 40:618–629.
- Fissore, C., C. P. Giardina, R. K. Kolka, C. C. Trettin, G. M. King, M. F. Jurgensen, C. D. Barton, and S. D. McDowell. 2008. Temperature and vegetation effects on soil organic carbon quality along a forested mean annual temperature gradient in North America. *Global Change Biology* 14: 193–205.
- Freschet, G. T., J. T. Weedon, R. Aerts, J. R. van Hal, and H. C. Cornelissen. 2012. Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. *Journal of Ecology* 100:161–170.
- Frey, S., E. T. Elliott, and K. Paustian. 1999. Bacterial and fungal abundance and biomass in conventional and no-tillage agroecosystems along two climatic gradients. *Soil Biology & Biochemistry* 31:573–585.
- Fujii, S., and H. Takeda. 2010. Dominant effect of litter substrate quality on the difference between leaf and root decomposition process above- and below-ground. *Soil Biology & Biochemistry* 42:2224–2230.
- Ganjegunte, G. K., L. M. Condron, P. W. Clinton, M. R. Davis, and N. Mahieu. 2004. Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management* 187:197–211.
- Garrett, L., M. Davis, and O. Graeme. 2007. Decomposition of coarse woody debris, and methods for determining decay rates. *New Zealand Journal of Forestry Science* 37:227–240.
- Giardina, C. P., C. M. Litton, S. E. Crow, and G. P. Asner. 2014. Warming-related increases in CO₂ efflux are explained by increased belowground carbon flux. *Nature Climate Change* 4:822–827.
- Giardina, C. P., and M. G. Ryan. 2000. Evidence that decomposition rates of organic carbon in mineral

- soil do not vary with temperature. *Nature* 404: 858–861.
- Gonzales, G., W. A. Gould, A. T. Hudak, and T. Nettleton Hollingsworth. 2008. Decay of Aspen (*Populus tremuloides* Michx.) wood in moist and dry boreal, temperate, and tropical forest fragments. *Ambio* 37:588–597.
- Hagemann, U., M. T. Moroni, J. Gleißner, and F. Makeschin. 2010. Accumulation and preservation of dead wood upon burial by bryophytes. *Ecosystems* 13:600–611.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Harmon, M. E., and C. Hua. 1991. Coarse woody debris dynamics in two old-growth ecosystems: Changbai Mountain Biosphere Reserve, People's Republic of China, and H. J. Andrews Experimental Forest, U.S.A. *BioScience* 41:604–610.
- Harmon, M. E., W. L. Silver, B. Fasth, H. Chen, I. C. Burke, W. J. Partons, S. C. Hart, W. S. Currie, and Lidet. 2009. Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. *Global Change Biology* 15:1320–1338.
- Heath, L. S., J. E. Smith, and R. A. Birdsey. 2003. Carbon trends in U.S. forestlands: a context for the role of soils in forest carbon sequestration. Pages 35–45 in J. M. Kimble, L. S. Heath, R. A. Birdsey, and R. Lal, editors. *The potential of U.S. forest soils to sequester carbon and mitigate the greenhouse effect*. CRC Press, Boca Raton, Florida, USA.
- Hendrickson, O. Q. 1991. Abundance and activity of N₂-fixing bacteria in decaying wood. *Canadian Journal of Forest Research* 21:1299–1304.
- Hermann, S., and C. E. Prescott. 2008. Mass loss and nutrient dynamics of coarse woody debris in three Rocky Mountain coniferous forests: 21 year results. *Canadian Journal of Forest Research* 38:125–132.
- Hicks, W. T. 2000. Modeling nitrogen fixation in dead wood. Ph.D. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Hicks, W. T., M. E. Harmon, and D. D. Myrold. 2003. Substrate controls on nitrogen fixation and respiration in woody debris from the Pacific Northwest, USA. *Forest Ecology and Management* 176:25–35.
- Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* 66:503–522.
- Holland, E. A., and D. C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* 68:425–433.
- Jastrow, J. D., J. E. Amonette, and V. L. Bailey. 2007. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. *Climatic Change* 80:5–23.
- Jurgensen, M. F., D. Reed, D. Page-Dumroese, P. Laks, A. Collins, G. Mroz, and M. Degórski. 2006. Wood strength loss as a measure of decomposition in northern forest mineral soil. *European Journal of Soil Biology* 42:23–31.
- Laiho, R., and C. E. Prescott. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Canadian Journal of Forest Research* 34:763–777.
- Mackensen, J., J. Bauhus, and E. Webber. 2003. Decomposition rates of coarse woody debris—a review with particular emphasis on Australian tree species. *Australian Journal of Botany* 51: 27–37.
- Manning, P., M. Saunders, R. D. Bardgett, M. Bonkowski, M. A. Bradford, R. J. Ellis, E. Kandeler, S. Marhan, and D. Tscherko. 2008. Direct and indirect effects of nitrogen deposition on litter decomposition. *Soil Biology & Biochemistry* 40: 688–698.
- Merckx, R., A. den Hartog, and J. A. van Veen. 1985. Turnover of root-derived material and related microbial biomass formation in soils of different texture. *Soil Biology & Biochemistry* 17:565–569.
- Milliken, G. A., and D. E. Johnson. 1984. Analyses of messy data. Volume I: Designed experiments. Van Nostrand Reinhold, New York, New York, USA, 473 pages.
- Miltner, A., and W. Zech. 1998. Carbohydrate decomposition in beech litter as influenced by aluminum, iron and manganese oxides. *Soil Biology & Biochemistry* 30:1–7.
- Mtambanengwe, F., P. Mapfumo, and H. Kirchmann. 2003. Decomposition of organic matter in soil as influenced by texture and pore size distribution. Pages 261–275 in A. Bationo, editor. *Managing nutrient cycles to sustain soil fertility in sub-Saharan Africa*. Academy Science Publishers and TSBF CIAT, Nairobi, Kenya.
- Nelson, P. N., A. R. Barzegar, and J. M. Oades. 1997. Sodicity and clay type: influence on decomposition of added organic matter. *Soil Science Society of America Journal* 61:1052–1057.
- Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322–331.
- Olsson, J., B. G. Jonsson, J. Hjalten, and L. Ericson. 2011. Addition of coarse woody debris – the early fungal succession on *Picea abies* logs in managed forests and reserves. *Biological Conservation* 144:1100–1110.

- Orchard, V. A., and F. J. Cook. 1983. Relationship between soil respiration and soil moisture. *Soil Biology & Biochemistry* 15:447–453.
- Osono, T., D. Hirose, and R. Fujimaki. 2006. Fungal colonization as affected by litter depth and decomposition stage of needle litter. *Soil Biology & Biochemistry* 38:2743–2752.
- Petersen, R. G. 1985. Design and analysis of experiments. Marcell Dekker Inc., New York, New York, USA, 429 pages.
- Remsburg, A. J., and M. G. Turner. 2006. Amount, position, and age of coarse wood influence litter decomposition in postfire *Pinus contorta* stands. *Canadian Journal of Forest Research* 36: 2112–2123.
- Saggar, S., A. Parshotam, G. P. Sparling, C. W. Feltham, and P. B. S. Hart. 1996. ¹⁴C-labeled ryegrass turnover and residence times in soils varying in clay content and mineralogy. *Soil Biology & Biochemistry* 28:1677–1686.
- Scott, N. A., C. V. Cole, E. T. Elliott, and S. A. Huffman. 1996. Soil textural control on decomposition and soil organic matter dynamics. *Soil Science Society of America Journal* 60:1102–1109.
- Silver, W. L., and R. K. Miya. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129:407–419.
- Six, J., R. Conant, E. A. Paul, and K. Paustian. 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant and Soil* 241:155–176.
- Smyth, C. E., B. Titus, J. A. Trofymow, T. R. Moore, C. M. Preston, C. E. Prescott, and CIDET Working Group. 2016. Patterns of carbon, nitrogen and phosphorus dynamics in decomposing wood blocks in Canadian forests. *Plant and Soil*. <http://dx.doi.org/10.1007/s11104-016-2972-4>
- Sørensen, L. H. 1981. Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biology & Biochemistry* 13:313–321.
- Steele, R. G., and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. Second edition. McGraw-Hill, New York, New York, USA.
- Stokland, J. N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. *Ecological Bulletins* 49:71–83.
- Stotzky, G. 1986. Influence of soil minerals on metabolic processes, growth, adhesion, and ecology of microbes and viruses. Pages 305–428 in P. M. Huang and M. Schnitzer, editors. Interactions of soil minerals with natural organics and microbes. Soil Science Society of America, Madison, Wisconsin, USA.
- Stotzky, G., and L. T. Rem. 2002. Influence of clay minerals on microorganisms. *Canadian Journal of Microbiology* 12:547–563.
- Strong, D. T., H. De Wever, R. Merckx, and S. Recous. 2004. Spatial location of carbon decomposition in the soil pore system. *European Journal of Soil Science* 55:739–750.
- Talhelm, A. F., K. S. Pregitzer, and C. P. Giardina. 2012. Long-term leaf production response to elevated atmospheric carbon dioxide and tropospheric ozone. *Ecosystems* 15:71–82.
- Tlalka, M., M. D. Fricker, and S. C. Watkinson. 2008. Translocation dynamics in *Serpula lacrymans*. *Applied and Environmental Microbiology* 74:2700–2708.
- Torn, M. S., S. E. Trumbore, O. A. Chadwick, P. M. Vitousek, and D. M. Hendricks. 1997. Mineral control of soil organic carbon storage and turnover. *Nature* 389:170–173.
- Townsend, A. R., P. M. Vitousek, D. J. Desmarais, and A. Tharpe. 1997. Soil carbon pool structure and temperature sensitivity inferred using CO₂ and ¹³CO₂ incubation fluxes from five Hawaiian soils. *Biogeochemistry* 38:1–17.
- Umar, S. 2010. Effect of clay on plant residue decomposition. Master of Agricultural Science-Thesis. School of Earth and Environmental Sciences, The University of Adelaide.
- Van der Wal, A., W. de Boer, W. Smant, and J. A. van Veen. 2007. Initial decay of woody fragments in soil is influenced by size, vertical position, nitrogen availability and soil origin. *Plant and Soil* 301: 189–201.
- Weedon, T. J., W. K. Cornwell, J. H. C. Cornelissen, A. E. Zanne, C. Wirth, and D. A. Coomes. 2009. Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters* 12:45–56.
- Winkler, J. P., R. S. Cherry, and W. H. Schlesinger. 1996. The Q₁₀ relationship of microbial respiration in a temperate forest soil. *Soil Biology & Biochemistry* 28:1067–1072.
- Woodall, C. W., L. S. Heath, and J. E. Smith. 2008. National inventories of down and dead woody material forest carbon stocks in the United States: challenges and opportunities. *Forest Ecology and Management* 256:221–228.
- Yatskov, M., M. E. Harmon, and O. N. Krankina. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. *Canadian Journal of Forest Research* 33:1211–1226.