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Article

Impacts of Prescribed Fire Frequency on Coarse Woody Debris Volume, Decomposition and Termite Activity in the Longleaf Pine Flatwoods of Florida

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Abstract: Longleaf pine (*Pinus palustris*) ecosystems have been reduced dramatically throughout their range. Prescribed burning is considered the best way to restore and maintain plant communities associated with longleaf pine, but little is known about its effects on coarse woody debris and associated organisms. We conducted a 5-year study on the Osceola National Forest in northeastern Florida to determine how dormant-season prescribed burns at different frequencies (annual, biennial, quadrennial or unburned) applied over a 40-year period affected coarse woody debris volume, decomposition and nitrogen content, and subterranean termite (*Reticulitermes* spp.) activity. Burn frequency had no effect on standing dead tree or log volumes. However, freshly cut longleaf pine logs placed in the plots for four years lost significantly less mass in annually burned plots than in unburned plots. The annual exponential decay coefficient estimate from all logs was 0.14 yr^{-1} (SE = 0.01), with the estimated times for 50 and 95% loss being 5 and 21.4 years, respectively. Termite presence was unaffected by frequent burning, suggesting they were able to survive the fires underground or within wood, and that winter burning did not deplete their food resources.

Keywords: coarse woody debris; decay; deadwood; decomposers; fire frequency; large fuel consumption; termites; Isoptera

1. Introduction

The importance of coarse woody debris (CWD), which includes standing dead trees or "snags" and large-diameter logs on the forest floor, in maintaining forest diversity is widely recognized [1–4]. For example, Elton [1] suggested that as many as one fifth of forest species are dependent on dead wood, and more recent estimates for European forests place the value as high as one third [5]. Clearly, forest management should consider this resource and how forestry practices affect its abundance and distribution. Most research on large woody debris and its function in North American forests has been conducted in the Pacific Northwest [2,6], and little is known about this important resource in forests of the Southeastern United States [7]. Longleaf pine (*Pinus palustris*) forests endemic to the region are of particular interest. These ecosystems once occupied >24 million hectares, but due primarily to harvesting, wild hogs, conversion to species with faster juvenile growth, and land use changes, less than 1.3 million fragmented hectares remained by the mid 1990's [8]. News of the impending demise of this species sparked a widespread, concerted effort by virtually all southern federal and state agencies, non-government natural resource organizations, and ecologically oriented private land owners to reverse the decline.

Prior to European arrival in North America, longleaf pine flatwoods communities were maintained by frequent fires (1–3 year intervals) started by lightning or Native Americans [9,10]. Prescribed fire, usually applied during the dormant season, has replaced these historic ignition sources and is the only known operational method (although mechanical or chemical pretreatments are sometimes necessary) for restoring and maintaining the full suite of ecosystem functions in longleaf pine and its associated plant communities [11]. Compared to research involving plant community response, efforts to determine how prescribed fire affects dead wood volumes and the decomposer community are largely lacking.

Fire can influence dead wood volumes in a variety of ways. These include direct or indirect inputs of dead wood through tree mortality or injury, consumption of woody fuel and effects on the decomposer community. Although fungi represent the primary decomposers in most ecosystems [12], wood-feeding insects such as termites and beetles can also play an important role. For example, in the longleaf pine forest of the Southern United States, subterranean termites belonging to the genus *Reticulitermes* are present in high numbers. Although efforts to quantify wood consumption by these organisms have not been made in such forests, studies carried out in other regions suggest their effects on decomposition processes may be substantial [13,14]. Efforts to determine how fire affects *Reticulitermes* are similarly lacking but studies on other termite taxa [15,16] suggest the low-intensity fires typical of longleaf pine forests may have little impact on these organisms.

The purpose of the current study was to determine how relatively low-intensity dormant season prescribed fires administered at different frequencies over a 40 year period in flatwood longleaf pine forests affected coarse woody debris volume (snags and logs), decomposition, and termite activity in Northern Florida. We theorized that frequent burning over such a long period of time would reduce the amount of coarse woody debris and slow decomposition rates through long-term depletion of resources for the decomposer community, including termites.

2. Materials and Methods

2.1. Study Site and Design

The study was conducted on the Osceola National Forest in Baker County, Florida on plots established in 1958 to examine effects of burning frequency on reducing understory and forest floor fuel loads, and thus the impact on wildfire suppression and damage. In 1958, the overstory trees were 45-year-old longleaf pine with a few slash pine (*P. elliottii*). Dominant trees averaged 20 m tall and 29 cm diameter at the start of the study. The presence of remnant longleaf pine trees that had been "boxed" or scarred for extraction of turpentine, a common practice from the early colonization of North America until the early 1900's, is strong evidence that the area was never cleared for agriculture, although it was extensively logged at the beginning of the 20th century. The understory consisted of typical flatwoods vegetation dominated by palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), *Vaccinium* sp. and wiregrass (*Aristida beyrichiana*) (see Glitzenstein *et al*. [17] for a complete floral description). The study was a randomized complete block design consisting 6 blocks of 4 treatments each (24 plots). Each plot was 0.8-ha (80 × 100 m) in size. The entire site received a low-intensity prescribed burn in the winter of 1956 to initialize the study area and treatments were applied as scheduled from 1958 to the present between December and early March (Table 1).

Table 1. Timeline from initial plot establishment through the present study showing when samples were collected and prescribe burning treatments applied for a long-term burn study on the Osceola National Forest in Florida.

Time	Treatment or Sampling Conducted
1956	Entire study area burned to initialize the study
1958–1964	Plots burned at 0, 2, 4 or 6 year intervals
1964–2012	Plots burned at 0, 1, 2 or 4 year intervals
November 1994	Present study begun, logs placed on the plots to measure decomposition
Winter 1994–1995	1 year interval plots were burned
April 1995	Termite blocks placed on plots and checked bimonthly
Winter 1995–1996	Logs sampled, 1, 2 and 4 year interval plots burned
Winter 1996–1997	Logs sampled, 1 year interval plots burned
September 1997	Termite blocks replaced and checked bimonthly
Winter 1997–1998	Logs sampled, 1 and 2 year interval plots burned
Winter 1998–1999	Logs sampled, 1 year interval plots burned
Winter 1999–2000	1, 2 and 4 year interval plots burned
December 2003	CWD surveyed on all plots

Initial treatments were winter burns applied every 2-, 4- or 6-years and unburned controls. However, after 1964 the 6-year interval treatment was replaced with annual winter burns. Fire intensity and severity varied from year to year depending on weather conditions (particularly wind and relative humidity), the Keetch-Byram Drought Index, available fuel (dead down material, groundcover and understory regrowth), dead fine-fuel moisture content (which ranged from about 9%–16%), and firing technique (headfire, flankfire or backfire). Our study was superimposed on this long-term winter burn study and began in the fall of 1994 with annual plots burned a few months later in early 1995 and then all, 1-, 2- and 4-year burn plots were burned a year later. The study continued for the full cycle of burn treatments (annual, biennial and quadrennial) ending after the 1-, 2-, and 4-year plots were again burned the winter of 1999–2000. Control plots had been unburned for 44 years at the close of our study.

2.2. Coarse Woody Debris

We initially surveyed coarse woody debris (defined in this study as larger than 10cm in diameter) on the plots in 1995. However, some unauthorized salvage cutting of lightning stuck trees had occurred on annual and biennial plots from 1989 through 1991. Since we were uncertain if our initial survey reflected natural levels of coarse woody debris input, we surveyed again in December 2003 to compare volumes between treatments. This gave us at least a 12-year period (1991–2003) during which no lightning-killed trees were removed from any plots. During the survey we measured down coarse woody debris (logs) on all plots by walking five, 10-m wide transects across the plots in the same direction resulting in samples of approximately 50% of the plot surfaces. The length and small- and large-end diameters of all down coarse woody debris >10 cm diameter within each transect was measured and recorded, but not differentiated by decay class. No adjustments were made in diameter readings to compensate for instances where the bark was gone. We used Huber's equation (volume = m × l; where, m = mid-point cross-sectional area and l = length) to estimate volume of dead wood [18]. The mid-point diameters of logs were estimated by taking the average of the end diameters. In addition, we conducted a 100% survey of standing dead wood (snags). Diameter at breast height (dbh) and height of each snag was measured in the field and the mid-point diameter was estimated using taper equations for coastal plain longleaf pine [19]. Huber's equation was then used to estimate volume after using the mid-point diameter to calculate the cross-sectional area.

2.3. Wood Decomposition and Nitrogen (N) Content

We were interested in determining if prescribed burning affected the rate of decomposition of longleaf pine. To measure decomposition rate, we placed four 1.3 m long sections of freshly cut longleaf pine (20.6–23 cm diameter) on each plot at the plot corners 10 m from each corner along the diagonal. Logs were laid on their sides on the accumulated leaf litter present at each location. No attempt was made to place logs in direct contact with mineral soil. During the third year (1997) we noticed mammals were beginning to forage in some previously sampled logs, so to prevent vertebrate fragmentation of the remaining logs we covered them with wire fencing (chicken wire with 2.5 × 2.5 cm openings) held in place with four tent stakes.

Wood decomposition rates were estimated by changes in mass over time. Just before placing the logs on the plots, a 5–7 cm wide cross-section was cut from one end of each log (96 sections) to obtain estimates of initial density. Density (g/cc) was measured by cutting a 60^{o} wedge from each debarked cross-section. The wedges were soaked in water for 7 days to ensure no air was in the wood and then volume was measured by water displacement. Afterward, wedges were air-dried for 24 h followed by oven-drying at 103 °C for 48 h and weighed. An additional wedge was cut from each cross-section, oven-dried at 60 °C for 48 h and stored for analysis of N content.

During January of each year, prior to prescribed burning, a cross-section was cut from the center of one of the four logs in each plot (*i.e.*, each log was sampled one time over the four-year period) and specific gravity was estimated in the same manner as above. By the third year the sections were beginning to fall apart after they were cut from the logs, so from then on, study wedges were cut and immediately enclosed in a bag constructed from fiberglass window screening for processing. The weight and volume of the bags were measured separately and subtracted from the total sample volume and weight to obtain density estimates for wood only.

Fungal colonization is the most important pathway for movement of N into coarse woody debris [20,21]. Similarly, the activities of termites and other wood-feeding invertebrates are thought to contribute to the release of N and other nutrients [22,23]. Thus, we measured N content in our logs to provide an indication of fungal and insect activity and a means to determine how prescribed burning affects nutrient dynamics in logs. Wood samples collected throughout the study (oven-dried at 60 °C for 48 h and stored at room temperature) were used for N content analyses. In 1999, the samples were ground in a Wiley mill to a particle size of 1 mm or less and analyzed for percent N by the University of Georgia's Soil, Plant and Water Testing Laboratory (Athens, Georgia) using an inductively coupled plasma emission spectrograph.

2.4. Termites

To measure termite abundance in the plots, we placed sampling blocks (a long-established method for monitoring subterranean termite activity, e.g., [24]) consisting of 25 cm long pieces of 5 × 10 cm kiln-dried pine wood on the plots in April, 1995. Ten blocks were placed on each plot in two lines spaced 20 m apart. Blocks were placed in direct contact with mineral soil and spaced 5 m apart within the lines. At that spacing, termites in each block likely represent a separate colony [25]. Blocks were checked for termite activity (*i.e.*, presence or absence of live termites) every 2 months for one year. A second set of blocks cut from the same wood as the first set was placed on the plots in November 1996 and monitored through September 1997. The number of blocks attacked was compared among treatments.

2.5. Statistical Analyses

Two-way analyses of variance were carried out using the SAS [26] General Linear Models procedure to determine if burn frequency affected the volume of standing dead trees, logs or both combined. Analyses of variance for a split-plot design (*i.e.*, with year being the subunit effect) were performed on mass loss and N content data. Percentage data on mass loss were arcsine square-root transformed to achieve normality prior to analysis [27]. When a significant treatment effect was detected, means were compared using the least significant difference method described by Dowdy *et al*. [28].

The most widely used equation to model wood decay is the single-exponential model [2]:

$$Y_t = Y_o e^{-kt} \tag{1}$$

where Y_t is the amount left at time t; Y_o is the initial amount; and k is the decay rate constant.

We estimated the decay rate constant from all wood samples combined and then used the above equation to estimate the time required for 50% and 95% of the initial mass to be lost. In four samples

(1 in 1997 and 3 in 1999) the density of decayed samples was higher than the original value so these outliers were not included in subsequent calculations.

To test for correlations between burn frequency and termite presence, the Mantel-Haenzel Chi-Square test was performed separately for each sampling period [29] (Note: data from November 1997 were not analyzed due to insufficient sample sizes).

3. Results

3.1. Coarse Woody Debris

The volume of snags, logs and total coarse woody debris volume (snags and logs) were the same regardless of prescribed burn frequency (Table 2). Since burn frequency had no effect on coarse woody debris volume, we calculated the average volume per unit area using the total volume per plot for the 24 plots. The mean volume was 6.54 m^3/ha (SE = 0.46) for snags and 2.09 m^3/ha (SE = 0.59) for logs yielding a total coarse woody debris volume of 8.63 m^3/ha (SE = 0.71).

Table 2. Volume (m^3/ha) of standing (snags) and down coarse woody debris (logs > 10 cm dia.) on longleaf pine plots on the Osceola National Forest (Baker County, Florida) burned at varying frequencies over a 40 year period.

Burn Frequency	N	Logs [1]	Snags [1]	Total [1]
Annual	6	3.9 ± 1.38 a	5.2 ± 1.44 a	9.1 ± 1.73 a
Biennial	6	1.9 ± 0.60 a	6.5 ± 1.00 a	8.5 ± 1.23 a
Quadrennial	6	1.6 ± 0.70 a	7.2 ± 1.48 a	8.9 ± 1.87 a
Unburned	6	0.8 ± 0.27 a	7.2 ± 0.81 a	8.0 ± 1.01 a

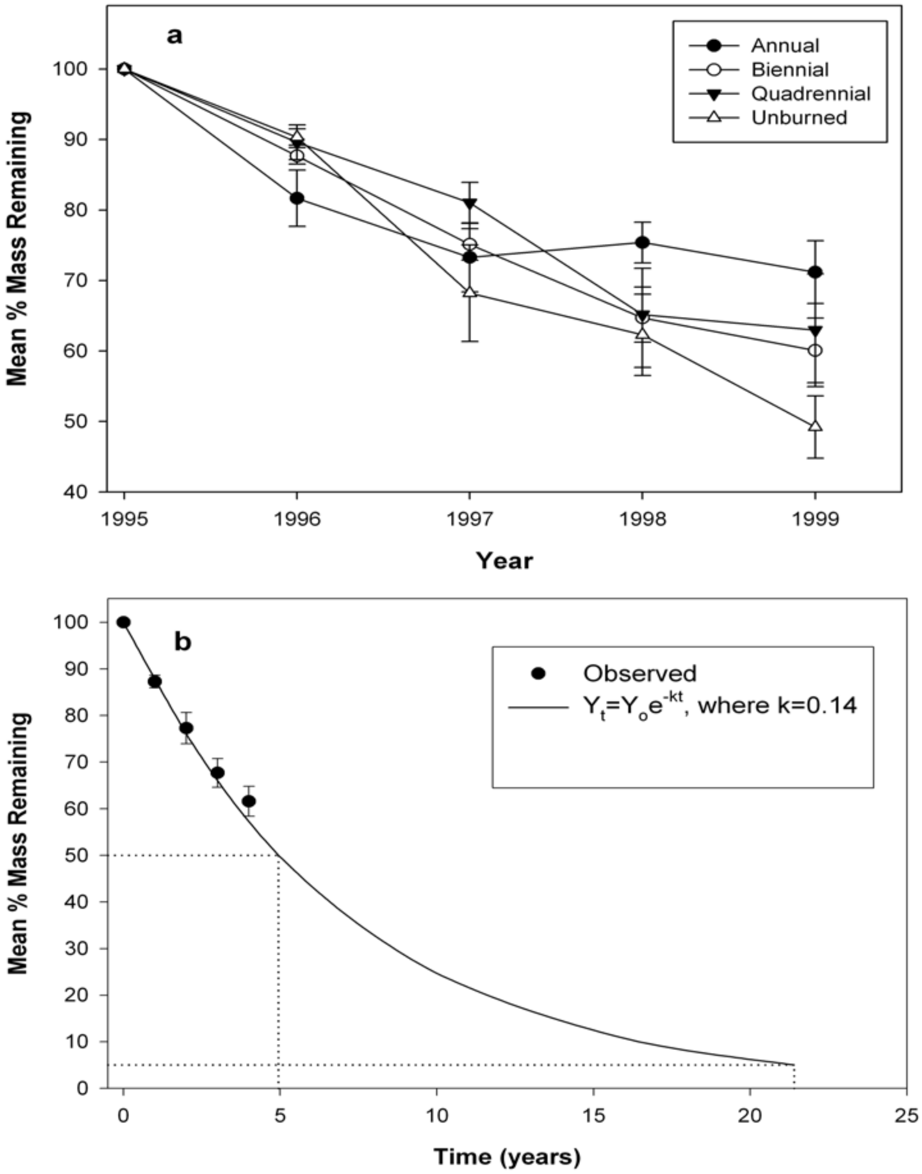
[1]: Means within columns followed by the same letter are not significantly different ($p < 0.05$; ANOVA; SAS 1987).

3.2. Wood Decomposition and Nitrogen (N) Content

Mass lost from logs placed in the plots at the beginning of this study varied significantly among treatments, blocks and years but there were no significant interactions between these terms (Table 3). Because a significant treatment effect was detected, transformed means were compared using a calculated least significant difference of 0.138. These comparisons indicate that log mass remaining was greater in quadrennially burned plots than in unburned plots in 1997 and greater in annually burned plots than unburned plots in 1998 and 1999. Although the difference detected in 1997 is not apparent in subsequent years based on Figure 1a, the difference between annually burned and unburned plots appears to be consistent and widening with time throughout the study.

Using the k value for all logs (0.14) in the exponential decay function, the estimated half-life of a longleaf log in the Florida flatwoods was 5 years and the time for 95% mass loss was 21.4 years assuming decay follows the single-exponential model (Figure 1b). Since annual burning reduced mass loss relative to the unburned controls during the four years of the study, we calculated the decay coefficients for logs on annually burned plots ($k = 0.138 \pm 0.018$ yr^{-1}, n = 24) and unburned controls ($k = 0.158 \pm 0.018$ yr^{-1}, n = 20) and used them in the exponential decay function to estimate half-life and time for 95% mass loss in those treatment plots. Logs on annually burned plots were estimated to lose 50% of their mass in 5.0 years and 95% in 21.7 years. On unburned control plots 50% mass loss was estimated to occur at 4.4 years and 95% loss at 18.9 years.

Figure 1. (**a**) Mean (±SE) percent of mass remaining in longleaf pine logs placed on plots receiving dormant season prescribed burns at different frequencies over 40 years on the Osceola National Forest, Baker County, Florida; (**b**) Observed mean (±SE) percent mass remaining for all logs sampled in a given year and the projected mass loss from logs assuming decay follows the single-exponential model and the decay coefficient estimated from the first four years of decomposition remains constant.

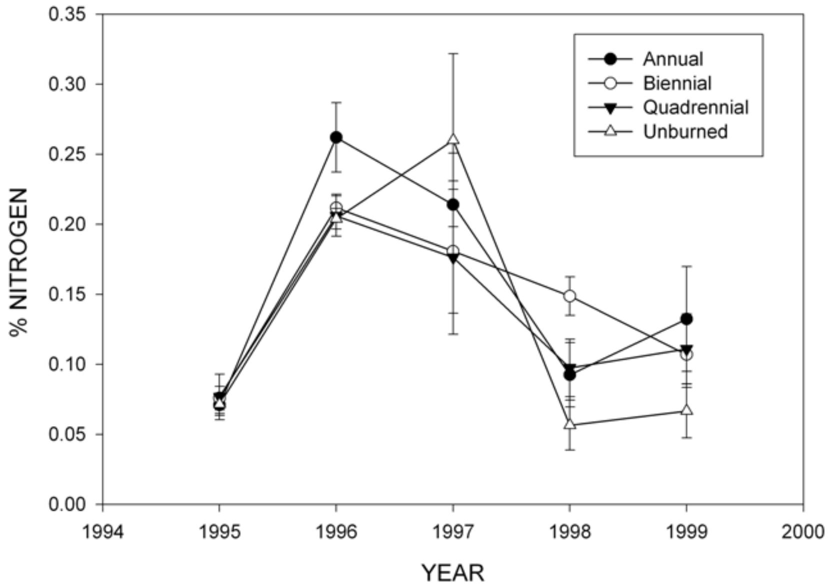


The nitrogen content of the logs varied among years but was unaffected by burn frequency (Table 3, Figure 2). On average, nitrogen content increased 3 fold from when the logs were placed on the site in December 1994 to when they were first sampled in January 1996 (0.07 ± 0.005% and 0.22 ± 0.01%, respectively). Levels remained relatively constant the following year, and then declined in 1998 and remained at the same level in 1999. Even in the last two years of sampling the overall nitrogen content was higher than the initial content when the logs were first cut.

Table 3. Results from ANOVA (split-plot design) for percent mass remaining and nitrogen N concentration.

Source	Mass remaining				Nitrogen			
	df	**MS**	**F**	**P**	**df**	**MS**	**F**	***p***
Whole unit								
Treatment	3	0.03	$F_{3,15} = 4.20$	0.02	3	0.01	$F_{3,15} = 1.13$	0.37
Block	5	0.03	$F_{5,15} = 4.10$	0.02	5	0.00	$F_{5,15} = 0.98$	0.46
Treatment* Block	15	0.01	$F_{15,55} = 0.37$	0.98	15	0.00	$F_{15,58} = 0.74$	0.74
Sub unit								
Year	3	0.41	$F_{3,55} = 24.74$	<0.01	3	0.10	$F_{3,58} = 15.98$	<0.01
Treatment* Year	9	0.02	$F_{9,55} = 1.46$	0.19	9	0.01	$F_{9,58} = 1.15$	0.34
Error	55	0.02	–	–	58	0.01	–	–
Total	90	–	–	–	93	–	–	–

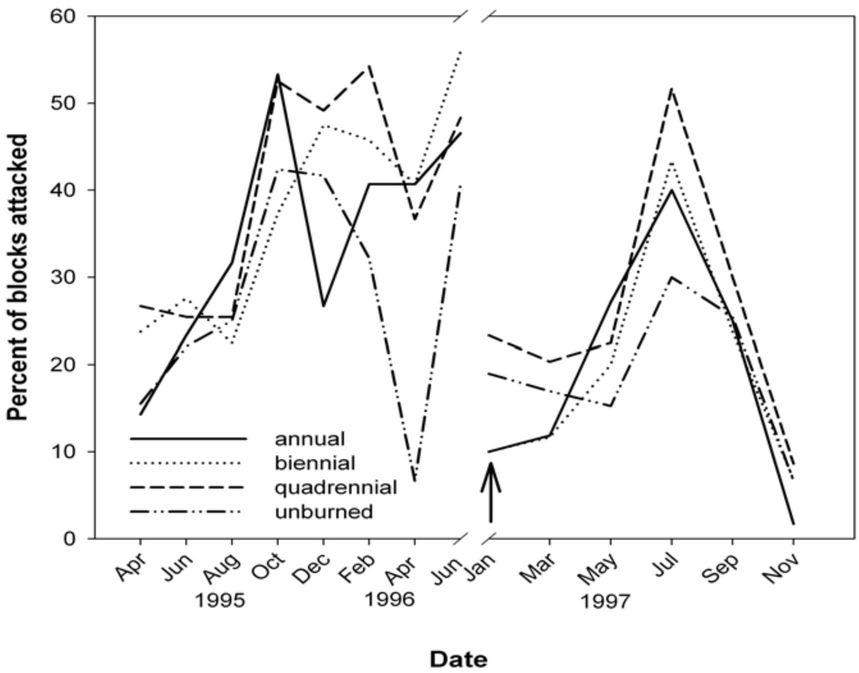
Figure 2. Mean percent nitrogen in longleaf pine logs placed on plots receiving dormant season prescribed burns at different frequencies over 40 years on the Osceola National Forest, Baker County, Florida.



3.3. Termites

Approximately 25% of the wooden blocks placed on the plots in March 1995 were infested within two months (Figure 3) and 46% had termites within eight months (October 1995). The second set of blocks was placed on the study site in November 1996 and approximately 40% of those had termites feeding on them by July 1997. Dormant season prescribed burning had little effect on termites. Only in April of 1996 was there a significant correlation between burn frequency and termite abundance, due to an unusually low proportion of blocks being infested in the unburned plots ($p < 0.0001$). Because this was the only time such differences were observed (Figure 3), this result may be due to chance.

Figure 3. Overall percentage of wooden blocks infested by termites at each burn frequency. The original blocks were replaced in November 1996. The x-axis break is used to separate the two sets of blocks and the arrow at January 1997 indicates the first reading taken from this second set of blocks. Mantel-Haenzel Chi-Square statistics were calculated separately for each sampling period. Significant results were obtained only for April 1996 (see results).



4. Discussion

Along with decomposition, insect consumption, and fragmentation by animals, fire is considered one of the main pathways by which dead wood is lost from ecosystems [30]. Little is known, however, about the relative importance of each pathway in different forest types. In the longleaf pine ecosystem studied in this project, 12 years of dormant-season prescribed burning (1991–2003) the period when no salvage logging had occurred) had no effect on coarse woody debris volume at any of the burn frequencies tested. Furthermore, standing dead tree or snag volumes were the same for all treatments indicating that recent (past 5 years) tree mortality [31] did not vary among burn frequencies. These findings are consistent with those of Ottmar and Vihnanek [32] who found no coarse woody debris consumption by dormant season prescribed burns on the Okefenokee National Wildlife Refuge (NWR) (longleaf and slash pine) and Piedmont NWR (loblolly, *P. taeda*, and shortleaf pine, *P. echinata*). Parresol *et al*. [33], however, found that longleaf pine coarse woody debris volumes were affected by the interaction of site index and the number of burns applied to the stands. They also found that time since the last burn was correlated with coarse woody debris volume in loblolly and slash pine stands but not longleaf pine. It is not clear how time since last burn affected coarse woody debris volumes in that study.

Although we were unable to find differences in the volumes of naturally-occurring coarse woody debris among treatments, fire did affect the decay rates of the log sections placed in the plots for four years based on our density measurements. Specifically, we found those placed in annually burned plots lost significantly less mass than those placed in unburned plots. Frequent dormant-season fires may slow wood decomposition by reducing the activities of fungi, microbes or invertebrates either directly or indirectly. For example, annually burned plots had about half of the litter and humus as plots burned on a 2- or 4-year cycle and 20 percent of the amount on unburned controls [34]. The lower amount of plant litter on the soil surface may have resulted in lower soil moisture that slowed decomposition. Research supporting a more direct effect of fire on wood-decaying fungi was conducted in northern Europe [35] where the fungal flora associated with fallen Norway Spruce were sampled before and after an intense burn in Finland. Many species of fungi were lost due to the fire, especially from moderately to strongly decayed logs and from those most strongly burned.

A long-term study similar to the present study was established in 1958 on the Francis Marion National Forest near Charleston, SC; but with a 3-year burn interval included and an overstory comprised mainly of loblolly pine (*Pinus teada*). Hurricane Hugo hit the area in September 1989 causing a large input of CWD on the study plots. Mayfield and Wade [36] examined the relationship between macrofungi and burn frequency by measuring fruiting bodies on three plots; an annual, triennial and unburned control during July 1991. Total fruiting body biomass averaged 989 grams on the unburned control plot, 9,183 grams on the triennial plot and 11,655 grams on the annual plot. Over 90% of the fruiting body mass occurred on the burn plots. Mayfield and Wade [36] also found higher levels of cellulase activity on burned than on the unburned plot suggesting that close-interval prescribed burns increased, rather than decreased decomposition of CWD on the forest floor.

Termites are thought to be the most important wood consuming insects in many forests [30]. Although termite abundance data from logs were not collected in this study, burn frequency did not affect the presence of termites according to data collected from the wooden blocks placed throughout the plots. This is perhaps not surprising considering the low intensities of the burns [37]. Although their heat tolerances (~44 °C) [38], fall far below the temperatures reached on the forest floor during typical burns [39], these organisms could have easily found refuge several centimeters beneath the soil surface [40]. They may also have been able to survive fires within dead wood as has been shown for other insects [41]. Furthermore, the availability of dead wood was not affected by fire frequency and charring does not deter feeding by these organisms [42] so their food resources were not affected. In the unlikely event food resources were reduced by prescribed burning in this region, termites would probably be unaffected since Horn and Hanula [43] found that three years of annual removal of all coarse woody debris did not significantly reduce termite abundance on large (9 ha) plots of mature pine forest in South Carolina.

Although this is the first attempt we are aware of to measure the effects of fire on *Reticulitermes* populations, a number of studies have been carried out elsewhere on other termite taxa. Abensperg-Traun and Milewski [44], for instance, sampled termites in burned and unburned habitats two years after an intense fire in Western Australia. They found wood-eating termites to be less numerous and diverse in previously burned areas whereas other taxa were not affected. Similarly, Davies [15] compared the species richness of termites in a seasonally-burned (low intensity) dry dipterocarp forest in Northern Thailand to that in an unburned forest nearby. He found termite richness to be slightly higher in the seasonally burned forest but relative abundance data were not collected. In an Australian tropical savanna, Dawes-Gromadzki [45] found termite abundance declined in tree patches following an early dry-season burn. Most recently, Davies *et al*. [16] found termites to be highly resistant to fire in African savannas although tolerance varied considerably among functional groups. It can be concluded from these results and those of the current study that termites vary greatly in their responses to fire depending on taxa and burn intensity.

We observed an initial large increase in nitrogen content of logs one year after placement followed by a general declining trend. That there were no differences in nitrogen content among treatments suggests that the balance of fungi and invertebrate decomposers and their effects on nutrient immobilization and release [22,23] were not significantly influenced by burn frequency. Taken together, the results from this study indicate that low intensity dormant season prescribed burns have little effect on the amount of coarse woody debris in longleaf pine forests and that termites and possibly other decomposers are highly resilient to the frequent fire regimes commonplace across the southeastern Coastal Plain [10]. These limited effects are no doubt largely due to the low intensity of the fires. In the western U.S., for example, where CWD tends to be considerably drier during prescribed burning due to lower precipitation and average daily relative humidity, Randall-Parker and Miller [46] found prescribed burns in ponderosa pine (*P. ponderosa*) stands consumed over 50% of logs and approximately 20% of snags.

With a half-life of just five years, our findings indicate wood decay proceeds quickly in the longleaf pine forests of the southeastern United States. This can probably be attributed largely to the warm and humid conditions characteristic of the region which apparently outweigh and limit the effects of fire on wood decomposition. For example, in our study the decay coefficient (k) for all samples combined was estimated to be 0.14 $year^{-1}$ (SE = 0.01). This is twice the rate reported for loblolly pine logging slash in a clearcut [47] where the logs were exposed to full sunlight, and half the value reported for loblolly pine in a forest in Tennessee [48] with a cooler climate. However, it was similar to the decay coefficient of 0.13 $year^{-1}$ reported by Eaton and Sanchez [49] for loblolly pine in a forest on the upper Coastal Plain of South Carolina. This study focused only on the decomposition of large-diameter woody debris. Previous studies on the Osceola National Forest long-term burn study plots examined fire effects on leaf litter and fine woody debris consumption and arthropod populations [34]. Also, just because termites were not noticeably affected in the current study, one should not conclude that fire is not relevant to wood-inhabiting arthropods. It is clear from research in other regions, for instance, that many wood-inhabiting insect species are strongly favored by or even dependent on fire [50,51]. The extent to which similarly pyrophilic species are present in the southeastern United States remains almost entirely unexplored and merits future investigation.

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Conflict of Interest

The authors declare no conflict of interest.

References and Notes

1. Elton, C.S. *The Pattern of Animal Communities*; John Wiley & Sons, Inc.: New York, NY, USA, 1966.
2. Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Gregory, S.V.; Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; Lienkaemper, G.W., Jr.; Cromack, K.; Cummins, K.W. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **1986**, *15*, 133–302.
3. Grove, S.J. Saproxylic insect ecology and the sustainable management of forests. *Ann. Rev. Ecol. Sys.* **2002**, *33*, 1–23.
4. Grove, S.J.; Hanula, J.L. Insect biodiversity and dead wood. In *Proceedings of a Symposium for the 22nd International Congress of Entomology*, Brisbane, Australia, 15–21 August 2004; U.S. Department of Agriculture, Forest Service, Southern Research Station: Asheville, NC, USA, 2006.
5. Dudley, N.; Vallauri, D. *Deadwood: Living Forests: The Importance of Veteran Trees and Deadwood to Biodiversity*; Technical Report for World Wildlife Fund: Washington, DC, USA, 2004.
6. Woldendorp, G.; Keenan, R.J.; Ryan, M.F. *Coarse Woody Debris in Australian Forest Ecosystems*; Bureau of Rural Sciences: Canberra, Australia, 2002.
7. McMinn, J.W.; Crossley, D.A., Jr. *Biodiversity and Coarse Woody Debris in Southern Forests*; U.S. Department of Agriculture, Forest Service, Southern Research Station: Asheville, NC, USA, 1996.
8. Outcalt, K.W.; Sheffield, R.M. *The Longleaf Pine Forest: Trends and Current Conditions*; U.S. Department Agriculture, Forest Service, Southern Research Station: Asheville, NC, USA, 1996.
9. Wahlenberg, W.G. *Longleaf Pine, Its Use, Ecology, Regeneration, Protection, Growth, and Management*; U.S. Department of Agriculture: Washington, DC, USA, 1946.
10. Landers, J.L. Disturbance influences on pine traits in southeastern United States. In *Proceedings of Tall Timbers Fire Ecology Conference*, Tallahassee, FL, USA, 30 May–June 2 1991; Tall Timbers Research Station: Tallahassee, FL, USA, 1993; pp. 61–98.
11. Brose, P.; Wade, D. Potential fire behavior in pine flatwood forests following three different fuel reduction techniques. *For. Ecol. Manag.* **2002**, *163*, 71–84.
12. Rayner, A.D.M.; Boddy, L. *Fungal Decomposition of Wood: Its Biology and Ecology*; John Wiley & Sons, Inc.: New York, NY, USA, 1988.
13. Abe, T. Studies on the distribution and ecological role of termites in a lowland rain forest of West Malaysia. 4. The role of termites in the process of wood decomposition in Pasoh Forest Reserve. *Rev. Ecol. Biol. Sol.* **1980**, *17*, 23–40.
14. Schuurman, G. Decomposition rates and termite assemblage composition in semiarid Africa. *Ecology* **2005**, *86*, 1236–1249.

15. Davies, R.G. Termite species richness in fire-prone and fire-protected dry deciduous dipterocarp forest in Doi Suthep-Pui National Park, Northern Thailand. *J. Trop. Ecol.* **1997**, *13*, 153–160.
16. Davies, A.B.; Eggleton, P.; van Rensburg, B.J.; Parr, C.L. The pyrodiversity-biodiversity hypothesis: A test with savanna termite assemblages. *J. Appl. Ecol.* **2012**, *49*, 422–430.
17. Glitzenstein, J.; Streng, D.R.; Wade, D.D. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and Northeast Florida, USA. *Nat. Area. J.* **2003**, *23*, 22–37.
18. Avery, T.E. *Natural Resources Measurements*; McGraw-Hill Book Co.: New York, NY, USA, 1975.
19. Clark, I.A.; Souter, R.A.; Schlaegel, B.E. *Stem Profile Equations for Southern Trees Species*; U.S. Department of Agriculture, Southeastern Forest Experiment Station: Asheville, NC, USA, 1991.
20. Ausmus, B.S. Regulation of wood decomposition rates by arthropod and annelid populations. *Ecol. Bull*. **1977**, *25*, 180–192.
21. Boddy, L.; Watkinson, S.C. Wood decomposition, higher fungi, and their role in nutrient redistribution. *Can. J. Bot.* **1995**, *73*, S1377–S1383.
22. Swift, M.J. The roles of fungi and animals in the immobilization and release of nutrient elements from decomposing branch-wood. *Ecol. Bull.* **1977**, *25*, 193–202.
23. Takamura, K. Effects of termite exclusion on decay of heavy and light hardwood in a tropical rain forest of peninsular Malaysia. *J. Trop. Ecol.* **2001**, *17*, 541–548.
24. Kofoid, C.A. *Termites and Termite Control*; University of California Press: Berkeley, CA, USA, 1934.
25. Forschler, B. Termite colony frequency in forests. Department of Entomology, University of Georgia, Athens, GA, USA. Personal communication, 1999.
26. SAS Institute. *SAS/STAT Guide for Personal Computers, Version 6 Edition*; SAS Institute: Cary, NC, USA, 1987.
27. Sokal, R.R.; Rohlf, F.J. *Biometry*, 3rd ed.; W.H. Freeman and Company: New York, NY, USA, 1995.
28. Dowdy, S.; Wearden, S.; Chilko, D. *Statistics for Research*, 3rd ed.; John Wiley & Sons, Inc.: Hoboken, NY, USA, 2004.
29. Stokes, M.E.; Davis, C.S.; Koch, G.G. *Categorical Data Analysis Using the SAS System*, 2nd ed.; SAS Institute: Cary, NC, USA, 2000.
30. Cornwell, W.K.; Cornelissen, J.H.C.; Allison, S.D.; Bauhus, J.; Eggleton, P.; Preston, C.M.; Scarff, F.A.; Weedon, J.T.; Wirth, C.; Zanne, A.E. Plant traits and wood fates across the globe: Rotted, burned, or consumed? *Glob. Chang. Biol*. **2009**, *15*, 2431–2449.
31. Conner, R.N.; Saenz, D. The longevity of large pine snags in eastern Texas. *Wildl. Soc. Bull.* **2005**, *33*, 700–705.
32. Ottmar, R.D.; Vihnanek, R.E. U.S. study of emissions of air pollutants from biomass fires in the United States: A progress report on fuel characterization—year 2. Department Agriculture, Forest Service, Pacific Northwest Research Station, Seattle, WA, USA. Unpublished work, 1997.

33. Parresol, B.R.; Shea, D.; Ottmar, R. Creating a fuels baseline and establishing fire frequency relationships to develop a landscape management strategy at the Savannah River Site. In *Proceeding Fuels Management—How to Measure Success*, Portland, OR, USA, 28–30 March 2006; Andrews, P.L., Bret, B.W., Eds.; U.S. Department Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2006; pp. 351–366.
34. Hanula, J.L.; Wade, D.D. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. *For. Ecol. Manag.* **2003**, *175*, 163–184.
35. Penttilä, R.; Kotiranta, H. Short-term effects of prescribed burning on wood-rotting fungi. *Silva Fenn.* **1996**, *30*, 399–419.
36. Mayfield, J.E.; Wade, D.D. Occurrence of macrofungi in burned and unburned hurricane-impacted loblolly pine forest. In *Proceedings of the 12th International Conference on Fire and Forest Meteorology*, Jekyll Island, GA, USA, 26–28 October 1993; Society of American Foresters: Bethesda, MD, USA, 1994; pp. 642–654.
37. Peterson, C.J. Review of termite forest ecology and opportunities to investigate the relationship of termites to fire. *Sociobiology* **1996**, *56*, 313–352.
38. Hu, X.P.; Appel, A.G. Seasonal variation of critical thermal limits and temperature tolerance in Formosan and eastern subterranean termites (Isoptera: Rhinotermitidae). *Environ. Entomol.* **2004**, *33*, 197–205.
39. Neary, D.G.; Klopatek, C.C.; DeBano, L.F.; Ffolliott, P.F. Fire effects on belowground sustainability: A review and synthesis. *For. Ecol. Manag.* **1999**, *122*, 51–71.
40. Massman, W.J.; Frank, J.M.; Shepperd, W.D.; Platten, M.J. *In situ* soil temperature and heat flux measurements during controlled surface burns at a southern Colorado forest site. In *Fire, Fuel Treatments, and Ecological Restoration*; Rocky Mountain Research Station: Fort Collins, CO, USA, 2003; pp. 69–87.
41. Ulyshen, M.D.; Horn, S.; Barnes, B.; Gandhi, K.J.K. Impacts of prescribed fire on saproxylic beetles in loblolly pine logs. *Insect Conserv. Divers.* **2010**, *3*, 247–251.
42. Peterson, C.J.; Gerard, P.D.; Wagner, T.L. Charring does not affect wood infestation by subterranean termites. *Entomol. Exp. Appl.* **2008**, *126*, 78–84.
43. Horn, S.; Hanula, J.L. Relationship of coarse woody debris to arthropod availability for red-cockaded woodpeckers and other bark foraging birds on loblolly pine boles. *J. Entomol. Sci.* **2008**, *43*, 153–168.
44. Abensperg-Traun, M.; Milewski, A.V. Abundance and diversity of termites (Isoptera) in unburnt versus burnt vegetation at the Barrens in Mediterranean Western Australia. *Aust. J. Ecol.* **1995**, *20*, 413–417.
45. Dawes-Gromadzki, T.Z. Short-term effects of low intensity fire on soil macroinvertebrate assemblages in different vegetation patch types in an Australian tropical savanna. *Aust. Ecol.* **2007**, *32*, 663–668.

46. Randall-Parker, T.; Miller, R. Effects of prescribed fire in ponderosa pine on key wildlife habitat components: preliminary results and a method for monitoring. In *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests*, Reno, NV, USA, 2–4 November 1999; Laudenslayer, W.F., Jr., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E., Eds.; U.S. Department Agriculture, Forest Service, Pacific Southwest Experiment Station: Albany, CA, USA, 2002; pp. 823–834.
47. Barber, B.L.; van Lear, D.H. Weight loss and nutrient dynamics in decomposing woody loblolly pine logging slash. *Soil Sci. Soc. Am. J.* **1984**, *48*, 906–910.
48. Harris, W.F. Nutrient release from decaying wood. In *Environmental Science Division Annual Report*; Auerbach, S.I., Reichle, D.E., Struxness, E.G., Eds.; Oak Ridge National Laboratory: Oakridge, TN, USA, 1976; pp. 169–170.
49. Eaton, R.J.; Sanchez, F.G. Quantitative and qualitative measures of decomposition: Is there a link? *S. J. Appl. For*. **2009**, *33*, 137–141.
50. Jonsell, M.; Weslien, J.; Ehnström, B. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiv. Conserv.* **1998**, *7*, 749–764.
51. Wikars, L.O. Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. *J. Insect Conserv*. **2002**, *6*, 1–12.