ECOSYSTEMS

Experimental Evidence that Forest Structure Controls Detrital Decomposition

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ABSTRACT

Much remains unknown regarding the linkages between forest structure and microclimate as they regulate detrital decomposition. In this study, we use a factorial field experiment that included canopy gap creation and downed woody material (DW) additions conducted in a mature northern hardwood forest. Our objectives were to (1) test the individual and combined effects of canopy gaps and DW additions on detrital mass loss; (2) determine whether the factors regulating mass loss are similar among leaf litter, experimental wood stakes, and coarse DW; and (3) assess the microclimatic variables that most strongly influence mass loss of these detrital types. After three years, leaf litter mass loss within gaps, without or with DW additions, was significantly greater than that of any non-gap treatments. Mass loss of stakes was significantly greater in gaps, intermediate in gaps with DW additions, and lowest in non-gap treatments. Mass loss of wood stakes after 8 years varied by species, with aspen (*Populus tremuloides*) losing up to 93% and sugar maple (*Acer saccharum*) up to 82% of its original mass. Fourteen years following treatment, the experimental logs lost 55–70% of their original mass, with ash (*Fraxinus* spp.) decaying faster than maple. Gap creation and DW additions individually, but not in combination, increased mass loss of coarse DW. For most substrates tested, gaps were consistently and positively related to mass loss, with approximately 10% greater mass loss in gaps compared to non-gaps. The presence of deadwood strongly moderated litter decomposition, had minimal effect on small woody substrates in the short-term after gap creation, but was influential on longer-term decay patterns of larger DW. Predictive models for each substrate varied, though shared some similar drivers. Litter mass loss was positively correlated to increasing gap size, canopy openness, and soil moisture. Stake mass loss was positively correlated to increasing gap size and canopy openness for maple, but soil temperature for aspen. Mass loss for logs was driven by increasing DW volume and gap size for ash, but soil temperature for maple. Smaller-sized materials may be more sensitive to environmental conditions as opposed to logs for which microclimatic influence may lag or remain a minor driver for at least the initial decade of decomposition. Regardless of substrate type, the findings of this work highlight the potential for greater rates of detrital mass loss from forest sys-

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tems under predicted increases in canopy disturbance rates with climate change and invasive insects and diseases.

Key words: forest carbon cycle; forest structure; leaf litter; Northern hardwoods; deadwood; downed woody material; wood decay.

HIGHLIGHTS

- Followed decomposition of litter, wood stakes and logs for 3, 8, and 14 years.
- Greater rates of detrital mass loss in canopy openings, but moderated by deadwood.
- Smaller sized material more sensitive to environmental conditions.

INTRODUCTION

Forests play a critical role in the global carbon cycle, given the sequestration and storage potential of live vegetation and the long-term storage by detritus. However, as detritus decomposes, its carbon is transferred to other pools, with most carbon ultimately being released to the atmosphere as CO_2. Detrital decomposition remains one of the least understood and inadequately quantified components of the forest carbon cycle, particularly considering the comparatively large body of literature on forest productivity. This knowledge gap arises from the complexity of the biotic and abiotic factors that interact to determine decomposition rates (Bradford and others 2014; Zanne and others 2015; Glassman and others 2018), as well as the long time period needed to track the more recalcitrant detrital components (McFee and Stone 1966; Kueppers and others 2004). A better understanding of the factors governing detrital decomposition rates is needed to improve process-based models of forest carbon dynamics used to simulate forest carbon management scenarios.

Numerous studies have shown that forest canopy openness—presumably through its influence on microclimate—alters leaf litter decomposition rates. However, studies addressing this issue have come to differing conclusions. Gliksman and others (2018) and Mayer and others (2017) report greater litter mass loss under canopy gaps, attributed to increased temperatures. In contrast, lower litter mass loss has been reported due to lower soil moisture and higher light intensity in gaps (Zhang

and Zak 1995) or altered freeze–thaw cycles in gaps (Tan and others 2020). Fewer studies have addressed the influence of canopy gaps on deadwood decomposition rates, but these too arrive at differing conclusions. Griffiths and others (2021) report greater deadwood mass loss under tropical canopy gaps (attributed to increased termite activity), and Shorohova and Kapitsa (2014) similarly report greater deadwood mass loss under open canopies. In contrast, Forrester and others (2015) report no difference in CO_2 flux rates (a measure of decomposition) from logs under canopy gaps and those under closed canopies four years after gap creation, although CO_2 flux from coarse deadwood was higher in canopy openings the first two years following gap creation (Forrester and others 2012). These inconsistent results for both leaf litter and deadwood decomposition emphasize the need for further study, as the influence of canopy structure appears to be region and context dependent as well as temporally dynamic.

This knowledge gap is particularly important considering that the projected increases in the frequency and intensity of extreme weather events (Seidl and others 2017) and non-native insects and diseases (Fei and others 2019) would create additional canopy disturbance and deadwood creation, in turn leading to altered decomposition rates. These considerations also lead us to question if the environmental conditions that regulate leaf litter decomposition are the same as those that regulate deadwood decomposition. Indeed, few field studies have simultaneously addressed decomposition rates of leaf litter and deadwood under various microclimatic settings.

Recently, fabricated wooden stakes or blocks have been used to assess wood decomposition, and their use is providing insights that had been previously underappreciated (see Bradford and others 2014; Meier and others 2010; Fraver and others 2018). Standard stakes provide the advantages of having known initial mass, being uniform in size and free from defects, and being fabricated from wood species of interest to a particular site. However, they may be best viewed as a proxy for small downed woody material (DW) (between 1–10 cm diameter), because of their typical small size and lack of bark. The degree to which inferences drawn from wood stakes can be extrapolated to coarse DW (that is, logs > 10 cm diameter) remains unknown, but this study provides an opportunity to evaluate how representative they are for larger material.

In this study, we use a factorial field experiment that included canopy gap creation and DW addi-

tions, conducted in a mature northern hardwood forest in Wisconsin, USA. Our specific objectives were to (1) test the individual and combined effects of canopy gaps and DW additions on detrital mass loss; (2) determine whether the factors regulating mass loss are similar among leaf litter, wood stakes, and coarse DW; and (3) assess the microclimatic variables that most strongly influence mass loss of these detrital types. We focus on early stages of leaf litter decomposition, when litter was shown to have the greatest effect on nutrient conservation or loss after disturbance (Vitousek and Matson 1984, 1985). We hypothesized that canopy gaps would increase decomposition rates, because increased radiative inputs combined with decreased evapotranspiration would lead to warm, moist conditions ideal for fungal activity and the degree of influence would increase with increasing gap size. We hypothesized that deadwood abundance would moderate decay among materials, due to additional variability in microclimate caused by the DW augmentations.

METHODS

Research Site and Experimental Design

The Flambeau Experiment was established to test the effect of forest structure on productivity, diversity and carbon and nutrient cycling in a second-growth northern hardwood forest. Experimental treatments were designed to isolate the effects of canopy gap size and DW abundance on multiple near- and long-term response variables. The study is established within the Flambeau River State Forest, a 36,500 ha forest in north-central Wisconsin, USA. The site is representative of the regional forest landscape, namely, maturing hardwood stands containing two co-dominant age cohorts. Sugar maple (*Acer saccharum*) dominates the overstory, with white ash (*Fraxinus americana*), basswood (*Tilia americana*), American elm (*Ulmus americana*), and bitternut hickory (*Carya cordiformis*) as co-dominants. Sugar maple is the dominant tree seedling, and sugar maple, white ash, and hop-hornbeam (*Ostrya virginiana*) are common saplings. The mesic site is gently sloping to flat, with silt loam soils (Glossudalfs) of the Magnor and Freeon series overlaying dense glacial till. Freeon, the moderately well drained series, is the dominant series across the site while Magnor occurs in lower or less sloping areas. January and July air temperatures (1980–1997) average − 12 and 19 °C, respectively (Daymet U.S. Data Center, http://daymet.org). The median length of the growing season is 105 days (base temperature = 0 °C) (1971–2000) (Midwest Regional Climate Center, http://mcc.sws.uiuc.edu). Mean annual precipitation averages 83 cm.

The experimental design includes factorial combinations of two factors: canopy gaps and DW with two levels of each factor. The resulting treatment combinations—gap creation, DW addition, gap creation plus DW addition, and unaltered control—were randomly applied to five replicate 80 × 80 m plots, for a total of 20 plots within a 280-ha area of the State Forest (Figure 1). Gap sizes (50, 200, and 380 m^2) were based on those natural canopy gaps found in regional old-growth hardwood forests; one gap of each size was created within each plot. A 50-m^2 gap approximates the average crown size of an old-growth hardwood tree and the median gap size in old-growth northern hardwoods (48 m^2; Dahir and Lorimer 1996). A 380-m^2 gap represents the upper end of the most frequently occurring gap sizes in old-growth hardwoods (Hanson and Lorimer 2007). These gaps and gap sizes serve as subplots; for consistency, same-sized subplots were established in the controls, even though no gaps existed.

Permanent 4-m^2 quadrats were established within subplots in cardinal and sub-cardinal directions (Figure S1). These quadrats provide a common framework for integrating analyses of structure, microclimate, and processes across differing temporal scales. This study utilized a portion of the quadrat layout that allows fine-scale delineation of aspect and gap-edge influence resulting from gap-creation treatments.

The DW treatments included: (1) DW augmentation up to that mass expected in old-growth northern hardwoods, 29 Mg ha^{-1} (Goodburn and Lorimer 1998), and (2) no change to background DW levels (2 Mg ha^{-1}; Forrester and others 2013). Trees harvested to create canopy gaps were either felled and left in place (GDW treatment) or redistributed within the site to DW addition plots (DW treatment). Augmentation occurred across the whole plot. All treatments were established in winter 2006–2007, when the ground was frozen and snow-covered.

Experimental treatments for the larger project were implemented in 2006–2007. In order to test the effects of the gaps and DW addition on decay rates, we monitored mass loss in three distinct substrates–leaf litter, fabricated wood stakes, and experimentally placed logs–each explained below.
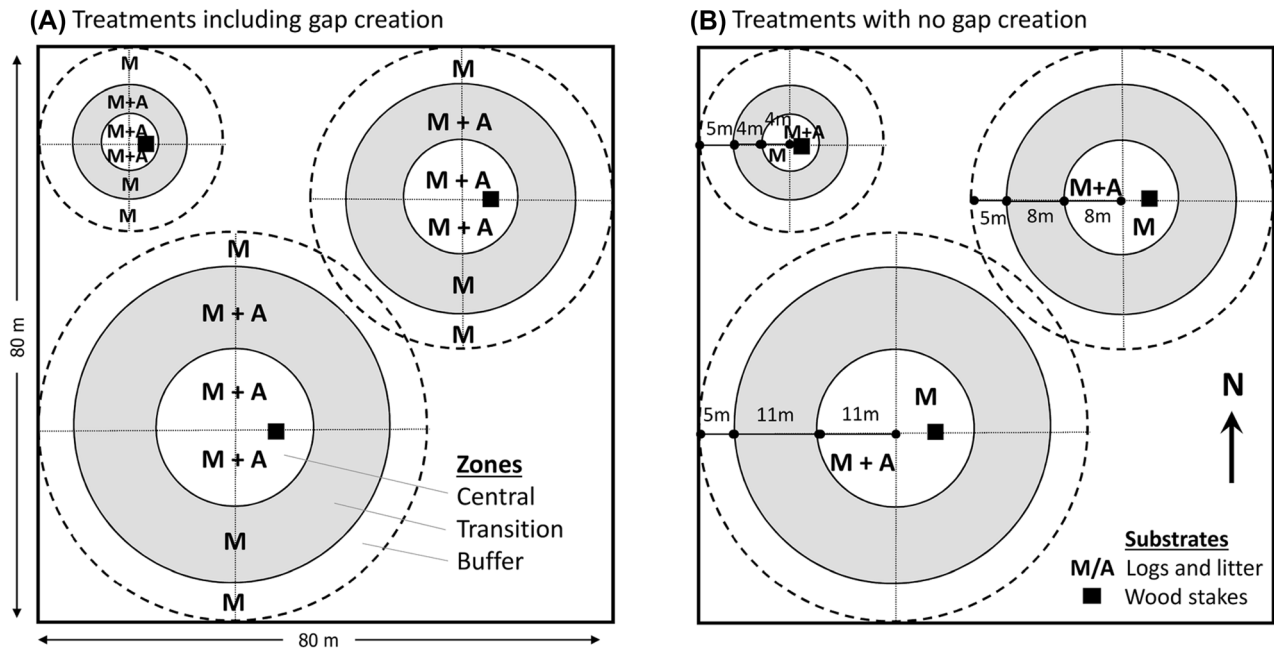
Figure 1. Layout of substrates in (A) two gap creation treatments (Gap only, Gap + DW) or (B) two treatments without gap creation (DW addition, control). Each whole plot includes three variable sized subplots composed of three concentric zones—central, transition and buffer listed from center out. The central zone was harvested in gap creation treatments. Letters indicate position of Maple or Ash logs (2 m long by 20 cm diameter). Litter bags were placed alongside logs at all 18 locations in the gap creation treatments and 6 locations in treatments without gap creation. Maple and aspen wood stakes were placed north of the understory vegetation quadrant symbolized with a square, east of subplot center.

Leaf Litter

Leaf litter was collected from the site in September and October 2008, dried, portioned into bags and distributed in the field in late fall 2008. Litterbags, measuring 20 × 20 cm, were made of polyester net with a mesh size of about 1 mm × 0.5 mm. Twelve replicate bags containing dried leaf litter (10 g) were strung together and placed on the forest floor in the north (3 each) and south (3 each) quadrats of each of three subplots in Gap and Gap + DW treatments (12 bags × 6 locations × 3 subplots for a total of $n = 216$ bags per plot) (Figure 1A). In non-harvest treatments (Control and DW) bags were placed at two randomly assigned locations within each subplot (12 bags × 2 locations × 3 subplots for a total of $n = 72$ bags per plot) (Figure 1B). Four replicates of litter bags were collected at the onset of each growing season from 2009 to 2011. After drying, any soil, plant or miscellaneous material adhered to the bags was removed and the remaining material within the bag was weighed to the nearest 0.01 g.

Fabricated Wood Stakes

Wood stakes were manufactured to 2.54 × 2.54 × 20 cm from the heartwood of un-treated, defect-free, regionally harvested sugar maple and aspen (*Populus tremuloides*). Aspen was chosen for comparability within a region-wide wood-decay study based on wood stakes. Before being deployed, all stakes were oven dried at 75 °C for 8 days to achieve constant mass, and each was weighed while dry to provide initial mass and density. A set of 8 stakes were placed 1 m north of permanently marked understory vegetation quadrats established 4 and 6 m to the east of subplot center in the medium and large subplots, respectively, and 2 m east of subplot center in the small subplot in gap creation, DW addition, Gap + DW addition, and control plots (Figure 1). This placement intended to minimize trampling by field crews. Each set included 4 sugar maple and 4 aspen stakes. Each stake was uniquely tagged and secured on top of the litter layer with a 15-cm landscaping staple with approximately 20 cm between each stake within the set. A total of 240 stakes of each species (4 stakes × 2 species × 3 subplots per plot × 5 plots per treatment × 4 treatments) were placed in July 2010. A stake was collected from every location in June or July of 2012, 2014, 2016, and 2018, that is, after two to eight years of decay on the forest floor. We note that ca. 5% of the stakes could not be found for collection. In the

laboratory, stakes were cleaned of debris and oven dried as above before being weighed to determine mass loss.

Experimentally Placed Logs

Sugar maple and ash logs (2 m long by approximately 20 cm diameter) were cut from material harvested from gap-creation treatments. A pair of logs (one of each species) was placed in the north and south positions within the central and transition zones of each subplot (Figure 1A). Logs of maple only were placed in additional locations north (1 log) and south of the harvested gap (2 logs). In non-gap addition treatments, logs were paired with the litter bags at two locations in each subplot (Figure 1B). Log length and diameter at three locations (ends and middle) were measured when logs were initially placed and re-measured nine years later.

To determine changes in wood density and mass, three small-diameter (5.2 mm) cores were extracted from each log at the onset of the growing season 1, 2 and 4 years after treatment. Cores were extracted at 0.5 m intervals along the length of the log (at 0.5, 1, and 1.5 m from end). By year nine, most logs had decayed to the point where core extraction was not feasible. Thus, in year nine and fourteen, one replicate plot from each treatment was randomly selected for more intensive sampling. As such, five 2-cm wide disks were cut from each log in this subset of plots, also at 0.5-m intervals along each log.

Upon collection, samples (cores or disks) were oven-dried (70–75 °C for at least 1 week) to constant mass. We estimated wood density (g cm^{-3}) as the ratio of wood oven-dry mass to volume. Core volume was estimated both by water displacement in a graduated glass cylinder and by direct measurements of core length and diameter. Disk volume was based on the average of three diameter and width measurements per disk. These measurements were recorded on freshly harvested disks and for a subset of disks (n = 83) after drying. Fresh disk volume was reduced by 12% based on the average difference in fresh and dry volumes so that wood density could be expressed as dry mass/dry volume.

Log volume was calculated using Newton's formula (Husch and others 2003). Wood density per log and time period were estimated using the average of the three cores or five disks. Total log mass loss was estimated by combining volume loss and density reduction, with ML = (V$_0$ × Dens$_0$) − (V$_T$ × Dens$_T$), where *ML* is mass loss, *V* is volume, *Dens* is density, and *0* and *T* are placement time (sound wood) and sample time, respectively (Grier 1978; Lambert and others 1980; Tyrrell and Crow 1994).

Environmental Data

Here, we test the effects of the changing conditions following experimental treatments established in 2006–2007. Measurements to describe the microclimate of the logs, stakes and litter bags were focused in the central zone of the large subplots (Figure 1). Discrete soil temperature was measured to 2 cm soil depth using a long-stem thermometer (model no. 15-078 k, Fisher Scientific) and soil moisture was measured using a portable TDR (Delta TH2O, Dynamax In., Houston, TX). Soil measurements were recorded monthly (April – Nov 2010 and 2011) from four permanent fixed locations. To avoid time-of-day sampling bias, we randomized the order in which plots were sampled on each sampling visit. Annual z-scores were calculated for both temperature and moisture and the two years were averaged, creating one temperature metric and one moisture metric capturing two growing seasons.

Hemispherical canopy photographs were taken at two permanent locations (north and south of subplot center) after full leaf-out in 2008 and 2016. Photographs were taken using a Nikon Coolpix 5000 with a FC-E8 fisheye lens mounted to a tripod, at 1.5 m height (for more information, see Forrester and others 2014). Woody understory was measured in permanent 2 × 2 m quadrats established in the cardinal directions from the center of the subplot. Understory was divided into the following height classes: 0–30 cm, 30.1 – 100 cm, 100.1–140 cm, and 140.1–200 cm). Stem counts were recorded in these height classes in 2007, 2010, 2014, and 2016. A complete inventory of downed woody material (> 10 cm diameter) was conducted on the 0.64-ha treatment plots in 2008 following methods described in Forrester and others 2013. Here, we used a summary of volume and biomass for the large subplots only.

We acknowledge that a range of soil properties may influence the decay dynamics we sought to test. However, previous studies from the same experimental site have analyzed soil properties (compaction and chemistry) and litterfall and did not reveal variation that would support including these properties in the present analysis (Forrester and others 2013; Sabo and others 2019; Perreault and others 2021).

Data Analyses

The effect of various treatment combinations on the proportion of mass remaining through time for each substrate type was assessed using linear models (PROC MIXED in SAS ver. 9.4) with treatments (4 levels) and subplots (3 sizes) as fixed effects, and plots nested within treatments as random effects. The models for the experimentally placed logs included repeated measures as well. Only substrates positioned in the central zones of the subplots were used to test these questions. In all cases a logit transformation was used for the proportion of mass remaining. Separate models were used for each species of wood stakes (maple and aspen) or experimental logs (maple and ash). The Kenward–Roger denominator degrees of freedom was used for the heterogeneous, first-order autoregressive covariance model (AR[1]) to better account for unequally spaced repeated measures for the experimental log analysis. Mean comparison tests with Tukey adjustments were performed to test differences among treatments or significant model parameters. For all analyses, probability values < 0.05 are considered significant, while those between 0.05 and 0.1 are considered suggestive.

To test if the location related to gap center influenced decomposition, we used a subset of measurements limited to plots where gaps were created only (Gap and Gap + WD treatments, $n = 10$). We tested if the mass remaining in one measurement year was effected by treatment, subplot, or location for litter and experimental logs. We used the final mass remaining at year 3 for litter and year 14 for experimental logs. The linear models included treatment, subplot (gap size) and location (see Figure 1A) as fixed effects, and plots nested within treatments as random effects.

Our intent was also to identify the primary environmental drivers of decomposition among the substrate types. We used a number of covariates that characterized the microenvironments in the large gap (excluding the small and medium subplots). These variables included soil moisture and temperature, canopy openness (measured via hemispherical photographs) and the volume and biomass of deadwood on the whole plot (Forrester and others 2014, 2016). Covariates were evaluated for collinearity using correlation analysis, variance inflation factors and tolerance levels. Deadwood biomass was highly correlated with volume and weakly associated with a few other variables, thus it was removed from the analyses. The logit transformed proportional mass remaining of each sub-

strate type (litter, stakes, logs) in the final time period was used as the response variable in generalized linear models (PROC GLMSELECT in SAS ver. 9.4, backward selection procedure). Model selection procedures eliminated predictor variables that did not have significant relationships with mass remaining ($p < 0.05$), and ranked the models based on the corrected Akaike's information criterion (AICc) scores. We selected the final model for each substrate type and species based on the lowest AICc and Mallow's Cp scores.

RESULTS

Mass Remaining

Leaf litter lost 62–78% of its original mass during the three-year study period (Figure 2A). The proportion of litter mass remaining among treatments varied significantly with time (time x treatment F value 11.8, $p = < 0.0001$) (Table 1). Within treatments, the proportion remaining decreased significantly each year. Mass remaining in the gap creation treatment was significantly lower than all other treatments within the first year (p values < 0.0001), and that difference was sustained throughout the study period. Initially the pairing of DW addition appeared to moderate mass loss in the gaps, though by year 2 the combined treatment had less mass remaining than the non-gap treatments (all p values < 0.04). After three years, mass remaining within gaps, without or with DW additions, was significantly lower than that of the controls or DW addition (that is, non-gap treatments). Though we expected the effects of gap size to differ according to treatment type, the effect was not consistent in either gap creation treatment (Figure S2).

Mass remaining of the stakes varied by species, with aspen losing up to 93% and maple up to 82% of its original mass after 8 years (Figure 2b). For maple, the pattern of mass loss through time varied by treatment and gap size (Time × Treatment × Size, $F = 1.9$, $p = 0.009$). Mass loss of maple stakes in large gaps of the gap-creation treatments accelerated 4 years after placement and remained significantly higher than that of both treatments without gap creation. After 8 years, the mass remaining was significantly greater in the control and DW treatments, intermediate in gaps with DW additions, and lowest in gaps only. These patterns were not apparent in the smaller-sized gaps. Gap size influenced decay patterns in the gap creation treatment only, with significantly less mass remaining in the largest gaps relative to the
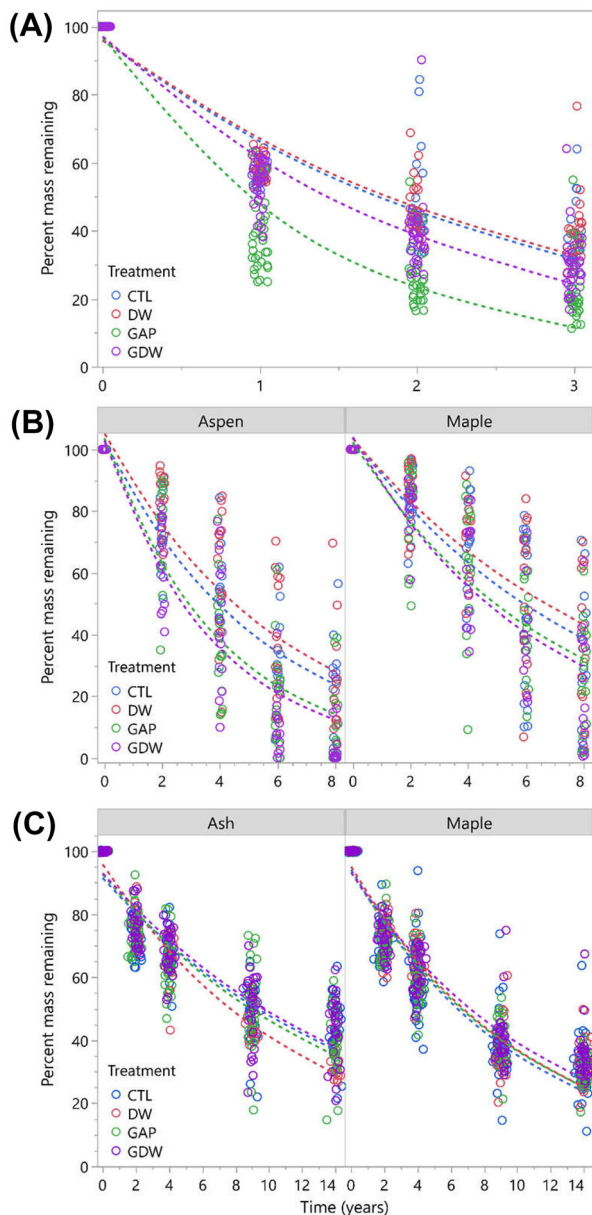
Figure 2. The percent mass remaining of (**A**) leaf litter, (**B**) wood stakes, and (**C**) experimental logs by treatment through time since harvest. Treatments include an unmanipulated control (CTL), dead wood addition (DW), gap creation (Gap), and gap creation + DW addition (GDW). Points represent sample mass by treatment and sampling period. Negative exponential models fit for each substrate, species and treatment are presented with dashed lines. Point data were logit transformed for statistical analyses (see text and Table 1).

small or medium sized gaps (*L* vs. *M*, $p = 0.0176$ and *L* vs. *S*, $p < 0.0001$) (Figure S3).

The mass remaining of aspen stakes also varied with treatment and gap size ($F = 1.9$, $p = 0.0074$). As with maple, variation in rates among treatments

became evident after four years in the large and medium sized gaps. Less mass remained in gap creation treatments across all subplot sizes, though variability was quite high in the largest gaps. The effects of gap size were limited to the Gap + DW treatment, where significantly less mass remained in the medium-sized gaps ($p = 0.0968$) (Figure S4).

The experimental logs lost 55–70% of their original mass over the fourteen years following harvest. Log decay progressed similarly for species and treatments for the first decade after placement, but then became more variable (Treatment × time, $p < 0.0001$ for ash and $p = 0.070$ for maple) (Figure 2C and Table 1). The treatments began to differentiate in year 9 (Trt*Time, slice = Y9, $p = 0.109$) and year 14 (Trt*Time, slice = Y14, $p < 0.001$) for ash and year 14 for maple (Trt*Time, slice = Y14, $p = 0.043$). The remaining mass of ash by year 14 did not differ between the control and Gap + DW treatments, was significantly lower in the gap treatment (*p* values all < 0.05), and was least in the DW treatment (*p* values all < 0.006). A marginal treatment-by-subplot interaction term indicates that the gap size also influenced mass remaining of ash ($p = 0.082$, Table 1). This is apparent in the highly variable and somewhat inconsistent patterns in mass loss among the gap creation treatments, relative to non-gap creation treatments (Figure S5).

Mass remaining of maple by year 14, was significantly greater in the Gap + DW treatment than the control ($p = 0.005$) or gap ($p = 0.074$) treatments, but did not differ from the DW treatment ($p = 0.112$) (Figure 2C). Overall maple mass remaining was generally lower than for ash, with the exception of the rate for ash in the DW treatment which was equivalent to rates for maple.

The location of logs relative to gap centers had little effect on patterns of mass remaining for the substrates tested, particularly leaf litter (Table S1). The effect of DW was much stronger ($F = 36$, $p = 0.0003$) than gap size, location or any interactions of these factors (Figure S6). Location of the maple experimental logs relative to the gap had a minor effect on the mass remaining depending on the treatment (Figure S7). Mass remaining did not differ between treatments in the Gap, but was significantly higher in the Gap + DW treatment versus Gap. The location again influenced ash experimental logs with less mass remaining in the transition (closed canopy) area north of gap center than logs in gap center (Figure S8).

Table 1. Results of Mixed Linear Models Identifying Factors That Describe Variation in Logit Transformed Proportion Mass Remaining of Substrates

Substrate	Factor	df	F	p
Litter	Time	(3, 388)	13,782	< 0.001
n = 451	TRT	(3, 16.3)	22.65	< 0.001
	Time*TRT	(9, 388)	11.82	**< 0.001**
	Subplot	(2, 389)	0.68	0.51
	Time*Subplot	(6, 388)	0.7	0.65
	TRT*Subplot	(6, 388)	2.43	**0.026**
	Time*TRT*Subplot	(18, 388)	0.5	0.96
Stakes				
Maple	Time	(4, 262)	1132.35	< 0.001
n = 284	TRT	(3, 19.2)	1.68	0.20
	Time*TRT	(12, 262)	1.08	0.38
	Subplot	(2, 266)	1.25	0.29
	Time*Subplot	(8, 262)	1.56	0.14
	TRT*Subplot	(6, 265)	9.52	< 0.001
	Time*TRT* Subplot	(24, 262)	1.88	**0.009**
Aspen	Time	(4, 267)	1156.05	< 0.001
n = 286	TRT	(3, 20)	12.71	< 0.001
	Time*TRT	(12, 267)	4.61	< 0.001
	Subplot	(2, 269)	3.27	0.04
	Time *Subplot	(8, 267)	2.26	0.02
	TRT*Subplot	(6, 268)	3	0.007
	Time*TRT*Subplot	(24, 266)	1.92	**0.007**
Logs				
Maple	Time	(4, 450)	16,550.8	**< 0.001**
n = 705	TRT	(3, 20.8)	0.93	0.44
	Time*TRT	(12, 503)	1.7	*0.064*
	Subplot	(2, 161)	1.76	0.17
	Time*Subplot	(8, 487)	0.45	0.89
	TRT* Subplot	(6, 161)	0.38	0.89
	Time*TRT* Subplot	(24, 521)	1.29	0.16
Ash	Time	(4, 344)	10,164.3	< 0.001
n = 510	TRT	(3, 21.9)	1.41	0.27
	Time*TRT	(12, 366)	4.04	**< 0.001**
	Subplot	(2, 109)	0.91	0.41
	Time*Subplot	(8, 360)	0.37	0.94
	TRT*Subplot	(6, 109)	1.93	*0.082*
	Time*TRT*Subplot	(24, 371)	1.27	0.18

Logs were analyzed as repeated measures. Significant main effects or their interactions are in bold; marginally significant effects are in italics. Sample sizes are included for each substrate, note zero values were added to each dataset for Time 0. Subplot indicates the gap size associated with harvested areas in gap treatments.

Environmental Variables

The changing abiotic and biotic properties affected by the experimental treatments were characterized periodically throughout the decade after treatment. Total groundlayer plant cover increased by at least 25% where gaps were created, and a midstory developed within nine years (Figure 3; Table 2). The density of vegetation at these heights reduced openness and altered the ground-level microclimate within gaps. Although canopy openness increased with gap creation, it returned to pre-gap creation values within nine years. Soil moisture was greater in the gap-creation and Gap + DW treatments, relative to control and DW additions (the treatment levels with no gap creation). Midday soil temperature patterns were inconsistent among treatments, but were generally more variable in gap-creation treatments. DW additions were substantial, and inventories quantified approximately 21–36 Mg coarse DW ha^{-1} in the addition treatments, compared to 2 Mg ha^{-1} in the treatments without additions (Forrester and others 2013).
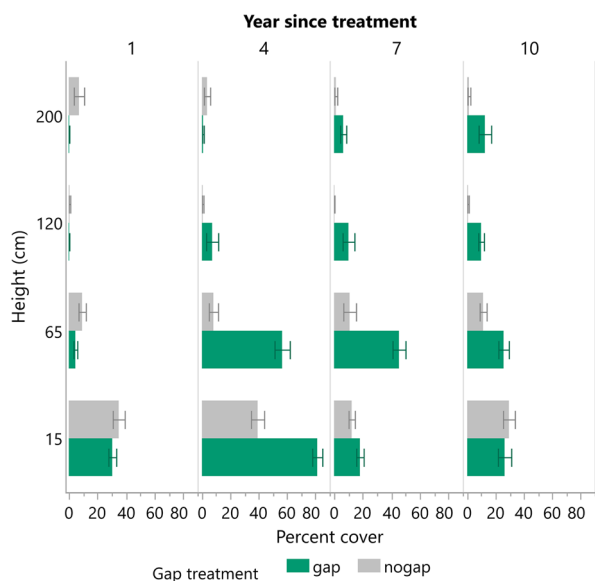
Figure 3. Understory vegetation height profiles at four time periods throughout the first decade following gap creation; data from the large subplots only (central zone). The green-filled bars represent average vegetation cover for gap creation treatments (Gap and Gap + DW), and the grey bars represent non-gap treatments (Control and DW).

Model selection procedures resulted in slightly different models for each substrate, with common drivers among models but in different combinations (Table 3). The amount of variation explained decreased substantially with the larger sized materials. Changes to litter mass loss were driven by increasing gap size, canopy openness, and soil moisture. Stake mass loss was driven by increasing gap size for both species, and openness for maple,

but soil temperature for aspen. Mass loss of ash logs was again driven by increasing gap size and DW volume. Mass loss for maple logs was driven by increasing DW volume and soil temperature. Thus, for all substrates tested except maple logs, gap size was consistently and positively related to mass loss. For example, by the end of the 3- or 8-year sampling period, litter and stakes (respectively) showed about 10% greater mass loss in gaps compared to non-gaps (Figure 4).

DISCUSSION

We compared the response of three substrates of common northern hardwood species to experimental manipulations of forest structure, including canopy gap creation and deadwood additions. Gap creation in particular enhanced mass loss for the finer materials—leaf litter and wood stakes—by approximately 10% after 3 or 8 years, respectively, and more mass remaining in both treatments where gaps were not created. Results for mass remaining of the larger material—20 cm diameter logs—were less clear, with mass remaining in gaps less than that of controls for ash and greater than controls for maple. Mass remaining for the DW addition treatments were again inconsistent, with lower mass remaining relative to controls for ash and greater than controls for maple. Our results highlight the benefit of long-term studies of decay, confirming that the trends in mass-loss (gap vs. non-gap treatments) seen early in the sequence persisted throughout, particularly for the finer materials. Our long-term study also revealed important changes in understory structure over time, namely greater vegetation density/cover

Table 2. Mean Values of Environmental Variables (± standard error) Characterizing the Location of Substrates in Large Subplots by Experimental Treatment

Treatment	Soil moisture	Soil temperature	Gap size (expanded gap)	Openness 2008	Openness 2016	DW volume 2008
	Z score	Z score	m^2	%	%	m^3 ha
Control	0.18 ± 0.44	− 0.20 ± 0.08	–	4.0 ± 0.2	5.9 ± 0.5	14.4 ± 5.1
DW addition	− 0.11 ± 0.34	− 0.10 ± 0.17	–	3.8 ± 0.1	5.7 ± 0.3	49.5 ± 6.6
Gap creation	0.15 ± 0.43	0.30 ± 0.29	366 ± 22 (625 ± 23)	11.0 ± 1.1	5.7 ± 0.5	23.0 ± 7.5
Gap + DW	− 0.22 ± 0.41	-0.01 ± 0.10	305 ± 17 (564 ± 35)	10.5 ± 0.7	7.2 ± 1.2	68.2 ± 13.9

Soil characteristics were measured in years 4 and 5 post-treatment, canopy openness was measured in years 2 and 10 post-treatment, and dead wood volume was measured year 2 post-treatment. Both gap size and expanded gap size were measured following Runkle (1992).

Table 3. Model Selection p values and Diagnostics (from SAS, PROC GLMSELECT) on Logit-transformed Proportion Mass Remaining of Detritus in Large Subplots (Moisture and Temperature Not Available for Small and Medium Subplots)

Substrate	k	Gap area	Canopy openness	DW volume	Soil moisture	Soil temp	AICc	ΔAIC	Cp	AdjR²
Litter	5	< 0.001	0.030	0.170	0.031	0.315	− 13.5		6	0.50
	4	< 0.001	0.043	0.214	0.043	–	− 15.4	1.9	5	0.50
	3	**< 0.001**	**0.017**	**–**	**0.078**		**− 16.5**	**3.0**	**4.7**	**0.49**
Stakes										
Maple	5	0.017	0.032	0.465	0.356	0.823	53.3		6	0.31
	4	0.005	0.023	0.466	0.319	–	48.1	5.1	4.05	0.36
	3	0.004	0.025	–	0.277	–	44.5	8.7	2.57	0.38
	2	**0.005**	**0.043**	**–**	**–**	**–**	**42.3**	**11.0**	**1.7**	**0.37**
Aspen	5	0.044	0.181	0.483	0.225	0.018	48.5		6	0.34
	4	0.049	0.216	–	0.277	0.019	44.4	4.1	4.52	0.37
	3	0.056	0.127	–	–	0.025	41.8	6.7	3.75	0.35
	2	**0.023**	**–**	**–**	**–**	**0.012**	**41.2**	**7.3**	**4.3**	**0.29**
Logs										
Maple	5	0.345	0.887	0.012	0.532	0.039	− 156.0		6	0.17
	4	0.343	–	0.010	0.478	0.027	− 158.6	2.6	4.02	0.19
	3	0.294	–	0.011	–	0.034	− 160.5	4.5	2.52	0.20
	2	**–**	**–**	**0.004**	**–**	**0.003**	**− 161.7**	**5.7**	**1.61**	**0.19**
Ash	5	0.351	0.279	0.112	0.557	0.244	− 91.2		6	0.10
	4	0.269	0.346	0.048	–	0.302	− 93.8	2.5	4.35	0.12
	3	0.192	–	0.077	–	0.382	− 95.5	4.3	3.25	0.12
	2	**0.060**	**–**	**0.036**	**–**	**–**	**− 97.3**	**6.1**	**2.01**	**0.13**

The full model for each substrate is indicated with k = 5, where k = the number of model parameters; p values are listed for individual factors, and a hyphen indicates that variable was removed from the model. The ''best'' model is indicated in bold font
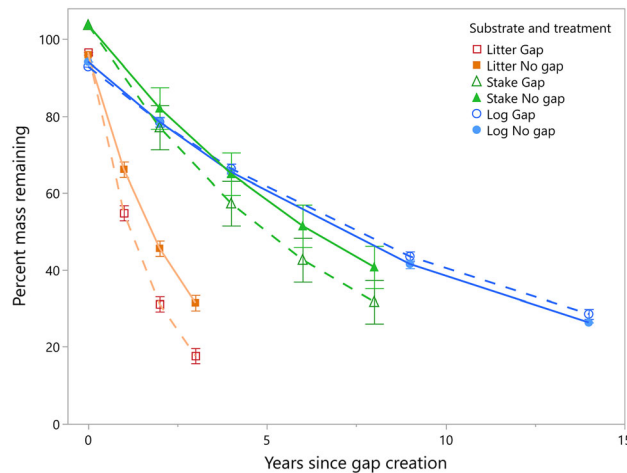

Figure 4. Comparative net mass remaining (± standard error) patterns for the three substrates (leaf litter, wood stakes, experimental logs) in this study. DW treatments and species were combined (large subplot only) to emphasize the strong influence of canopy gaps on decomposition rates (Gap = Gap and Gap + DW treatment levels; No gap = Control and DW treatment levels). Exponential decay models were fit to points for display purposes.

developing in gaps (Figure 3), which altered near-ground microclimates and in turn altered net mass remaining for some of the finer materials.

Our finding that leaf litter mass remaining was significantly lower in gaps, corroborates a number of previous studies (Ritter 2005; Mayer and others 2017; Gliksman and others 2018). However, contrary to previous studies, we did not find that soil temperature (for example, Salinas and others 2011) enhanced litter mass loss. Leaf litter breakdown is

an integrative ecosystem process that involves numerous organisms and links biogeochemical cycles. Its decomposition in gaps is moderated by complex interactions of moisture, litter chemistry, canopy structure, within-gap understory vegetation, and the activity/diversity of soil organisms (Adair and others 2008; Zhang and Zak 1995; Prescott 2010; Mayer and others 2017). In addition, solar radiation and its interaction with the canopy influences the microenvironment (that is, temperature, water) where litter decomposition occurs, plays a key role in determining the structures and functions of decomposers, and directly causes photodegradation of compounds in litter (Austin and others 2016; Ma and others 2017). Therefore, creating openings in the canopy, whether from natural or anthropogenic cause, seems likely to increase litter decay rates. However, studies have found that openings created through forest harvest have increased, decreased or had no effect on wood decay rates (Prescott 2010; Gonzalez and others 2014; Zhang and Zak 1995). This variation in response is likely due to more local effects of gap size that influence a number of microclimate factors, which interact to alter moisture patterns (Gray and others 2002), as well as differences in fungal species composition among substrates, given that fungal composition is known to influence decay rates (Lindner and others 2011). Climate differences may also be a factor at a larger scale, as latitude will influence the mean annual temperature and precipitation that influences decay rate (Prescott 2010).

We are not familiar with any previous study assessing the effect of deadwood abundance on leaf litter decomposition. We found that the presence of deadwood strongly moderated litter decomposition, had minimal effect on small woody substrates in the short-term after gap creation, but was influential on longer-term decay patterns of larger woody material. The presence of deadwood is important for nutrient cycling, soil forming processes, and regeneration niches. The physical presence of deadwood shades the soil, decreasing the temperature and altering the moisture dynamics (Gray and Spies 1998). The waterlogging of soils near deadwood may inhibit decomposition processes (Hagemann and others 2010), but it also might help stabilize the microclimate by preventing diurnal fluctuations (Zalamea and others 2016). The initial lag in litter mass loss in DW treatment may reflect the localized moderation of microclimate by deadwood in this study. Moisture patterns are not consistently responsive to deadwood, with some evidence of very similar deadwood and soil

moisture dynamics (Green and others, 2022). Soil under decaying wood has been found to have fewer roots, less variable soil temperature, and lower nutrient availability depending on the species and decay stage of the wood (Goldin and Hutchinson 2015; Zalamea and others 2016; Perreault and others 2020). Clarifications of these relationships are needed as those managing forests for multiple resources including productivity and biodiversity will face conflicting opinions of the role of deadwood and the implications of global change.

Fabricated wood stakes or blocks have been used as a surrogate for deadwood decay in a number of recent studies. Such stakes or blocks are not intended to directly track decay of large stem wood, given their small size, surface area: volume ratio, and lack of bark. However, their mass loss over time has allowed investigators to compare decay rates among biomes (Gonzalez and others 2008), assess the importance of local-scale factors that govern decay rates (Bradford and others 2014), quantify wood strength reductions (Jurgensen and others 2006, Fraver and others 2018), and evaluate the relative role of termites and fungi in wood decay (Cheesman and others 2018), among others. Our wood stake results showed greater mass loss occurring in gaps –similar to our litter bag results—as has been shown for wood blocks in tropical rainforests (Griffiths and others 2021). However, our wood stake results differed from those of the experimental logs (coarse DW), which did not show a difference in decay between gap and non-gap treatments. Nevertheless, we note that at the temporal limit of our wood stake experiment (eight years), the percent mass remaining in maple stakes was very similar to that of maple logs at that time (ca. 45%), suggesting similar decay rates, albeit apparently driven by different biotic or abiotic factors. We also point out the large stake-to-stake variability in mass loss (Figure 2 and personal observations at other sites), which may suggest that a large number of stakes may be needed to detect differences among treatments. Overall, stakes still appear to be a reasonable proxy for fine woody material, which tends to get overlooked compared to large DW, and which provides substrate for wood-inhabiting species and in some systems still retains substantial carbon, because of its sheer abundance.

Large diameter DW decomposes slowly relative to other substrates and here, relative to other locations that are warmer and/or more humid. Unlike leaf litter and wood stakes, where mass loss was strongly influenced by canopy gaps, mass loss

from logs was influenced primarily by DW volume, with greater resident DW leading to greater mass loss. The lack of difference between log decay in canopy-gap vs non-gap treatments is consistent with findings of Forrester and others (2015), who, working at this same site, report no difference in log CO_2 flux between those treatments after four years, despite differences in temperature (gaps warmer). The ''neighborhood'' volume of DW may have enhanced the colonization of nearby logs by wood-decay fungi, as some such species appear to be limited in successful colonization beyond the scale of a few meters (Jönsson and others 2008). Thus the more rapid mass loss associated with high volumes of DW may be associated with the fungal community that was added along with the large volume of deadwood (Brazee and others 2014; Perreault and others 2023). The fact that gap treatments enhanced mass loss in the smaller substrates (litter, stakes) but not logs initially, may imply that the smaller materials may be more sensitive to environmental conditions.

Differences in log decay attributable to gaps were not seen until after fourteen years of decomposition and were not apparent for both species. The lower mass remaining with ash is consistent with what would be expected for its litter relative to sugar maple given its higher quality. Future measurements will be important in documenting any shifts in drivers that may occur, and particularly following this by species. These species specific decay rates indicate that the unique pattern of a co-dominant species might be lost from this system over time with the spread of Emerald ash borer (*Agrilus planipennis*).

Early observations of logging slash highlight several important factors that may help explain variability in decay rates we quantified here. Under certain conditions, case hardening of deadwood pieces occurs, forming an extremely hard, decay-resistant outer shell (Spaulding and Hansbrough 1944). High exposure to sunlight and extreme temperature were found to promote the phenomenon (Harmon and others, 1986), conditions common following large canopy disturbances. Spaulding and Hansbrough (1944) noted favorable conditions for decay are found under a moderately broken canopy cover—conditions that may hasten decay by about 20%. In addition, waterlogging can slow decay, as it creates anaerobic conditions unsuitable for fungal activity (Raynor and Boddy 1988), with the decay period for waterlogged material being up to twice as long as the average (Spaulding and Hansbrough 1944). Our experimental manipulations created conditions that could lead to case-hardening and/or waterlogging, both of which influence wood decay rates and should be tracked in future studies. The longer term nature of this work allowed us to document the decline in canopy openness over time, which would serve to reduce moisture loss over time as well.

The initial fungal colonization at the onset of wood decomposition has been shown to influence the mass loss of large woody material (Lindner and others 2011), and the composition of the wood-decay fungal community is likely the most important predictor of mass loss in well decayed woody material (van der Wal and others 2015). We note that the response variables we explored accounted for a third to a half of the variation in mass remaining for leaf litter and wood stakes but only a tenth of the variation in mass remaining of for large DW. Factors influencing light availability or microclimate were significantly related for fine material mass loss, but the ''neighborhood'' volume of coarse DW was most related to log mass loss. Based on other data collected at this study site, we speculate that the large unexplained variation in mass loss of DW may be attributed to differences in fungal community composition among logs or locations, particularly where large volumes of DW are present. (This hypothesis is addressed by Perreault and others 2023.)

CONCLUSIONS

A time-series approach to investigating decomposition provides the best resolution for measurements describing long-term patterns of decomposition and avoids uncertainties in substituting space for time. Here, we followed decomposition of leaf litter, wood stakes, and experimental logs, for 3, 8, and 14 years, respectively. Although the approach requires a large investment of time and resources, the effort is justified, particularly when linking decomposition to experimental treatments and associated temporal changes in microclimate. Our analyses of the effects of gap creation and DW additions confirm that variation in both the horizontal and vertical structure of the forest influences ecosystem processes. Faster decomposition of fine materials (for example, leaf litter and wood decay stakes) following gap creation leads to faster turnover and possibly resource availability. Yet, when more DW is present this can reduce the magnitude of the canopy effect. Coarse material is not equally responsive as finer materials and varies by species.

Those interested in managing forests for sustainability, biodiversity, and carbon objectives may

use our results to gauge the costs and benefits of gap creation and leaving more residual deadwood following harvests or disturbance events. DW additions as well as the denser ground-layer vegetation that develops following gap creation can buffer dramatic changes in microclimate that occur immediately following canopy disturbance creating critical "safe sites" for taxa sensitive to extreme changes in microenvironment. And although gap creation generally leads to more rapid decomposition of fine materials (that is, more CO_2 emitted to the atmosphere), this must be weighed against the increase in carbon sequestration as tree establishment and rapid growth take place in the gap. Moreover, the additional adaptation pathways generated by increasing structural and functional diversity through gap creation and deadwood retention should also be considered against these outcomes, particularly for systems simplified by historic land use, like those examined in this study.

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