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Bedding of Wetland Soil: Effects of Bed Height and Termite Activity on Wood Decomposition

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Microorganisms and termites are the primary wood decay agents in forests of the southeastern United States, whose activity can be affected by forest management practices. Bedding establishes raised planting beds on poorly-drained soils, but little is known about the effect of bedding or soil bed height on wood decomposition. Therefore, a four height bedding study was conducted on a wetland soil in eastern South Carolina: flat (no bedding), half (7.5 cm), single (20 cm), and double (30 cm) above the original soil surface. Aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.) wood stakes were inserted to 30-cm soil depth, sampled over 23 mo, and decomposition (mass loss) by soil microorganisms and termites assessed. Microbial decay of both aspen and pine stakes increased as bed height increased, approaching 50% mass loss in double beds at the end of the study. Termites were not present in the flat (unbedded) soil, only damaged <1% of stakes in half beds, but were very active in single and double beds. Termites damaged or consumed 43% of aspen stakes in the double beds, which increased aspen mass loss by 30%. In contrast, termites attacked only 11% of pine stakes in double beds, and had little impact on mass loss. Stake decomposition was highest at the 5-cm soil depth and was affected by soil microsite variability among soil bed heights. Soil bedding increased wood decomposition by both soil microorganisms and termites, and their impact on soil organic matter content and productivity deserves more attention.

Abbreviations: OM, organic matter.

C oarse woody debris is an important structural and functional component of forest ecosystems, and is considered an important terrestrial carbon (C) sink because of its slow decomposition rate (Harmon et al., 1986; Woodall et al., 2013). Many factors control the rate at which coarse woody debris decomposes, such as wood species, size, and location (Edmonds and Vogt, 1986). Forest management can also impact soil properties, which subsequently could alter organic matter (OM) decomposition (Grigal and Vance, 2000; Page-Dumroese et al., 2006). Therefore, land managers and climate-change modelers need to understand how wood decomposition rates and subsequent soil C sequestration are affected by various forestry operations.

There have been numerous studies on wood decomposition in which fungi are the main biological drivers of the decay process (e.g., Rayner and Boddy, 1988; van der Wal et al., 2015). However, in many ecosystems termites have an important role in soil processes, such as OM decomposition, methane production, and pedogenesis (Sugimoto et al., 2000; Ulyshen 2016). Considerable information is available on species richness, abundance, and biomass consumption by mound-building termites in tropical and sub-tropical ecosystems (e.g., Bignell and Eggleton, 2000; Takamura 2001), but much less is known on the distribution and activity

Core Ideas

- **Wood stake decomposition is a function of both microbial and termite attack in raised beds in the US southeast.**

- **Microbial decay was greater in single and double beds than in half beds and unbedded soil.**

- **Mass loss was similar for both aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.).**

- **Termites were active only on aspen stakes in single and double beds, where they increased mass loss 20-30%.**

- **As wood stakes decomposed, soil microsite variability of mass loss increased.**

of subterranean termites in temperate forests. While there are many studies on the life cycle, community structure, population size, and impacts of subterranean termites on wooden structures in urban areas (e.g., Vargo and Husseneder, 2009; Suiter et al., 2012), much less information is available on termites in forest soils (Maynard et al., 2015).

Subterranean termites are found in a wide variety of US soils and forest types (e.g., Wang and Powell, 2001; Bradford et al., 2014), but their distribution is generally controlled by temperature, and are largely absent in soils that freeze in the winter (King et al., 2013). Numerous laboratory studies have examined the rate of wood decomposition by subterranean termites, but very few have been conducted in forest ecosystems, mostly in southern pine and hardwood stands (e.g., Gentry and Whitford, 1982; Ulyshen 2014; Ulyshen et al., 2014). Termites impact wood decomposition by direct consumption, but they can indirectly affect wood decay rates by changing fungal community structure and activity (Ulyshen et al., 2016). However, the high spatial variability of both termite populations and woody residue distribution in many soils make it very difficult to extrapolate laboratory and small field plot studies to termite impacts on wood decomposition at the stand or forest level.

Bedding is an important management practice on poorly-drained soils in the southeastern United States, in which surface soil is formed into mounds (beds). The mixing of surface organic debris (forest floor) with the mineral soil into raised planting beds improves soil aeration, raises soil temperature, and increases nutrient availability (Morris and Lowery, 1988; Kelting et al., 2000; Trettin et al., 2011). Such changes in soil properties increase tree survival and growth (e.g., Gent et al., 1983; Fox et al., 2007; Maier et al., 2012), which increase with bed height (Mann and McGilvray, 1974; Outcalt, 1984; VanderSchaaf and South, 2004). The incorporation of surface OM during bedding operations increase initial mineral soil C contents (Maier et al., 2012), but there is little information on how bedding or the height of the soil beds impacts subsequent OM decomposition or termite activity.

Therefore, the objective of our study was to assess the effect of soil bed height on microbial wood decomposition and termite activity in a mineral wetland soil in the lower coastal plain of the southeastern United States. Wood was selected as the OM substrate because it is a normal component of forest soils, would be incorporated into the beds, and its decomposition is affected by soil properties and micro-climate over long time periods (Chen et al., 2000). This study entailed using wood stakes and separating them into two groups after sampling: (1) no evidence of termite damage, which assumes all wood decomposition is done by microorganisms, and (2) evidence of termite activity (feeding, tunneling, or missing) and assumes wood decomposition is a function of both microorganisms and termites. We hypothesized that: (1) decomposition of wood stakes in this poorly-drained soil would increase as bed height increased, (2) the proportion (fraction) of wood stake decomposition occurring at deeper soil depth would decrease as bed height increases, and (3) termites

become more important in the wood decomposition process as bed height increases.

METHODS
Study Site and Experimental Design

The study was located near Summerville, SC, USA on land owned by Westvaco Corporation, which previously had a 25-yr-old loblolly pine stand that was clear-cut harvested in October 1993. In August 1995 the soil was sheared, roll-chopped in May 1996, and a soil bedding height study established in June 1996. The soil is a poorly-drained, sandy-surface Rains series (fine-loamy, siliceous, semiactive, thermic Typic Paleaquults) that had a thick residual root mat from an ericaceous understory. Loblolly pine (*Pinus taeda* L.) seedlings were planted on the top of each bed on a 1.82 m spacing in January 1997. The area was treated with Arsenal at 0.29 L ha^{-1} (isopropylamine salt of imazapyr; BASF Corp.), Oust at 0.22 L ha^{-1} (sulfometuron methyl; DuPont Inc.), and Escort at 0.36 L ha^{-1} (metsulfuron methyl, DuPont, Inc.) herbicides in March 1997, and fertilized with 224 kg ha^{-1} of triple super-phosphate (0–45–0) in October 1996.

Bedding Treatments

Four bed height treatments were established in June 1996 using a D8 Caterpillar tractor equipped with a V-shearing blade on front and a standard Savannah bedding plow: (1) flat, no bedding; (2) half bed, 7.5 cm; (3) single bed, 20 cm; and (4) double bed, 30 cm above the original soil surface. The half-height beds were formed by raising the bedding plow up slightly, as might occur when beds are formed under unfavorable conditions. Single beds were formed in a single pass, and this is considered the standard height in most soil bedding operations (Mann and McGilvray, 1974; Outcalt, 1984). Double beds were formed by making two passes with the packing wheel removed on the second pass. Three replicates were established containing three rows of each soil bed height spaced 3.4 m apart. Each row had four trees, for a total of 12 trees per replicate.

Wood Stakes

Stakes of both trembling aspen (*Populous tremuloides* Michx.) and loblolly pine were used as standard substrates, as wood of these two species have different lignin types, lignin to cellulose ratios, and nitrogen (N) contents, which would favor the development of a different wood-decomposing microbial community (Blanchette, 1984). Two field stakes (2.5 by 2.5 by 30 cm) were cut from kiln-dried, knot-free 70-cm long aspen and pine sapwood "mother" stakes, and the top of each stake was treated with a neoprene sealant to reduce moisture change after installation. The 10-cm center section was used as a control (time = 0) to determine wood mass loss during the study.

In December 1999, 25 stakes of each species were spaced 30 cm apart and inserted vertically to a 30-cm soil depth between loblolly pine trees growing in three soil beds of each height per replicate, for a total of 600 wood stakes used in the study ($n = 3$ replicates × 4 bed heights × 2 wood species × 5 sample dates ×

5 stakes). A soil core was removed with a square 2.5-cm by 2.5-cm metal coring tool to reduce soil compaction around the stakes during installation. For more information on wood stake production and placement, see Jurgensen et al. (2006).

Originally, five stakes of each species were to be randomly sampled from each soil bed height per replicate at 5, 9, 15, 23, and 30 mo after insertion. However, beginning at the second sampling (9 mo) some stakes selected for removal were completely gone from termite activity ("tag-only stake"), so adjacent stakes were sampled until a total of 15 aspen and 15 pine stakes were obtained from the three soil bed height replicates. The "tag-only" stakes (assumed 100% termite removal) were also included as stakes sampled, so the total stake sample size of both wood species from soil bed replicates at the 9, 15, and 23 sample dates was often greater than 15. Consequently, not enough stakes remained in many soil beds for an adequate sample at 30 mo, so the study was ended after 23 mo. All samples were shipped to Michigan Technological University (Houghton, MI, USA) for wood mass loss determination.

In the laboratory, all stakes were cleaned of adhering soil, dried at 105°C for 48 h, weighed, and each stake was examined for termite damage, such as external surface feeding and/or tunneling (See Supplemental Fig. S1). Stakes with termite damage were also examined for soil moved into the wood by termites, and if present, physically removed with small scrapers. All stakes without termite damage had a 2.5-cm long block cut at the 5-, 15-, and 25-cm soil depth to assess the effect of soil depth on decomposition.

Wood decomposition (mass loss) during each sampling period was measured by comparing dry weight of each field stake to the weight of its corresponding control section (t_0). Mass loss averages for each replicate (n = 5 to 8 stakes) were used as a treatment observation in the statistical analyses. The relative impact of termites on wood decomposition was determined by comparing mass loss from stakes with both termite plus microbial decay to mass loss from stakes with only microbial decomposition.

Statistical Analysis

All analysis were conducted using SAS version 9.4 (SAS Institute, Cary, NC) and assessed at α ≤ 0.05 significance level. An analysis of variance (ANOVA) was conducted for this factorial design using SAS PROC GLM. Stake weight reductions at each sampling date were used as the observation for each treatment combination in the analysis. Two datasets were created: (1) all stakes with mass loss from microbial decay plus termite damage, and (2) a subset of all stakes with mass loss from only microbial decay. Factors in the analysis were: sample date (5, 9, 15, and 23 mo), soil bed height (double, single, half, and flat), and soil depth (5 cm, 15 cm, and 25 cm). The response variable was stake weight loss as a proportion of original weight, and each factor and all possible interactions were considered in the model.

The arcsine square root transformation was used to homogenize the error term (Steele and Torrie, 1980). While this transformation provided better adherence to the assumptions of the ANOVA than the untransformed data, the Levene's Test still indicated heterogeneity of variance. The Kruskal–Wallis non-parametric procedure was performed, and the results were consistent with those reported in the initial ANOVA analysis, so we report the results from the ANOVA approach. When significant effects and interactions were identified, post-hoc assessments were made with Tukey's range test. Standard deviations of stake mass loss were compared with two-sample t tests using SAS PROC TTEST with results considered for pooled or unpooled variance, as indicated by preliminary F-tests for homogeneity of variance.

RESULTS

Both soil microorganisms and termites were factors in the decomposition of wood stakes placed in soil beds on this poorly-drained soil. Of the 495 aspen and pine stakes sampled, ~14% had termite damage or were totally removed by termites. By comparing stakes decayed by soil microorganisms to stakes decomposed by both microorganisms and termites, the relative impact of soil bed height on the activity each wood decomposer group during the study was determined (Supplemental Table S1).

Bed Height
Aspen

Microorganisms. Increased soil bed height had a large positive effect on aspen wood decomposition by soil microorganisms (Fig. 1A). While no significant mass loss occurred during the cool, wet winter and spring (5 mo), microbial decay increased during the warm summer (9 mo). In the following autumn and winter (15 mo) conditions were more favorable for microbial activity in double beds than in the other soil beds, but microbial decay in single beds greatly increased during the second summer. Therefore, by the end of the study (23 mo) mass loss in the single and double beds were similar (~45%) and significantly higher than in half beds (32%) and flat (unbedded) soil (20%).

Termites. Soil bed height also had a major impact of termites on aspen decomposition. After 23 mo termites increased aspen stake mass loss in single beds from 44% (only microorganisms) to 71% (microorganisms plus termites) and from 47% to 76% in double beds (Fig. 1B). The probability of termites finding aspen stakes in the single and double beds increased with time, as over 60% of the stakes sampled at 23 mo had termite damage or were gone (Table 1). However, a greater incidence of termite-feeding activity was evident in the double beds, which had 13 "tag-only" stakes, as compared to only 7 "tag-only" stakes in single beds. In contrast, termites had no measurable effect on aspen mass loss in the half bed, as only 4 of the 75 aspen stakes sampled during the study had termite damage, and we found no evidence of termites in the flat soil.

Pine

Microorganisms. Similar to aspen, decomposition of pine stakes by soil microorganisms was enhanced by increased soil bed height (Fig. 1C). The temporal pattern of microbial decay was also similar to aspen, with little decomposition in the cool,
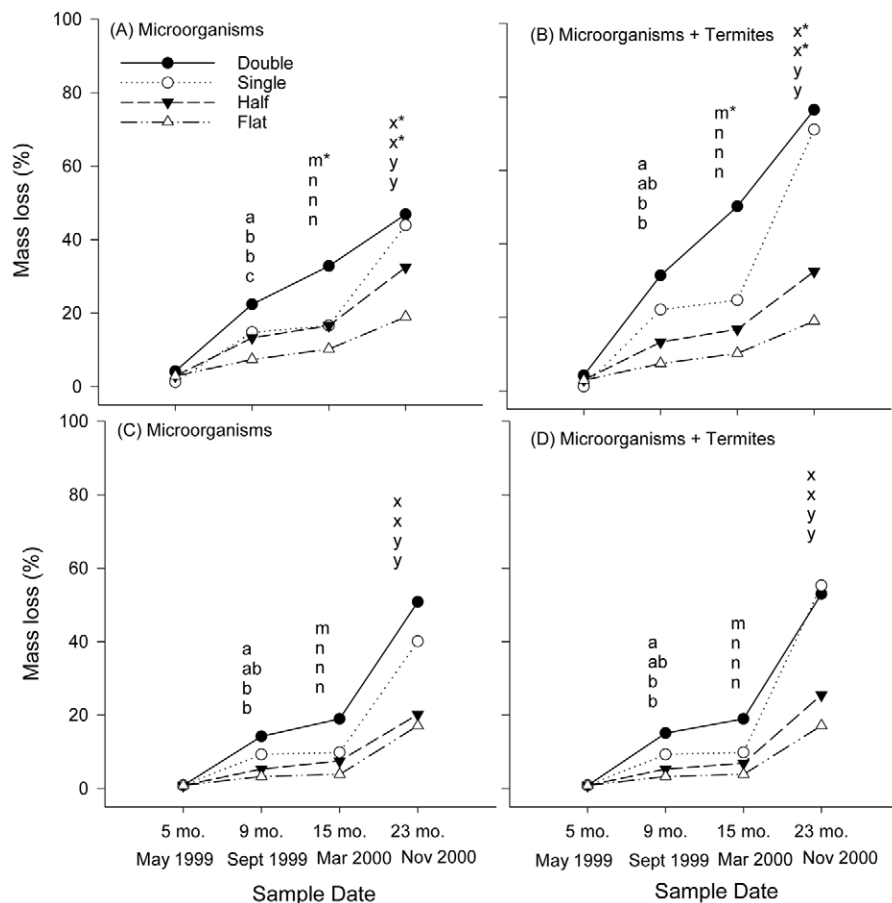
Fig. 1. Effect of soil bed height on aspen (A, B) and pine (C, D) stake mass loss by microorganisms and microorganisms plus termites in a mineral wetland near Summerville, SC. Different letters indicate significant differences among soil bed heights at the same sampling date, $p \leq 0.05$. Asterisks (*) indicate significant mass loss difference between only microorganisms and microorganisms plus termites at the same sample date and bed height, $p \leq 0.05$. There was no termite activity in flat soil across panels by wood stake species.

wet winter and spring months, and significantly higher mass loss in single and double beds by the end of the study. As expected, decomposition of pine stakes was significantly less than aspen across all bed heights (Supplemental Table S1), except at the last sample date (23 mo), when mass loss among soil bed heights was significantly different, but not between aspen and pine stakes (Fig. 2). This surprising result, which is likely related to the different number of aspen stakes (13) and pine stakes (23) taken

from single and double beds on this sample date, will be examined in greater detail in the Discussion.

Termites. In contrast to aspen, termites had little effect on the decomposition of pine stakes (Fig. 1D), which resulted from a lower incidence of termite attack (Table 1). Of the 93 pine stakes in the single and double beds sampled over the two year study, only 11 had termite damage (12%), as compared to 43 aspen stakes with termite damage out of 110 stakes sampled (39%). Similar to aspen, termites were not a factor in pine decomposition in half beds, as only 3 of the 75 stakes sampled had termite damage (<1%), and no termites were found in the flat soil.

Soil Depth

The impact of soil depth on stake decomposition was confounded by the presence of termites only in the single and double bed treatments. Therefore, we ran an analysis on stakes from all four soil bed heights that only had microbial decay, and a separate analysis on stakes with microbial decay and termite damage from single and double beds. Since there was no significant soil depth × bed height interaction for either wood species, mass loss at each soil depth for all sample dates was averaged across the four bed heights (Table 2). Except for the first sampling (5 mo), aspen and pine stake mass loss was highest at the 5-cm soil depth and decreased significantly with each depth increment. The proportion of total stake mass loss that occurred at each soil depth was also similar across sample dates and averaged 53% at 5 cm, 29% at 15 cm, and 18% at 25 cm.

Since many termite-damaged stakes were fragmented and incomplete, only 14 whole aspen stakes across all sample dates could be used to assess the effect of soil depth on termite damage.

Table 1. Mass loss of aspen and pine stakes by microorganisms and microorganisms plus termites in single and double soil beds in a mineral wetland near Summerville, SC, USA. Termites were not a factor in stake mass loss in the half bed and flat soils.

	Single bed					Double bed				
	Microbial decay		Microbial + termite decay			Microbial decay		Microbial + termite decay		
Time in soil	Stakes	Mass loss	Stakes	Mass loss	Incidence†	Stakes	Mass loss	Stakes	Mass loss	Incidence
mo	*n*	%	*n*	—— % ——		*n*	%	*n*	—— % ——	
				Aspen						
9	15	14.8	4	38.7	21	14	22.4	6	44.0	30
15	11	16.4	4	39.3	27	14	32.8	7	100	33
23	7	43.9	11	93.9	61	6	47.0	11	91.8	65
				Pine						
9	15	9.3	–	–	–	13	14.2	2	20.2	13
15	14	8.7	1	4.6	6	15	18.9	0	–	–
23	10	41.0	5	70.1	33	13	50.8	3	52.3	19

† Percentage of total stakes with termite-damage or gone at each sample date.
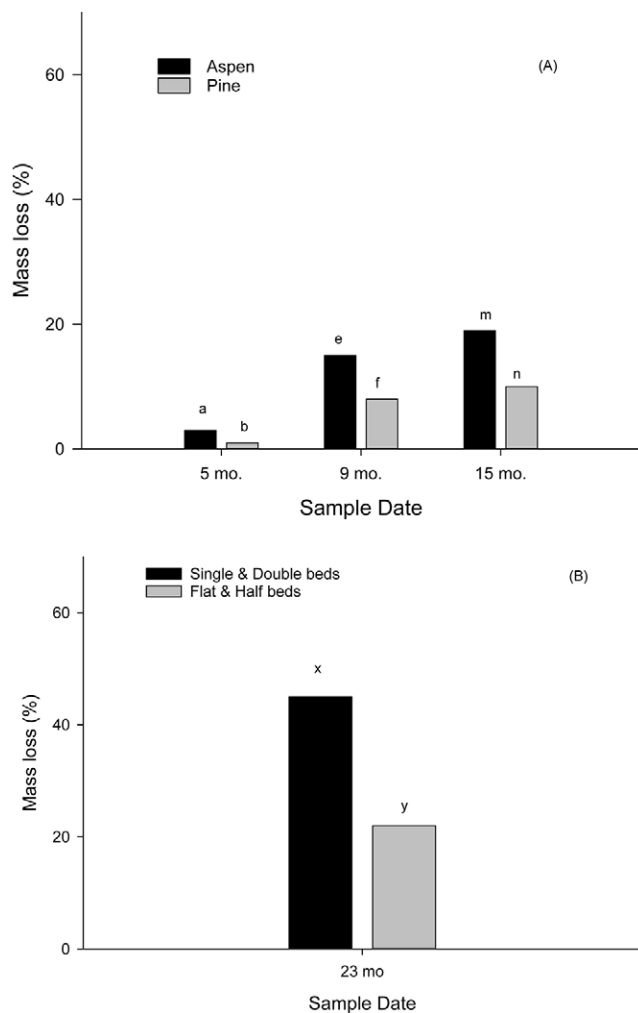
Fig. 2. Mass loss of aspen and pine stakes by microorganisms averaged (A) by species and (B) across soil bed heights in a mineral wetland near Summerville, SC. Different letters indicate significant differences between wood stake species at the same sampling date, $p \leq 0.05$.

Similar to microbial decay, mass loss in termite-damaged stakes was significantly higher at the 5-cm soil depth, but not different at the 15- and 25-cm depths. There were not enough suitable samples for an analysis of soil depth effects on termite-damaged pine stake decomposition.

Soil Microsite Variability

Decomposition of wood stakes in the soil beds reflect the biotic (e.g., microbial community, termite activity) and abiotic (e.g., temperature, water content) conditions of the soil around each stake. Small-scale (microsite) differences in soil properties could affect the decay rate (mass loss) of individual wood stakes, which would become more variable as the stakes decompose. Therefore, we used differences in mass loss among wood stakes (expressed as standard deviations) at each sampling date to estimate the effect of bed height on soil microsite variability (Table 3). Standard deviations of aspen stake mass loss from microbial decay increased over the four sample dates, especially in single and double beds, and when averaged over the study, microsite variability of wood decomposition increased as soil bed

height increased. The mass loss variability of termite-damaged aspen stakes in single and double beds were significantly larger than stakes with only microbial decay. However, mass loss standard deviations showed little change across sample dates, which likely indicates the probability of termites finding individual stakes in the soil beds, rather than the variability of soil microsite properties that affect wood decay.

The effect of soil bed height on microsite variability was less pronounced on pine decomposition than aspen (Table 3). Standard deviations of pine stake mass loss from microbial decay increased as time in the soil increased, but differences among bed heights averaged over the study were not significant. Similar to aspen, mass loss variability of pine stakes with termite damage were larger than for stakes without termite damage.

DISCUSSION
Soil Bedding

Increased soil volume above the water table, and the physical mixing of surface OM with mineral soil by bedding equipment, improves the soil macropore to micropore ratio, lowers bulk density, increases N availability, and most importantly, increases soil oxygen levels in poorly-drained soils (Kelting et al., 2000; Neaves et al., 2017). The average height of the double beds in our study was 30 cm, but varied from a minimum height of 23 cm to a maximum of 43 cm above the original wetland soil surface (P. Dougherty, pers. comm., 2018). Similar variations in soil bed height occurred in the single (average 20 cm ± 7 cm; max 30 cm) and half beds (average 7.5 cm ± 3 cm; max 12 cm). Small differences in bed heights were likely a major factor in microsite wood decay variability within and among soil beds. Bed height was an important component of a soil microsite quality index developed in Louisiana for pine seedling survival after planting (Khanal et al., 2018).

Microbial Decomposition

Our study shows that bedding a poorly-drained South Carolina soil increased microbial wood decomposition, which was affected by soil bed height and microsite variability. Trettin et al. (1996) reported increased loss of soil OM after beds were established on a poorly-drained, clear-cut harvested forest soil in northern Michigan, which they attributed to increased microbial activity from higher soil temperatures and a more favorable soil oxidation status. Soil micro-climate conditions in our soil beds were monitored by Westvaco Company personnel, but the data collected during our study period could not be found. However, soil bed measurements for 21 mo prior to the beginning of our study (February 1997 to October 1999) showed that increased soil bed height decreased volumetric soil moisture contents and increased soil oxygen status (Supplemental Fig. S2). The effect of bed height on soil moisture and aeration follows the seasonal pattern of wood stake mass losses found in our study.

Microbial decomposition of both aspen and pine stakes were highest near the soil surface in all bed heights and decreased at lower soil depths. Similar results have been reported in many litter

Table 2. Effect of soil depth and incubation time on aspen and pine stake mass loss from microbial decay in a mineral wetland near Summerville, SC, USA. Values averaged across soil bed heights.

Soil depth	Incubation time							
	5 mo		9 mo		15 mo		23 mo	
	Mass loss	Proportion†	Mass loss	Proportion	Mass loss	Proportion	Mass loss	Proportion
cm					%			
				Aspen				
5	5.0a‡	60	26.3e	61	31.1l	54	48.9x	51
15	2.5b	26	12.4f	25	17.6m	28	27.0y	29
25	1.3b	14	6.8g	14	10.8n	12	17.1z	20
Average	3.0		14.5		19.3		33.0	
				Pine				
5	1.9a	40	12.6e	54	16.0l	58	42.4x	52
15	1.3a	31	6.4f	29	8.8m	30	27.3y	52
25	1.1a	29	3.7g	17	4.0n	12	19.0z	30
Average	1.4		7.6		9.6		28.8	

† Percentage of total stake mass loss at each soil depth.

‡ Values with different letters indicate significant differences ($p \leq 0.05$) among soil depths for each species.

bag decomposition studies, in which soil temperature has been the major controlling soil variable (e.g., Gill and Burke, 2002; Berhe, 2013). However, in contrast to our hypothesis, the proportion of stake mass loss at each soil depth was consistent across the four bed heights, even though there were large differences in total stake mass loss among them. This indicates the relationship of soil oxygen to soil depth was similar among bed heights, and likely related to weather-induced lowering of the water table, especially in the half bed and flat soil (P. Dougherty, pers. comm., 2018).

Initially, aspen stakes decayed more rapidly than pine in all soil beds, which met expectations since the lower aspen lignin concentration and C to N ratio has been correlated with higher

Table 3. Standard deviations of aspen and pine stake mass loss as affected by soil bed height and incubation time in a mineral wetland near Summerville, SC, USA. Termites were not a factor in stake mass loss in the half bed and flat soils.

Bed height	Incubation time					
	5 mo	9 mo	15 mo	23 mo	Average	p-value
	Standard deviation of mass loss					
			Aspen			
Double						
Microorganisms	0.051a†	0.069a	0.096ab	0.127b	0.085A‡	0.006
Microorganisms + termites	–	0.196	0.267	0.260	0.239	
Single						
Microorganisms	0.018x	0.083y	0.075y	0.186z	0.082A	0.054
Microorganisms + termites	–	0.193	0.187	0.258	0.213	
Half						
Microorganisms	0.020	0.048	0.047	0.123	0.060B	
Microorganisms + termites	–	–	–	–	–	
Flat						
Microorganisms	0.029	0.032	0.035	0.058	0.038C	
Microorganisms + termites	–	–	–	–	–	
			Pine			
Double						
Microorganisms	0.020	0.071	0.111	0.125	0.082	0.029
Microorganisms + termites	–	0.236	0.247	0.207	0.230	
Single						
Microorganisms	0.018	0.069	0.077	0.173	0.084	0.157
Microorganisms + termites	–	0.094	0.176	0.300	0.193	
Half						
Microorganisms	0.026a	0.045b	0.041b	0.176c	0.072	
Microorganisms + termites	–	–	–	–	–	
Flat						
Microorganisms	0.029x	0.026x	0.035x	0.097y	0.046	
Microorganisms + termites	–	–	–	–	–	

† Values with different lowercase letters are significantly different ($p \leq 0.05$) across incubation times.

‡ Values with different capital letters are significantly different ($p \leq 0.05$) among bed heights without termites.

Table 4. Impact of subterranean termites on wood decomposition in field and laboratory studies.

Forest type	Wood blocks/dowels		Mass loss			Length of study	Reference
	Species	Size	Total	Termites only	Blocks with termites		
		cm		———— % ————			
			South Carolina				
Loblolly pine	*Pinus taeda*	2.5 × 2.5 × 12	55	12	9	23 mo	This study
	Populus tremuloides	2.5 × 2.5 × 12	75	39	28	23 mo	This study
Turkey oak	*Pinus* spp.	5.1 × 5.1 × 10.2	7	80	3	9 mo	Gentry and Whitford (1982)
Longleaf pine	*Pinus* spp.	5.1 × 5.1 × 10.2	18	65	15	9 mo	Gentry and Whitford (1982)
Lowland hardwood	*Pinus* spp	5.1 × 5.1 × 10.2	9	70	4	9 mo	Gentry and Whitford (1982)
			North Carolina and Georgia				
Hardwood/pine	*Pinus taeda*	8.8 × 8.8 × 3.5	6	57	4	20 mo	Ulyshen (2014)
Hardwood/pine	*Triadica sehifera*	20 × 0.2–2.5	–	–	9–10	8–20 mo	Stoklosa et al. (2016)
			Oklahoma				
Loblolly pine	*Pinus taeda*	12.7 × 1.8 × 0.6	38–51	54	32–39	426 d	Zhang et al. (2016)
			Laboratory				
	Pinus strobus	10 × 10 × 1.25	10	–	5	25 wk	Neupane et al. (2015)
	Acer rubrum	10 × 10 × 1.25	13	–	3	25 wk	Neupane et al. (2015)
	Quercus rubra	10 × 10 × 1.25	10	–	<1	25 wk	Neupane et al. (2015)
	Betula alleghaniensis	10 × 10 × 1.25	9	–	<1	25 wk	Neupane et al. (2015)

wood decomposition rates (Laiho and Prescott, 1999; Weedon et al., 2009; Wang et al., 2018). Our aspen stakes had an average lignin concentration of 21% and a N concentration of 0.11%; whereas loblolly pine stakes had an average lignin concentration of 31% and a N concentration of 0.077 (Wang et al., 2018). However, the similar mass loss of termite-free aspen and pine stakes in the single and double beds at 23 mo was a surprise, and may be explained by the low sample size of termite-free aspen stakes, compared to the larger number of pine stakes sampled. Since our study results show that aspen stakes are more likely to be found and consumed by termites than pine stakes (discussed below), the termite-free aspen stakes in the single and double beds may have been located at soil microsites unfavorable to termite activity (i.e., higher water contents, less oxygen), and would also be less suitable for microbial decay. In contrast, the higher number pine stakes without termite damage was likely due to termites not finding them or a low feeding preference for pine wood, rather than the pine stakes being located at unfavorable soil microsites. Therefore, the similar mass loss of pine and aspen stakes in the single and double beds at this sample date may reflect a higher number of pine stakes located at soil microsites more favorable to microbial decay than the few remaining aspen stakes.

Termites

As indicated by the lack of wood stake termite damage, this poorly-drained wetland did not have an active termite population before the soil was bedded. However, termites are present and active in the single (20 cm) and double (30 cm) beds, where they increased aspen stake mass loss by more than 20% after 2 yr in the soil. In a similar poorly-drained Georgia soil, Forschler and Henderson (1995) found very wet soil conditions caused by heavy winter rainfall greatly reduced *Reticulitermes* colony populations the following spring. Ulyshen (2014) reported that termites were less active in seasonally-flooded than in unflooded mineral soil in Mississippi hardwood/pine forests, but the incidence of termites in logs placed on the surface of both soils was not significantly different. This raises the question if termites can survive in such flooded ecosystems, or if they have to recolonize after the water recedes. A laboratory study by Forschler and Henderson (1995) suggests that *Retimlitermes* spp. do not try to escape high soil water contents, but enter a state of quiescence to survive until soil conditions improve. Braccia and Batzer (2001) found a few termites in floating woody debris in a seasonally-flooded South Carolina bottomland hardwood forest, but no termites were present in wood on the soil surface during the wet or dry season. However, Su et al. (1993) reported finding termites in standing dead oaks above the waterline after a southeastern Florida wetland soil was flooded. While flooding and high year-round rainfall has eliminated subterranean termites from some tropical forest ecosystems (Bignell and Eggleton, 2000), there is little information on the effect of wet soil conditions or soil drainage class on termite occurrence and activity in North American forests.

Surprisingly, we could not find any studies on the effects of soil beds or other forest management practice on termite activity. As discussed earlier, soil bedding would facilitate termite colonization by reducing soil bulk density and increasing soil oxygen levels (Kelting et al., 2000; Neaves et al., 2017). Timber harvesting may increase root decomposition by termites, as they accounted for ~50% of coarse root mass loss after trees were cut on a West African farm (Manlay et al., 2004). In contrast, management-prescribed, low-intensity fires would likely have little impact on subsequent termite activity, as Peterson et al. (2008) found that charred wood had no effect on termite-feeding preference.

As compared to mound-building termites, there is relatively little information in the literature on the impact of termites on wood decomposition in temperate forests (Table 4). Overall, termites removed <15% of surface wood biomass in studies conducted for 1 yr or less, but losses up to 39% occurred in

longer studies (1.5 to 2 yr). The effect of study length was clearly shown by Gentry and Whitford (1982), who found that >65% of their wood samples had termite damage after 9 mo, but total mass loss was <15%. In contrast to wood block/ stake studies, loblolly pine bolts (56 cm × 22.5 cm) lost 20.5 and 13.7% of their specific gravity after 31 mo in flooded and unflooded Mississippi hardwood/pine stands (Ulyshen, 2014), and Maynard et al. (2015) estimated that *Reticulitermes* spp. consumed 10% of annual dead wood litter in some eastern deciduous forest ecosystems.

Our study results showed that aspen stakes were attacked more often than pine stakes in both single and double beds. Since termites would likely have an equal probability of finding aspen and pine stakes if they forage randomly through the soil beds (Su et al., 1984), the higher incidence of termite attack suggests that aspen might have a soil "signal" that attracts termites (Grace and Campora, 2005). Such a signal could be a metabolite from microorganisms actively decaying aspen wood, or a chemical released during the wood decomposition process (Cornelius et al., 2003). Brown-rot fungi appear to have such a role, as some termite species have shown a preference for wood colonized by this fungal group (Getty and Haverty, 1998; Maynard et al., 2015).

Another possibility is that termites encountered pine stakes as often as aspen, but they preferred to feed on aspen wood. As multiple stakes (food sites) are found, foraging termites decide where to allocate their feeding efforts, since not all food resources may be equally acceptable (Waller and LaFage, 1987; Oi et al., 1996; Lee and Forschler, 2016). Aspen has a high cellulose to lignin ratio and a lower wood density (0.35 g cm^{-3}) than pine (0.50 g cm^{-3}), which makes it more favorable to termite attack (Bultman and Southwell, 1976; Ohkuma, 2003; Judd and Corbin, 2009; Shanbhag and Sundararaj, 2013). However, field and laboratory studies have shown that wood of pine species is readily consumed by termites (e.g., Arango et al., 2006; Lee and Forschler, 2016), so it is not clear why pine stakes in our study had a low incidence of termite damage.

Management Perspectives

The establishment of raised planting beds on poorly-drained soils is an important management practice in the southeastern United States, and greatly improves the survival and growth of planted seedlings (e.g., Morris and Lowery, 1988; Kelting et al., 2000; Fox et al., 2007). The incorporation of surface OM during bedding operations initially increases mineral soil C and N concentrations (Maier et al., 2012), but McKee and Shoulders (1974) reported soil OM concentrations were significantly lower 8 yr after bedding. Neaves et al. (2017) also found a similar reduction in soil C content 25 yr after soil bedding. Such long-term C reductions in bedded soils are likely caused by increased OM decomposition by soil microorganisms, such as was shown in our study. However, none of the above studies examined soil beds for presence or activity of termites.

Termites were not present in our poorly-drained wetland soil before it was bedded. However, the establishment of 20-cm and 30-cm high soil beds allowed termites to colonize the soil and increase the decomposition of wood. Termites can increase C pools by defecation and nest construction in the mineral soil (e.g., Nutting et al., 1987; Myer and Forschler, 2018), but OM passage through termite guts may make the added soil C more susceptible to microbial decomposition and subsequent C loss (Dahlsjo et al., 2014). Termites could also increase soil productivity by fixing atmosphere N$_2$ (Nardi et al., 2002; Yamada et al., 2006), but they also emit methane, a potent atmospheric green-house gas (Sugimoto et al., 2000).

Future changes in climate could affect the role of termites in OM decomposition, especially in poorly-drained soils, since termite activity is correlated with seasonal changes in soil temperature and moisture (Haverty and Nutting, 1974; Houseman et al., 2001). Unfortunately, the tools to assess the potential effects of termites and climate on soil properties are few, as a recent examination of 23 soil biogeochemical C models indicated that only six have a separate modules for wood decomposition, and none included termites or other soil invertebrates (Dai, unpubl. data, 2018).

While bedding wetland soils is clearly beneficial to tree growth and stand productivity (Gent et al., 1983, VanderSchaaf and South, 2004), the possible long-term impact of soil bed C loss from microbial and termite activity on future soil productivity is unknown. Such information on how soil bedding and other forest management practices affect OM decomposition rates and subsequent soil C sequestration is important to managers, scientists and climate change modelers. Therefore, the impact of soil beds and soil bed height on OM decomposition and termite activity deserves greater attention.

SUPPLEMENTAL MATERIAL
Supplemental material is available with the online version of this article. The supplemental file contains Fig. S1, Representative aspen and pine stakes showing only microbial wood decay and both microbial wood decay and termite activity; Fig. S2, Effect of bed heights on soil moisture content and soil aeration in a poorly-drained wetland soil near Summerville, SC, February 1997 to October 1999; and Table S1, Full ANOVA model for: 1) wood stakes with microbial decay plus termite damaged and 2) wood stakes with only microbial decay.

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