

Vegetation dynamics, coarse woody debris, and nitrogen cycling over 20 years in a virgin hemlock-hardwood forest recovering from catastrophic disturbance

Maggie Wagner, B.S. Honors thesis
University of Michigan

Mentor: David Orwig, Harvard Forest

Abstract

Primary forests provide a valuable opportunity to study forest processes in a natural environment, uncomplicated by anthropogenic disturbance. We surveyed two transects covering 0.57 ha of the Harvard tract of Pisgah forest in southeastern New Hampshire, one of the few parcels of old-growth forest remaining in New England. The surveys were conducted in 1989 and 2009. In each 10x10 meter plot, we measured and mapped every tree (live stems ≥ 2.5 cm diameter at breast height) and every piece of coarse woody debris (CWD; all downed wood with an average diameter ≥ 10 cm). In 2009 we also surveyed the understory vegetation and analyzed the C and N contents of soil from under CWD and soil that has incorporated recently decayed CWD. Censuses showed natural thinning of all major tree species, with Eastern hemlock (*Tsuga canadensis*) suffering mortality at less than half the rate of the hardwoods (*Acer rubrum*, *Fagus grandifolia*, and *Betula* spp.). The CWD pool decreased from 354.6 m³/ha to 215.5 m³/ha, but is still much larger than is typical for old-growth forests in New England. The vast majority of this CWD is the legacy of a catastrophic 1938 hurricane that destroyed the old-growth hemlock and white pine (*Pinus strobus*). As of 2009, white pine is almost completely absent from the forest. Between 1989 and 2009, total basal area increased from 35.5 to 41.8 m²/ha, while density decreased from 2793 to 1768 stems/ha. Plots differed in community structure, with tree density negatively correlated with average tree size. Trends over the topographic gradient indicates that slope and aspect influence both community structure and CWD stores. Nitrogen was scarcer in soil under CWD and in soil incorporating decayed wood than in control soil ($p < 0.05$), indicating that CWD effects on soil nutrition add another element of spatial heterogeneity to the forest floor. Finally, we found 20 species of herbs and shrubs covering 4.42% of the study area, as well as 10 species of tree seedlings covering an additional 5.45% of the site. Our results show that despite its recent history of catastrophic blowdown, Pisgah retains many structural features typical of old-growth forests (especially huge CWD pools and microtopography related to natural disturbances) and supports more diverse vegetation than is found in New England second-growth forests. These findings are useful for foresters wishing to design a balanced management plan that maximizes forest health, and for conservation biologists aiming to restore a damaged landscape as close as possible to its original pristine condition.

1. Introduction

Virgin forests are widely appreciated as study systems for basic forest ecology research as well as for their intrinsic value as habitat for plants and wildlife (Foster et al. 1996). Conservation biologists and restoration ecologists often use old-growth characteristics as a goal for the protection

and rehabilitation of disturbed ecosystems. For this reason, many studies have emphasized comparisons between old-growth or virgin forests and secondary growth, i.e., forests growing on abandoned agricultural land or recovering from intensive logging (Mladendoff et al. 1993, Angelstam 1998). Similarly, modern ecological foresters seek to develop selective logging regimes that imitate natural disturbance processes in old-growth forests in order to maximize forest health (Attiwill 1994, Franklin et al. 2002, Atlegrim and Sjojberg 2004). Among the most important features of virgin forests are their biodiversity (Halpern and Spies 1995, Angelstam 1998, Thomas et al. 1999) and their stores of dead wood, referred to as coarse woody debris (Sturtevant et al. 1997, Siitonen et al. 2000).

A diverse plant community has repeatedly been shown to be important for forest ecosystem functions (Hobbie 1992, Hooper and Vitousek 1997), so the preservation of biodiversity has become a priority for foresters and restoration ecologists. Comparative studies of old-growth, managed, and clear-cut forests have revealed major differences in community composition. Several studies have found that understory herb diversity is much lower in secondary forests than in old-growth forests, even decades after the original clear-cut (Duffy and Meier 1992, Moola and Vasseur 2004). Rare animals and specialists—including birds (Hansen et al. 1995), small mammals (Carey and Johnson 1995), and amphibians (Petranka et al. 1994)—are particularly dependent on old-growth habitat. One study (Maguire et al. 2004) found a direct correlation between the persistence of many taxa of fungi and birds and the percentage of live trees spared during harvesting activities. Another (Marshall 2000) found that clear-cutting significantly reduces soil faunal and floral diversity. Even if alpha biodiversity is constant between clear-cut and mature forests, the species themselves may differ markedly (Gilliam et al. 1995), fundamentally altering the natural ecosystem. In contrast, the strategic creation of canopy gaps in wisely managed forests may actually increase

biodiversity by opening niches for fast-growing, shade-intolerant plant species and associated taxa, while preserving the old-growth characteristics and mature canopy that others depend on (Attiwill 1994).

Directly related to forest biodiversity is decaying wood, or coarse woody debris (CWD), defined here and in other studies (e.g., Foster and Lang 1982, Brais et al. 2006, Gough et al. 2007) as downed logs and branches more than 10 cm in diameter. Many studies have shown that CWD stores are much higher in old-growth forests than in secondary or harvested forests (Sturtevant et al. 1997, McGee et al. 1999, Ziegler 2000, D'Amato et al. 2008). This is a major concern of restoration ecologists because CWD is an important structural feature of healthy forest ecosystems. CWD promotes biodiversity by creating microhabitats for a variety of flora and fauna (Harmon et al. 1986, Carroll 1993, Freedman et al. 1996) and is a major source of fuel for wildfires (Uhl and Kauffman 1990), which also promote biodiversity in forests where fires were historically important disturbances (Angelstam 1998, Allen et al. 2002). Decaying CWD also is an important part of the global carbon cycle, returning vast amounts of carbon to the atmosphere and also sequestering a considerable amount in the soil as humus (Berg and McClaugherty 2008).

Related to its role in the carbon cycle, but less clearly understood, is its function as a long-term nutrient source in forest ecosystems. CWD decays slowly; reported half-lives for CWD range from 7 years in tropical forests (Lang and Knight 1979) to 300 years in conifer forests of the Pacific Northwest (Sollins et al. 1987). Thus, CWD has the potential to store and supply nutrients for long periods of time. The extent to which CWD meets this expectation, however, is ambiguous. A review of the subject by Laiho and Prescott (2004) concluded that CWD contributes much of the biomass but only a small percentage of the total nitrogen input to the typical northern coniferous forest. This is likely due to the consistently low initial nitrogen concentrations in wood. For instance, Hart

(1999) found that only 4 to 6% of plant nitrogen uptake originated in CWD. In addition, mortality from normal senescence and self-thinning is not sufficient to generate large inputs of CWD on a regular basis (Fahey 1983). Thus, the role of CWD in the cycling of nitrogen and phosphorous is much less significant than its role in the carbon cycle (Laiho and Prescott 2004).

The same review, however, identifies certain cases in which this pattern may not hold. CWD in old-growth forests, for instance, represents a more substantial nutrient pool than the CWD in younger forests, due to the relative

immensity of the downed boles (Laiho and Prescott 2004). This view is shared by Lang and Forman (1978), who suggest that nutrient contributions from CWD are substantial but hard to detect because of a long time lag, during which wood carbon content slowly declines. Alternatively, young forests in the early stages of succession may also store larger amounts of nitrogen in their CWD pools, which are also unusually massive due to the numerous downed stems (Fahey 1983). These special cases, however, are precluded by salvage logging, which mostly negates these great pulses of CWD (Lindenmayer and Noss 2006).

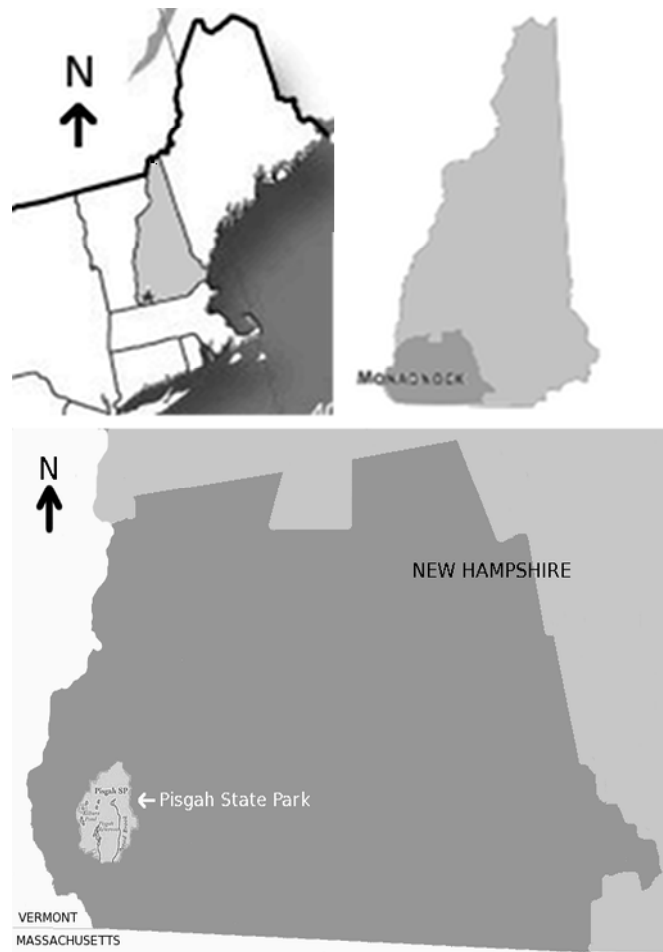


FIGURE 1. Location of study site, Pisgah State Park, in the Monadnock region of New Hampshire, USA. Maps modified from the Nations Online Project (<http://www.nationsonline.org>) and the New Hampshire Department of Resources and Economic Development (<http://www.visitnh.gov>).

The current thesis investigates the relationships between vegetation dynamics, CWD flux, and nitrogen cycling. The study site is an unmanaged, unsalvaged hemlock-hardwood forest recovering from a catastrophic hurricane that replaced its old-growth stands in 1938. Thus, we expect this forest to contain an especially large amount of nitrogen in its CWD pool, due to the simultaneous input of numerous very large trees during the hurricane. Moreover, because this wood has been decaying for over 70 years, the effects of this pulse of nitrogen should be detectable. This would be impossible in more recently disturbed forests, because coniferous CWD must decompose for several decades before it begins to release its nitrogen back into the ecosystem (Alban and Pastor 1993). The results of this study will help resolve how CWD contributes to forest nutrition, a question with important implications for both foresters and conservation biologists. More generally, this thesis also attempts to create a cohesive picture of natural forest succession 60 to 70 years after a stand-replacing disturbance, including understory and overstory vegetation, coarse woody debris stores, and carbon-nitrogen contents of soil and downed wood. Such a description will provide a useful comparison for forests recovering from clear-cutting or regenerating from pastures or farmland.

2. Methods

Study site and ethical considerations

The study area is located in the Pisgah State Park in southwestern New Hampshire (42°49' N, 72°27' W) (Figure 1). In 1927, Harvard Forest purchased an 8.1 ha tract near the center of the forest in order to protect it from logging, which was rampant in the early 20th century. The tract was chosen for its magnificent old-growth white pine (*Pinus strobus*) and Eastern hemlock (*Tsuga canadensis*), as well as for its isolated location and rugged terrain, which precluded logging in its immediate vicinity. The most prominent topographical feature is a low ridge (214 to 397 m above

sea level) running north-south through the tract (Henry and Swan 1974, Foster 1988). The soil is thin and rocky, and bare stone faces are exposed in some areas of high relief. The climate is temperate, with an average annual precipitation of 96.5 cm, distributed over all four seasons, and a typical growing season of approximately 120 days (U.S.D.A. 1941, Henry and Swan 1974).

The great hurricane of 1938 destroyed most of the old growth in Pisgah (Figure 2), and Harvard Forest chose not to salvage the uprooted trees within its protected parcel. In contrast, the numerous fallen trees were quickly harvested from the rest of the forest. Post-hurricane succession was allowed to proceed naturally in the Harvard Tract, which now consists almost entirely of five species: Eastern hemlock, red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), paper birch (*Betula papyrifera*), and black birch (*Betula lenta*). The tract remains untouched, a rarity in New England (Orwig et al. 2001, D'Amato et al. 2006), and is insulated from development by the 5300 ha State Park that was established in the late 1960s after decades of decreasingly intensive management. As a well-protected remnant of virgin forest, it provides a valuable opportunity to study ecological processes in a truly natural setting, and is the site of several past and ongoing studies of its fifteen permanent plots (Henry and Swan 1974, Foster 1988, Schoonmaker 1992).

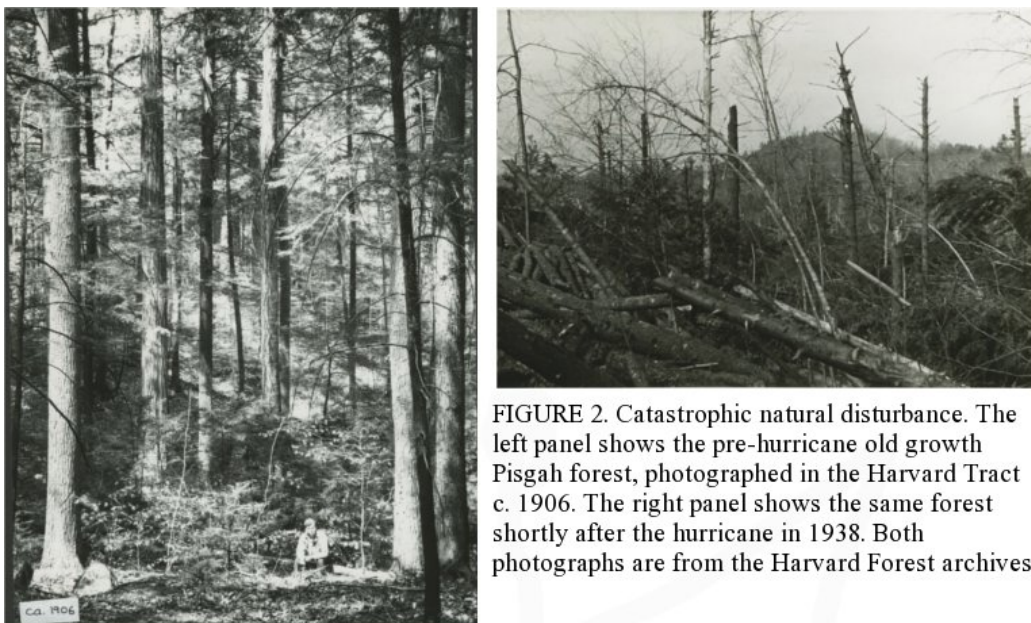


FIGURE 2. Catastrophic natural disturbance. The left panel shows the pre-hurricane old growth Pisgah forest, photographed in the Harvard Tract c. 1906. The right panel shows the same forest shortly after the hurricane in 1938. Both photographs are from the Harvard Forest archives.

The natural purity of our study site introduced special ethical consequences to our research (Minteer and Collins 2005). Much of Pisgah's value comes from its legacy as a native forest that has not been directly disturbed by humans. Out of respect for the entire ecosystem as well as the individual organisms that comprise it, we made every effort to minimize our impact as we worked. Our gravest concern was the spread of the hemlock woolly adelgid (*Adelges tsugae*), the exotic sap-sucking insect that is decimating Eastern hemlock over much of its eastern range (Orwig and Foster 1998), including a stand about 50 m from the parking lot at Harvard Forest, Petersham, Massachusetts, where our research team was based (M. Wagner, personal observation). The adelgid has been known to disperse via wind, animal, and automobile vectors (McClure 1990). We reasoned, however, that our odds of introducing the pest to Pisgah forest are no greater than those of any given visitor to the State Park. We recognize, too, that our daily 60-mile commute consumed more petroleum and emitted more carbon dioxide than should be allotted to such a small group of people. We sincerely hope that our research will support the development of practical knowledge that improves the health of Pisgah forest or of the Earth in general, so as to offset any damage our work may have caused.

Vegetation surveys

This study focuses on two permanent transects that run magnetic west to east across the width of the Harvard tract, spanning the entire topographic gradient. The parallel transects, 20 m apart, are divided into 10 m x 10 m plots. One transect was 300 m long and the other was 270 m long, for a total of 57 plots covering 0.57 ha. All four corners of each plot were marked with upright PVC pipe. The southwest corners were labeled with aluminum tags inscribed with the number of

their respective plots. For analyses of spatial patterns, plots were pooled into 27 groups of two and 3 groups of one based on their position along the topographic gradient (Figure 3).

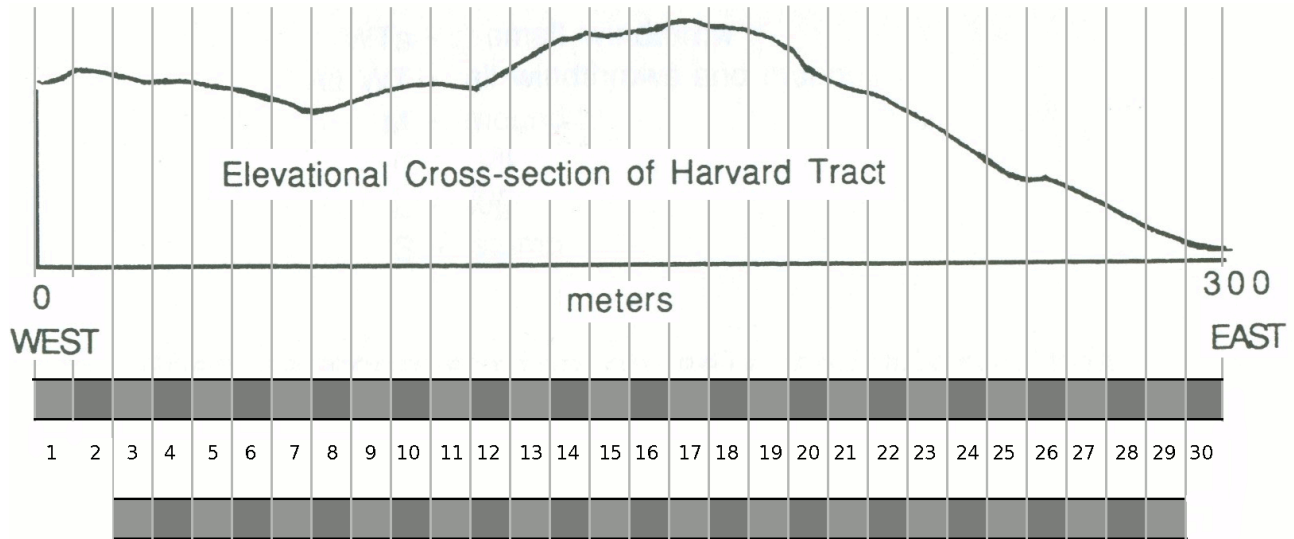


FIGURE 3. Diagram of sampling design—two transects, composed of 10 m by 10 m plots, with each plot's position along the elevational gradient of the Harvard Tract. Modified from Schoonmaker 1992.

To investigate the dynamics of the forest community over the past 20 years, we repeated the original surveys conducted by P.K. Schoonmaker (1992) when he established the transects in 1989. Schoonmaker inventoried every tree (stems ≥ 2.5 cm dbh) in the two transects, mapped their locations, and recorded diameter at breast height (dbh) and growing substrate. Schoonmaker used over a dozen different categories of substrate, but to simplify interpretation we condensed these into three major groups: soil, rock, and tip-up (i.e., the protruding roots of an older windthrown tree; see Figure 4). Schoonmaker's maps also showed the major topographical features of each plot, such as rocks and the mounds and pits created by uprooted trees. We used these maps to locate each tree. We recorded any trees not listed in the 1989 data as ingrowth, mapped and measured them, and recorded their species. Trees listed in 1989 that could not be located were recorded as missing, and assumed dead. We noted a missing tree's fate whenever possible (e.g., if it had become visible woody debris), but usually this was impossible and the tree was simply listed as missing. It should

be noted that because 20 years elapsed between surveys, our records of both mortality and ingrowth are probably underestimates—it is likely that some seedlings became established, died, and disappeared in between samplings. We take this fact into account when interpreting our data.



FIGURE 4. A paper birch growing on the exposed roots of a large white pine that was uprooted in the 1938 hurricane. Photographed in Pisgah forest by Tawny Virgilio, 2009.

By compiling and comparing our own data with Schoonmaker's, we created a master dataset that describes the fate of every tree living in the transects in 1989. For those that were still alive in 2009, we calculated their growth (as increase in dbh). By subtracting the trees that had died and adding the new trees, we created a second database that described the composition of these transects in summer 2009. We also constructed updated maps of the plots, showing all trees present in 2009 (Figure 5). Using these data, we analyzed patterns of mortality and changes in overstory structure over the past 20 years. All statistical analyses were conducted using the programming environment R (R Development Core Team 2009).

We also surveyed understory vegetation in each plot, which included saplings (stems < 2.5 cm dbh), root sprouts, seedlings, ferns, and herbaceous seed plants. We did not inventory the non-vascular flora. We used the Braun-Blanquet cover scale (Poore 1955) to characterize the understory in each plot. Plants occurring only once or twice in a plot were given the lowest ranking (*r* for rare),

and excluded from our final analysis of the community. All other plants were assigned to one of six categories depending on their estimated percent cover. Species that were sparsely present were presumed to cover 0.1% of a plot and grouped together; the other groups consisted of species covering least 1%, 5%, 25%, 50%, and 75%.

Coarse woody debris surveys

Schoonmaker's original surveys also included inventories of all aboveground coarse woody debris. CWD included stumps (rooted dead wood shorter than breast height) and boles (downed wood). Snags (rooted dead wood higher than breast height) were tallied separately.

Schoonmaker identified every piece of CWD to species (when possible), measured their volume, and drew them to scale on the vegetation maps.

Snapped and uprooted trees of appropriate size and age (mostly large *Tsuga canadensis* and *Pinus strobus*), and lying at an orientation of 270 to 330°, were linked to the hurricane of 1938.

Using these maps, we marked each piece of CWD on the 1989 list as either “missing” (assumed decayed) or “present.” A piece of wood was considered “present” if any part of it was visible. We also identified new CWD to species when possible; severely decayed CWD was instead identified to genus, as a hardwood or softwood, or recorded as unknown and excluded from analysis of species differences. We measured the volumes of new CWD and drew them onto the updated plot maps. Whenever possible, new CWD was cross-referenced to a tree that had died since 1989. New CWD was also assigned a decay class based on visual cues and physical traits, according to



FIGURE 5. Example of a working map for one 10x10 m plot. Numbered dots are trees; stumps, CWD, and topography (rocks, tip-ups, pits, etc.) are also sketched.

the five-level system described by Sollins *et al.* (1987). Logs and stumps were assigned as follows: class I if the wood was newly dead or fallen, still solid with bark intact and possibly with twigs still attached; class II if the wood showed early signs of decay, with minimal missing bark, no twigs, and sapwood beginning to soften; class III if the wood retained its shape but was soft through to the heartwood, with bark sloughing off; class IV if the wood was losing its shape, missing its bark and at least some sapwood, and heartwood beginning to decay; and class V if the wood was extremely decayed, had lost all of its bark and much of its sapwood and heartwood, and was severely misshapen. We altered the system slightly for birch detritus, due to the unusual resistance of birch bark.

We measured the dbh of snags using diameter tape. Volumes of stumps and boles were calculated from length and average diameter. For both boles and stumps, length from the tip to the base, or just above the root-ball if roots were also exposed, was measured using meter tape. Using 50-cm calipers, we measured the width of the stump twice at each end, on perpendicular axes. The average diameter of the stump was calculated as the mean of all four measurements. The same approach was used to measure downed wood. We took two width measurements on perpendicular axes at each end of the bole, and averaged all four values to calculate the final diameter. If a bole fell partially out of the plot, we measured its end diameter at the point of intersection with the plot boundary, and only measured its length up to the plot boundary line. All downed wood with an average diameter of < 10 cm was considered fine woody debris, and was neither mapped nor recorded.

This methodology deviates from both conventional and expertly recommended techniques for measuring CWD (Harmon and Sexton 1996). For instance, we had to exclude downed wood that was ≥ 10 cm diameter at one end but tapered so that its average diameter was < 10 cm. Our priority

in this study, however, was to compare data from 1989 and 2009, requiring us to be consistent with the methods used in 1989 (Schoonmaker 1992). As a result, we probably underestimated the amount of CWD that has entered the system since 1989. We take these consequences into account when interpreting our results.

As we did for the vegetation surveys, we compiled data into two sets: one describing the fate of all CWD present in 1989, and another reflecting the current CWD pool in these transects. Missing CWD was excluded from the updated maps, while new CWD was added. Due to time constraints, we did not re-measure old CWD for partial volume loss or change in decay class. We consider the resulting underestimate of decomposition when interpreting our results. Again, we conducted all statistical analyses using the programming language R.

Using our records of CWD that decayed completely between surveys, we were able to roughly estimate decay rates based on volume loss. We calculated the decay constant k from Olson's (1963) single negative exponential model using the formula:

$$V=V_0*e^{-kt}$$

where V is the volume of CWD in 2009, V_0 is the volume in 1989, and $t = 20$ years. The parameter k is used widely in the literature to describe decay rates, although it is almost always calculated from data on mass loss (Guo et al. 2006), density loss (Ganjegunte et al. 2004), or carbon dioxide efflux (Sollins et al. 1987) rather than volume loss. In addition, our values of k are almost certainly underestimates because they do not take into account volume lost from CWD that was still present in 2009, and also because they do not take into account mass and density loss that may have occurred without changing the apparent volume. Therefore, we do not attempt to compare these decay rates to those from other studies, but only use them to describe and predict CWD fluxes within our own study system, and interpret them accordingly.

Nutrient analysis

To examine the effect of CWD on soil richness, we took soil samples from 1) underneath CWD, 2) spots on the forest floor where CWD was present in 1989, but has since decayed completely, and 3) next to CWD, one meter away in a random direction. We also collected samples of the CWD itself, in order to examine nutrient dynamics of wood of different species, at various levels of decomposition. The individual pieces of CWD chosen for nutrient analysis were randomly selected from the 2009 pool of CWD on one of the transects. We only selected CWD belonging to three species: *Tsuga canadensis* ($N=13$), *Pinus strobus* ($N=6$), and *Fagus grandifolia* ($N=4$). Locations of soil samples from sites of completely decayed CWD were chosen in a similar manner, except that they were based on the pool of CWD that was present in 1989 but missing in 2009. These soils were from the former sites of randomly selected *T. canadensis* ($N=6$) and *P. strobus* ($N=6$) CWD, all originating in the 1938 hurricane (Schoonmaker 1992).

TABLE 1. Population sizes of all tree species in two transects (0.57 ha total) of the Harvard Tract in Pisgah forest, NH in 1989 and 2009.

Species	1989 population	Deaths	Ingrowth	2009 population	Net % decline	Annual % decline
<i>Tsuga canadensis</i>	582	120	29	491	15.6	0.85
<i>Acer rubrum</i>	350	169	7	188	39.9	2.55
<i>Betula lenta</i>	272	149	2	125	46.3	3.11
<i>Fagus grandifolia</i>	208	86	3	125	54.3	3.92
<i>Betula papyrifera</i>	127	69	0	58	54.0	3.89
<i>Fraxinus americana</i>	7	1	0	6	14.3	0.77
<i>Betula allegheniensis</i>	10	5	0	5	50.0	3.47
<i>Acer saccharum</i>	8	3	0	5	37.5	2.35
<i>Picea rubens</i>	5	2	0	3	40.0	2.55
<i>Quercus rubra</i>	3	0	0	3	0.0	0.00
<i>Prunus serotina</i>	2	0	0	2	0.0	0.00
<i>Pinus strobus</i>	1	0	0	1	0.0	0.00
<i>Ostrya virginiana</i>	1	0	0	1	0.0	0.00
<i>Ulmus americana</i>	1	1	0	0	100.0	
All species	1577	605	41	1013	35.7	2.21

All soil samples, taken from the organic layer only, were collected using a garden spade and taken back to the lab in labeled and sealed plastic bags. We filtered the soils through a 2 mm sieve to remove roots, wood chips, and other debris. Soils were dried at 60° C for 3 days and finely ground using the 110V heavy duty Wig-L-Bug grinding mill, which we cleaned with ethanol and de-ionized water between samples to prevent cross-contamination. Woods were dried at 100° C for one week, splintered using a razor blade, and finely ground using the Wig-L-Bug mill. Gloves were worn at all times while handling both soils and woods. We analyzed the carbon and nitrogen contents of the prepared samples with an Elementar Vario MICRO Cube.

As for the vegetation and CWD surveys, statistical analyses were conducted with the R programming language (R Development Core Team 2009). To address whether CWD affects the nitrogen richness of soil in this forest, we compared the mean percent nitrogen, mean percent carbon, and mean C:N of the three soil treatments (away from CWD, under CWD, and formerly under CWD) with one-way ANOVA. Pairwise comparisons were made with Welch's two-sample t-test. We also compared the mean percent nitrogen, mean percent carbon, and mean C:N of CWD samples, using species and decay class as explanatory variables. For some CWD samples, nitrogen content was so low that the machine could not detect it accurately; these samples were excluded from ANOVA tests for percent nitrogen and C:N.

3. Results

Vegetation surveys

Censuses of all species from 1989 and 2009 revealed a 36.7% decrease in density from 2793 stems/ha to 1768 stems/ha. The 615 deaths

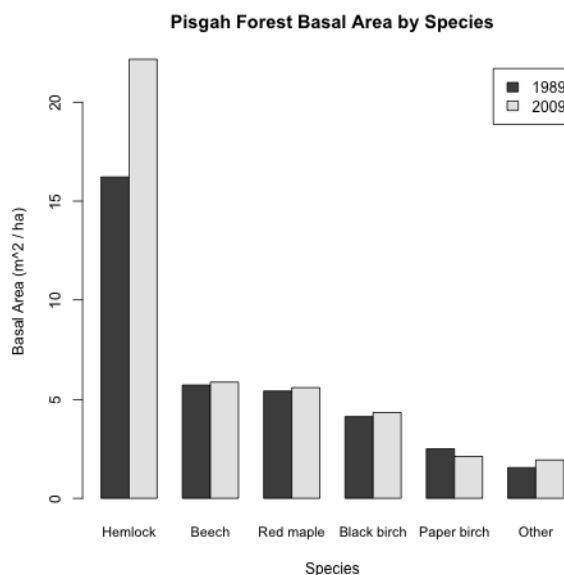


FIGURE 6. Total live basal area in 1989 and 2009, broken down by species.

were distributed unequally among species (Pearson chi-square, $p < 0.001$), ranging from 20.7% of hemlocks to 55.1% of black birches (Table 1). We recorded only 36 new stems, of which 26 were hemlocks. In both 1989 and 2009, over 97% of live stems belonged to one of the five dominant species (Eastern hemlock, red maple, American beech, paper birch, or black birch). Populations of all species declined over the 20-year interval, except for three sparsely present species, which remained stagnant (Table 1). The relative densities and basal areas of the five dominant species, however, shifted noticeably in favor of hemlock at the expense of the birches (Figure 6). This reflects both uneven mortality and uneven growth (Table 2; ANOVA, $p < 0.001$) among species. Total basal area increased from 35.5 m²/ha to 41.8 m²/ha.

Preferential thinning of birches and red maple since 1989 (Table 1) suggests that shade-tolerant Eastern hemlock is enjoying a selective advantage. This competition probably also explains the observed high mortality rates of trees growing on the exposed roots of massive windthrown trees (“tip-ups”); although tip-ups are an unstable substrate and are expected to cause mortality when they eventually degrade and collapse, as of 2009 most tip-ups were still quite solid. Therefore, death rates in these microhabitats were higher because most (72.2%) of the trees that established there were shade-intolerant birches. In contrast, only 14.9% of trees growing in soil and 18.2% of trees growing on bare rock were birches.

TABLE 2. Species-specific and overall growth of trees in the Harvard Tract of Pisgah forest, NH from 1989 to 2009.

Species	Mean dbh growth (cm)	Net Δ basal area (m ² /ha)		% of total basal area in 1989	% of total basal area in 2009
		+	-		
<i>Tsuga canadensis</i>	2.99	5.93		45.6	52.7
<i>Fagus grandifolia</i>	2.94	0.15		16.1	14.0
<i>Acer rubrum</i>	2.05	0.17		15.3	13.3
<i>Betula lenta</i>	2.44	0.20		11.7	10.4
<i>Betula papyrifera</i>	2.28		0.39	7.0	5.0
Other	3.71	0.25		4.3	4.6

All species	2.72	6.44	100.0	100.0
-------------	------	------	-------	-------

Growing substrate also affected mortality rates (Pearson chi-square, $p < 0.01$). Trees growing on tip-ups suffered 50.0% mortality, compared to only 36.7% for trees growing in soil and 35.4% for those growing on bare rock. Among all surviving trees, however, substrate did not affect growth (ANOVA, $p = 0.2349$).

Both tree density and mean dbh changed in roughly opposite manners depending on location along the transect; as a result, their effects clashed so that basal area had no relationship with location (Figure 7). Single linear regression of density and mean dbh showed a strong negative correlation (Figure 8; $p < 0.001$ for data from both 1989 and 2009). Understory vegetation, however, was less predictable. Plots showed variation in both species richness and percent ground cover, but no trends were apparent along the transect (Figure 9). Furthermore, single linear regressions revealed that percent cover was not related to tree density ($p = 0.293$), tree basal area ($p = 0.1703$), or volume of CWD ($p = 0.5248$). Similarly, herb species richness showed no correlation with the same parameters ($p = 0.179$, $p = 0.5610$, and $p = 0.246$ respectively).

A total of 26 species (including 16 herbs and shrubs and 10 species of tree seedlings) were recorded in the understory. The most abundant were hemlock seedlings, ferns in the genus *Dryopteris*, beech seedlings, and lowbush blueberry. The most widespread (i.e., recorded in the most plots) were beech seedlings, red maple seedlings,

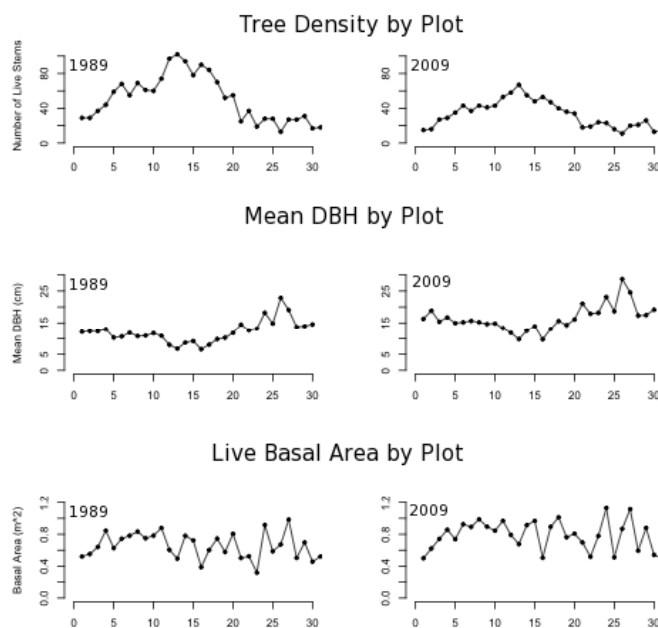


FIGURE 7. Trends in tree density and size along the topographic gradient (see Figure 3) in 1989 and 2009.

hemlock seedlings, and Indian pipe (Table 3). Notable areas for understory vegetation were the top of the ridge (plots 15-16), which were dense with blueberry, and the low end of the transect (plots 28-30), which supported thick patches of ferns (Figure 9-b). The entire understory covered 9.87% of the available area in the study site; without woody seedlings, saplings, and root sprouts, this figure drops to 4.42%.

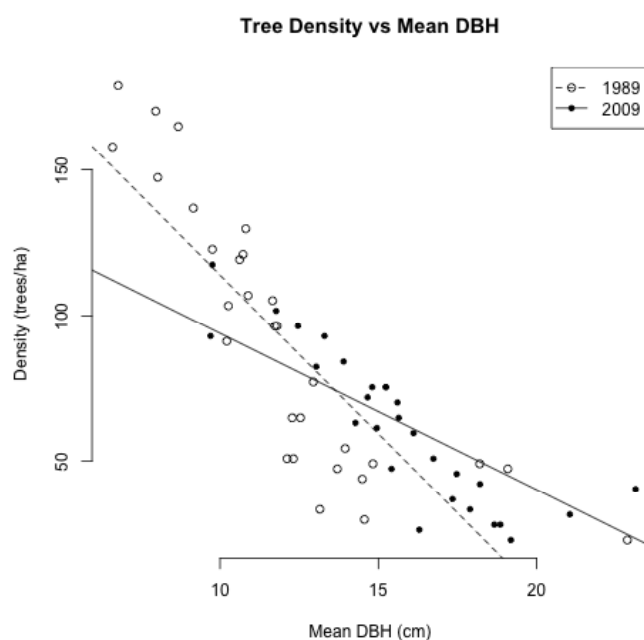


FIGURE 8. Strong negative correlation between density and tree size, showing differences in community structure between plots.

CWD surveys

Between 1989 and 2009, a total of 153.7 m³/ha of CWD decayed completely, and only 14.7 m³/ha of new CWD were added to the system, resulting in a net decrease of 139.0 m³/ha of wood. Most (87.8% by volume) of the CWD that decayed completely between inventories was pine or hemlock. However, initial volumes of CWD of these species were so high that even in 2009, they represented most of the CWD

pool despite suffering the greatest losses to decay (Figure 10). They also accounted for the majority of new inputs to the CWD pool (Table 4), despite the fact that living pine was nearly absent from the community in 1989 and hemlock suffered the lowest mortality rates of any species since then. The large influx of pine CWD resulted from a few massive hurricane-killed snags that fell into one plot, causing the addition of 4 pieces of wood with an average volume of 0.69 m³—much higher than 0.02 m³, the average volume of all other new CWD (this event is visible as a spike in Plot 12 in Figure 11-c). The abundance of hemlock in the input CWD pool, in contrast, is an artifact of the

initial abundance of this species in 1989 (45.6% of live basal area) as well as hemlock's relative success at establishment since then (53.4% of ingrowth basal area). The basal area of snags increased slightly from 2.64 to 2.78 m²/ha. Both total CWD input and total volume varied by plot, but no trends along the transect were apparent (Figure 11). In single linear regressions, CWD input was not correlated with 1989 basal area ($p = 0.882$), 1989 tree density ($p = 0.125$), or mortality ($p = 0.161$).

TABLE 3. List of all species present in the understory, along with their abundances.

Species	Occurrence (% of plots)	Coverage (% of transect area)
<i>Tsuga canadensis</i>	66.67	3.62
<i>Dryopteris sp.</i>	43.33	2.44
<i>Fagus grandifolia</i>	86.67	1.40
<i>Vaccinium angustifolium</i>	23.33	1.35
<i>Acer pennsylvanicum</i>	13.33	0.25
<i>Polystichum sp.</i>	13.33	0.25
<i>Polypodium vulgare</i>	20.00	0.18
<i>Acer rubrum</i>	80.00	0.16
<i>Monotropa uniflora</i>	66.67	0.07
<i>Trientalis borealis</i>	26.67	0.03
<i>Aralia nudicaulis</i>	13.33	0.01
<i>Arisaema triphyllum</i>	6.67	0.01
<i>Betula papyrifera</i>	6.67	0.01
<i>Carex sp.</i>	13.33	0.01
<i>Dennstaedtia punctilobula</i>	6.67	0.01
<i>Gaultheria procumbens</i>	6.67	0.01
<i>Lycopodium lucidulum</i>	10.00	0.01
<i>Lycopodium obscurum</i>	6.67	0.01
<i>Maianthemum canadense</i>	10.00	0.01
<i>Medeola virginiana</i>	13.33	0.01
<i>Mitchella repens</i>	10.00	0.01
<i>Aster acuminatus</i>	3.33	0.00
<i>Betula lenta</i>	3.33	0.00
<i>Polygonatum commutatum</i>	3.33	0.00
<i>Viburnum acerifolium</i>	3.33	0.00
<i>Viburnum alnifolium</i>	3.33	0.00

TABLE 4. Flux by volume, estimated decay rate, and estimated half-life of CWD in the Harvard Tract of Pisgah forest, NH from 1989 to 2009.

Species	Input (m ³ /ha)	Output (m ³ /ha)	k (years ⁻¹)	Half-life (years)
<i>Pinus strobus</i>	4.87	19.73	0.04745	14.6
<i>Tsuga canadensis</i>	3.47	115.21	0.00535	129.5
<i>Fagus grandifolia</i>	2.49	3.54	0.01391	49.8
<i>Betula</i> spp.	2.47	5.44	0.04319	16.0
<i>Acer</i> spp.	0.86	2.15	0.03054	22.7
Other	0.52	7.65	0.03925	17.7
All species	14.68	153.72	0.02486	27.9

Nutrient analysis

In this study, CWD appears to decrease the nitrogen content of the soil beneath it. Percent N was lowest in “under” soil presently underneath CWD, intermediate in “incorporated” soil associated with recently decayed CWD, and highest in control soil with no recent exposure to CWD (Figure 12-b). Accordingly, C:N shows the

opposite trend (Figure 12-c). The C:N of control soil was significantly lower than those of both “incorporated” and “under” soil ($p < 0.05$ and $p < 0.01$, respectively), but the C:N of “incorporated” and “under” soil was the same ($p = 0.6586$). There were no differences in % carbon between soil categories (Figure 12-a; ANOVA, $p = 0.7002$).

For CWD itself, species and decay class explained variance only in %C (ANOVA; $p < 0.01$ for both). Analyses were hampered by small sample sizes; no pairwise comparisons could be made for CWD in decay class I. Comparisons of the remaining groups were ambiguous. Percent N varied significantly only between decay classes II and V, whereas mean C:N distinguished only decay

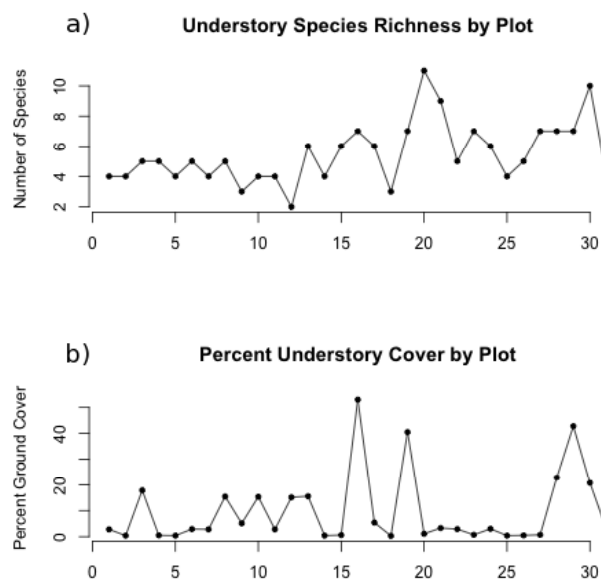


FIGURE 9. Spatial variation in understory richness and abundance along the topographic gradient (see Figure 3). This figure includes both herbs and woody seedlings, saplings, and root sprouts.

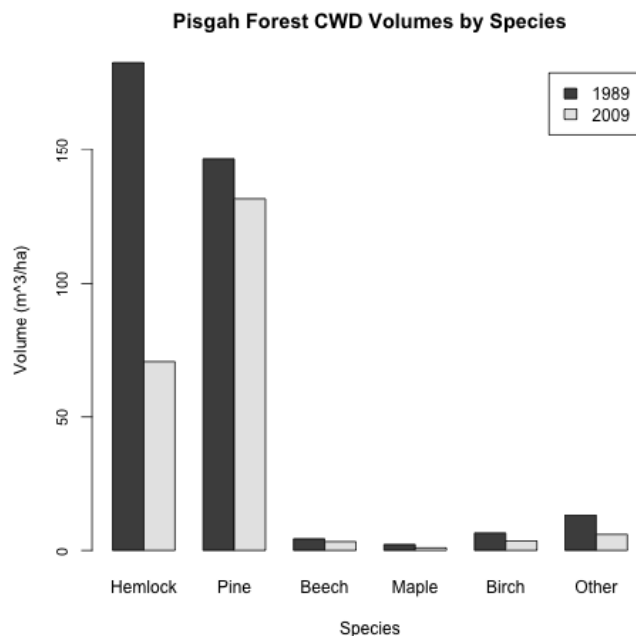


FIGURE 10. Total volumes of CWD in 1989 and 2009. See Table 4 for a breakdown of the change in volume for each species.

class II from class IV (Welch two-sample t-test, $p < 0.05$ in both cases). Percent C, in contrast, differed significantly between decay class V and classes II, III, and IV (Welch two-sample t-test, $p < 0.05$, $p < 0.01$, $p < 0.001$ respectively). This reflects the low variance in percent C between the four lower classes (all between 47.0% and 49.0%) followed by the sudden spike in decay class V (Table 5). Anomalous behavior of decay class V is also evident in trends in percent N

and C:N. Relative N content increases steadily with decay class from 15.5% to 49.1%, but then drops abruptly in class V. Similarly, C:N decreases steadily as decay class increases, but spikes again in decay class V (Table 5). Similarly, %C differed between American beech and both softwood species ($p < 0.01$ for pine, $p < 0.001$ for hemlock) but not between the softwoods themselves ($p = 0.3799$). No species differed significantly in either %N or C:N. In general, N content was highest in pine CWD, intermediate in hemlock CWD, and lowest in beech CWD (Table 5). Percent C and C:N showed the opposite trend. Qualitatively we can say that N content is higher in CWD than in fresh wood; none of our fresh wood samples contained enough N for the elemental analyzer to detect, whereas we were able to obtain N data for most of the CWD samples.

4. Discussion

Even-aged succession in Pisgah Forest

Over the past 20 years, the tree community in the Harvard Tract of Pisgah forest has changed in a predictable way, given the life histories and ecological requirements of the major species involved (Halpern 1989). Reconstructions (Henry and Swan 1974, Foster 1988) reveal that the old-growth vegetation in the early 20th century consisted mostly of massive *Pinus strobus* and *Tsuga canadensis*.

After the forest was leveled by the 1938 hurricane, white pine never recovered. Foster (1988) posits that some qualitative difference in the forest floor—possibly the absence of fire in recent decades—prevented white pine from re-establishing during early succession, when the light-loving species could have thrived. Instead, a variety of hardwoods—notably opportunistic birches and red maple—rose to prominence under the newly wide-open canopy. Meanwhile, hemlock remained important, keeping up with the faster-growing hardwoods during early succession. It appears that the first hemlocks to reach the new overstory were already seedlings or saplings at the time of the hurricane, survived the devastating winds, and were released from suppression when the formerly dense canopy was opened by the storm (Foster 1988). Tree density skyrocketed immediately after the hurricane, and basal area plummeted; but as the overstory grew in, density gradually decreased while basal area increased, a pattern that has continued through 2009.

TABLE 5. Nitrogen contents of CWD of different decay classes and species.

Attribute	CWD decay class				
	I	II	III	IV	V
mean % N	15.50 §	25.76 a	37.40 ab	49.05 ab	36.82 b
mean C:N	303.87 §	207.42 c	158.99 cd	122.32 d	181.18 cd
	CWD species				
	<i>Pinus strobus</i>	<i>Tsuga canadensis</i>	<i>Fagus grandifolia</i>		
mean % N	43.72	37.35	29.89		
mean C:N	158.79	172.13	183.93		

Notes: For decay classes, different letters denote significance at $p < 0.05$ using Welch two sample t-test.

No means were significantly different between species.

§ Significance could not be tested for decay class I due to small sample size ($N = 5$).

The topographic gradient of our study site appears to play some role in overstory structure. The tree community is less dense in the eastern third of the transect, which corresponds to a pronounced slope with an eastern aspect (see Figure 3). In addition, the trees are also larger than average here. Because the 1938 hurricane approached from the east (Foster 1988), the thinner forest here is not unexpected. It seems that if this area suffered heavier casualties during the hurricane, some legacy of CWD should remain, especially at the bottom of the slope (where falling boles are naturally more likely to land). Instead, however, we see an unusually small CWD pool that decreases along with elevation (Figure 11). The distinctiveness of this part of the transect suggests some qualitative difference and merits further investigation.

Because of the coarse temporal resolution of this study, we know only that the relative density and relative basal area of Eastern hemlock have increased over the last 20 years. Sampling at a finer scale would allow us to determine whether rates of population change are increasing, decreasing, or remaining constant. In addition, a finer temporal resolution would prevent the underestimation of both ingrowth and mortality rates, thus allowing a more accurate and descriptive record of tree community dynamics. Based on these imperfect data, our best prediction for the future of

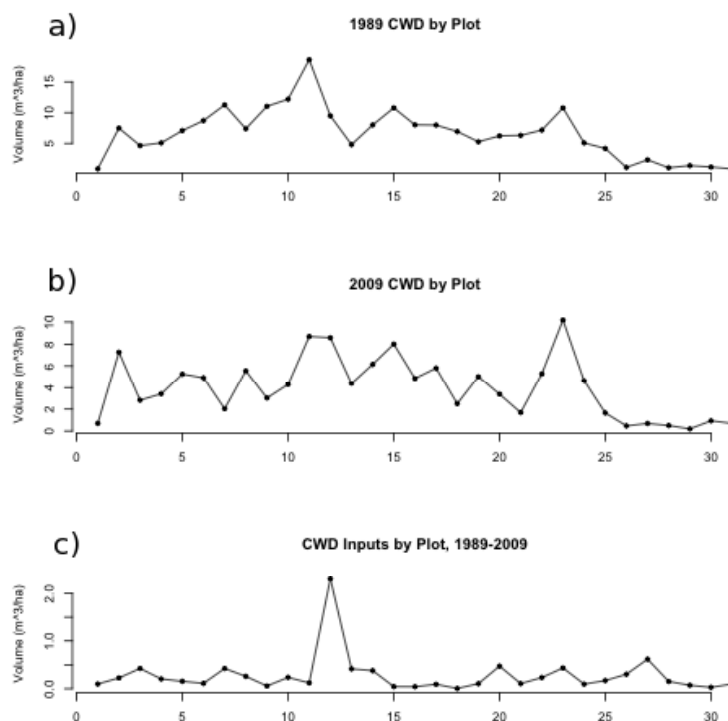


FIGURE 11. Spatial variation in total CWD volume in 1989 and 2009, and in CWD input between surveys, over the topographic gradient (see Figure 3).

Pisgah is decelerating mortality towards a climax community dominated by *Tsuga canadensis*, with significant populations of *Fagus grandifolia* and *Acer rubrum*. An intermediate disturbance regime may create canopy gaps that allow r-selected species such as *Betula lenta* and *B. papyrifera* to persist in small stands, eventually resulting in a forest with a more complex age structure (D'Amato et al. 2008). Succession is not completely understood and difficult to predict, but even subtle variations in disturbance history have been shown to impact vegetation patterns (Halpern 1989, McLachlan et al. 2000, Busby et al. 2008). Therefore, we expect that community dynamics will proceed differently in Pisgah forest than in forests with histories of clear-cutting or agricultural use.

Such disturbance-related differences in forest composition also extend to the herb community (Duffy and Meier 1992, Gilliam et al. 1995, Thomas et al. 1999, Moola and Vasseur 2004). Currently, the understory vegetation at our study site is similar to that of other old-growth hemlock forests in the region. For instance, a recent article by D'Amato *et al.* (2009) reported a total of 26 herb species from 16 old-growth sites in western Massachusetts, covering on average about 4% of the forest floor. Sixteen of these species co-occurred in Pisgah, which had 20 species covering 4.42% of available area. It is worth noting that the Pisgah data represent a much larger sampling area (5700 m² compared to 384-640 m²); the average of 14 species found in each 24-40 m² plot by D'Amato *et al.* is probably higher than what a similar sampling design would reveal in Pisgah forest. Nevertheless, the Pisgah understory is more similar to the old-growth vegetation than the secondary vegetation reported by D'Amato *et al.* This suggests that land-use history exerts a strong influence on the understory community, because a diverse herb and shrub community has persisted in Pisgah despite a catastrophic disturbance that opened the canopy and drastically altered the overstory, whereas many understory species have not repopulated forests that were cleared for agriculture. D'Amato *et al.* (2009) suggest that the availability of natural disturbance-related

microhabitats (e.g., CWD, pits, tip-ups, canopy gaps) promoted understory richness. Similarly, del Rio (2006) found that the herb community was altered by the salvaging of downed wood, resulting in clear differences even between forests disturbed by the same windstorm. In this thesis, however, we found no links between either CWD or basal area and understory composition in Pisgah forest.

Coarse woody debris flux

The CWD pool at Pisgah forest has diminished significantly since 1980, indicating the steady decomposition of the last major pulse of CWD in 1938. In pristine forests during succession, the CWD pool is logically expected to be representative of the climax vegetation at the time of the most recent major disturbance (excluding fires). Pisgah is no exception; even in 2009, the vast majority of the CWD pool is white pine and hemlock, which made up a similar proportion of the total woody biomass at the time of the hurricane (Foster 1988). As this wood continues to decompose and slowly disappears, it will no longer swamp new inputs to the pool, and CWD stores will begin to resemble more closely the post-disturbance community. Repeated surveys at this site, if conducted at a finer temporal resolution—about 5 year increments, recommended by Harmon and Sexton (1996)—are expected to reflect the process of succession. More generally, the size and species composition of

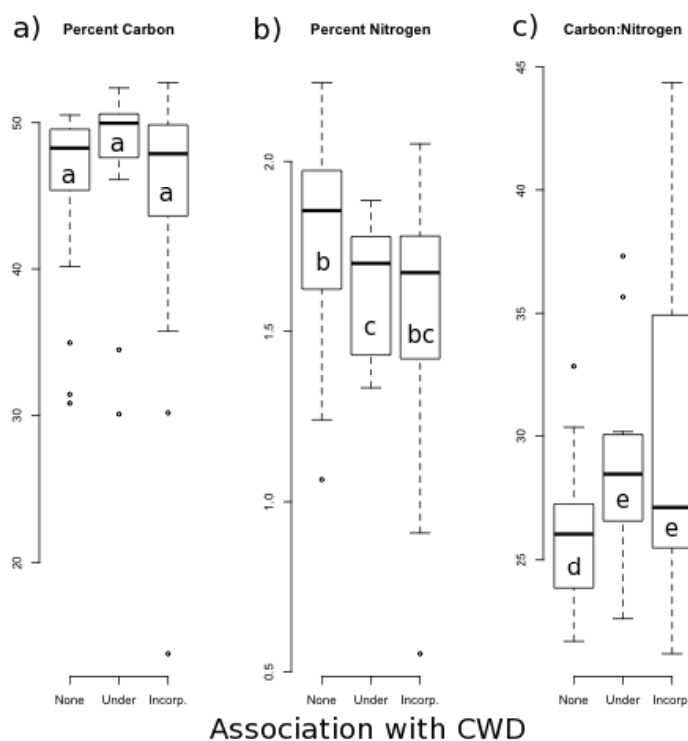


FIGURE 12. Carbon and nitrogen contents of soil affected by association with CWD. “None” refers to control soil “Under” refers to soil collected from beneath CWD, and “Incorporated” refers to soil collected from sites where CWD has completely decayed within the past 20 years. Plots with different letters are significantly different (Welch two-sample t-test, $p < 0.05$).

the CWD pool should track the total biomass and species composition of the woody community at any given time, with a time lag of some decades depending on tree senescence rates, CWD decay rates, and the frequency and intensity of disturbance. A comprehensive model linking CWD stores and vegetation has not yet been developed, although such relationships have been used qualitatively to reconstruct forest history at the landscape level (Henry and Swan 1974).

Even after 70 years of decay, the CWD pool in Pisgah forest is substantially larger than those in typical New England secondary hemlock forests, and even other primary hemlock forests (Table 6). Our recorded value of 215.8 m³/ha is particularly striking because it is almost certainly an underestimate, given our unusually strict definition of CWD (see Methods). The markedly high volume of CWD compared to similar old-growth forests is due to the relatively recent catastrophic disturbance and the slow decomposition of the resulting downed trees. As this major pulse of CWD gradually disappears, we expect the total volume of CWD at Pisgah to decline and reach equilibrium between decay and new mortality (Tyrell and Crow 1994). Because no trees are harvested and removed from this ecosystem, we expect its volume of CWD at equilibrium to remain higher than volumes in partially or entirely harvested hemlock forests. The frequency and intensity of future disturbances—particularly ice storms and small-scale windstorms—will likely be important controls on the CWD pool (D'Amato et al. 2008), because rates of standing mortality due to normal senescence are relatively slow among the long-lived Eastern hemlock, compared to species such as *Betula* spp. (Tyrell and Crow 1994).

Our records of complete decomposition of CWD between 1989 and 2009 allow us to draw some broad conclusions about CWD decay rates in Pisgah forest. Between 1989 and 2009, white pine CWD decayed more slowly than any other species by an order of magnitude. If it continues to decay at the same rate, about four centuries will pass before only 5% of its volume remains. In

contrast, all red maple CWD currently in the system is expected to decay within just over 20 years. Because of our rough methodology, these CWD lifespans are probably overestimates (see Methods). Nevertheless, an impressively small proportion of pine CWD decomposed during the last 20 years. This relatively low decay rate, coupled with the very high initial volume of white pine CWD, suggests that evidence of *Pinus strobus* will remain in Pisgah forest for many decades after its live population was wiped out.

TABLE 6. Comparison of CWD stores and basal areas of New England forests differing in community composition and disturbance history.

CWD (m ³ /ha)	Basal area (m ² /ha)	Disturbance / succession level	Forest type	Location	Source
216	41.8	Pristine; even-aged maturing	Hemlock/hardwood	Southeastern NH	This thesis
135	44.8	Pristine; old-growth	Hemlock	Western MA	D'Amato <i>et al.</i> 2008
33	41.2	Secondary growth	Hemlock	Western MA	D'Amato <i>et al.</i> 2008
109	NA ‡	Secondary growth	Hemlock/hardwood	Central ME	Fraver <i>et al.</i> 2002
32	61.2	Pristine; old-growth	Hemlock	Central MA	Orwig <i>et al.</i> 2001
126	NA ‡	Old-growth	Hemlock/hardwood	Eastern NY	Ziegler 2000
63	NA ‡	Post-fire secondary growth	Hemlock/hardwood	Eastern NY	Ziegler 2000
65	47.0	Old-growth	Hemlock/hardwood	Northern MI and WI	Tyrell & Crow 1994
69	18.2	Partially harvested, uneven-aged	Hardwood	Eastern NY	McGee <i>et al.</i> 1999
139	33.7	Old-growth	Hardwood	Eastern NY	McGee <i>et al.</i> 1999
61	29.1	Maturing, even-aged	Hardwood	Eastern NY	McGee <i>et al.</i> 1999

‡ Data not reported.

Nitrogen cycling

Because CWD is so abundant in Pisgah forest, we discuss here its possible effects at the ecosystem level, which might be missing from overharvested forests with unnaturally small stores of downed wood (Currie and Nadelhoffer 2002). Specifically, we go beyond the well-established impacts of CWD (creating microhabitats, promoting seedling establishment, fuelling wildfires, etc.) and address instead its ambiguous role in the nitrogen cycle. Unfortunately, without mass or density

measurements we could not estimate the total amount of N stored in the woody litter in Pisgah forest. The %N by mass in CWD was quite low, but such a huge amount of even poor-quality CWD could represent a formidable N pool (Laiho and Prescott 2004). In addition, CWD appeared to accumulate N. Past studies also have found that the nitrogen content of CWD increases with time (Holub et al. 2001). In the current study, however, N content increased with decay class only for classes I through IV (Table 5). Possibly, decay class V describes the point at which the N in CWD begins to be released into the ecosystem. If this is so, future studies might concentrate on extremely decayed wood in order to describe the endpoint of the decomposition process, as far as N is concerned.

In this study, the effects of CWD on soil nitrogen are more interesting than the nutrient contents of the wood itself. Aber *et al.* (1989) identified soil C:N as an important indicator of forest N status, which in turn exerts an important control on many aspects of ecosystem functioning, notably primary productivity (Aber et al. 1995, Vitousek et al. 1997). CWD significantly decreased the amount of N in the organic soil layer, even after the wood had decomposed entirely. This shows that CWD's effects are detectable both before and after it is incorporated into the soil, suggesting that its mere physical presence is enough to alter soil nutrition (although chemical or biological processes may also eventually come into play). Differences in soil nutrition add another element of spatial heterogeneity to the forest floor, and can therefore be expected to influence the spatial arrangement of future vegetation (D'Amato et al. 2009). More detailed research is necessary to investigate the possible mechanisms by which CWD decreases soil N:

- 1) Logs intercept rain containing dissolved nitrogen, a common form of pollution in New England (Driscoll et al. 2003, Campbell et al. 2004). Experiments in other mixed forests (Schimel and Firestone 1989) and in nearby Harvard Forest (Micks et al. 2004) have

shown that decaying wood acts as a sink for anthropogenically supplemented N—another potential mechanism for N accumulation in CWD. Another Harvard Forest study, however, indicated that soil stores more exogenous N than does wood or other litter (Magill et al. 2004), which would explain why less N was detected even in soil that has already incorporated the decayed CWD. This hypothesis merits further investigation, because N deposition has the potential either to enhance forest productivity (Nadelhoffer et al. 1999) or to damage ecosystem health (Aber et al. 1995, Magill et al. 2004).

- 2) CWD blocks inputs of leaf litter, which tends to contain more nitrogen than woody litter (McClaugherty et al. 1985). Because humus consists largely of decomposed plant litter, the organic layer of exposed soil should contain much more leaf material than soil that has been sheltered by wood for decades. This observation explains not only why the control soil in our study was richer than soil associated with CWD, but also why soil currently under CWD had slightly less N than soil under totally decayed CWD (Figure 12)—probably, the “incorporated” soil has recently had a few years of leaf input. In general, then, the N content of soil under CWD should decrease consistently with time and then increase after the log is gone—an hypothesis easily testable either in woody litter chronosequences or through long-term experimentation (e.g., intercepting and removing leaf litter).
- 3) Fungi living in humus and on woody litter have been shown to move soil nitrogen into CWD (Schimel and Firestone 1989), a biological explanation for the scarcity of N beneath logs. The presence of CWD also affects the soil biotic community, especially organisms involved in the decomposition of plant litter. For instance, CWD promotes species richness of basidiomycetes and other soil fauna (Nordén et al. 2004), with

important implications for many ecosystem functions (Coleman and Whitman 2005).

Spears *et al.* (2003) found that soil beneath CWD is warmer than control soil, and while microbial biomass was not affected, the metabolic rates and N utilization may have been enhanced by higher temperatures beneath logs.

5. Conclusion

The characteristics of Pisgah forest described in this thesis reinforce previous studies' conclusions that land use history exerts a crucial influence on ecosystem processes. The old-growth stands that once dominated the forest were almost completely eliminated by the hurricane of 1938, and yet the structure of the forest today is very different from the structure of forests that suffered similarly intense disturbance at the hands of humans. In particular, the evidence suggests that completely natural forests such as Pisgah store much more carbon and nitrogen in the form of coarse woody debris and support a wider variety of herbaceous species than do second-growth forests in the same region. This study also shows that CWD is involved in nitrogen cycling and alters the nutrition of the soil beneath it. Thus, it contributes a great deal of spatial heterogeneity to the forest floor, not only as microhabitat for plants and animals, but also through its effect on soil N content even after it is completely decayed. Because biodiversity and N cycling are so crucial to ecosystem functioning, therefore, the impacts of land use resonate through many dimensions of forest health. Because of its recent history of catastrophic disturbance, Pisgah has provided an outstanding opportunity to observe succession in a totally natural setting, and an excellent case study in basic forest ecology and forest history. Its unique CWD pool, protected status, well-documented history, and ownership by a Long-Term Ecological Research program also make it an ideal study site for more detailed CWD decomposition studies in the future. This thesis is the first attempt at quantifying decay rates at Pisgah, and has set a precedent for nutrient analysis as well.

More frequent surveys of CWD including density measurements, quantification of a wider array of nutrients, and more detailed soil profiling should yield valuable insights into relationships between disturbance, succession, and forest nutrition.

Acknowledgements

Many thanks to Dave Orwig, Audrey Barker-Plotkin, and David Foster for their guidance during this project, and to Brendan Gallagher for his help with data collection. This project was funded by Harvard University, Harvard Forest, and the National Science Foundation through the Research Experience for Undergraduates program.

Works Cited

- Aber, J., A. Magill, S. McNulty, R. Boone, K. Nadelhoffer, M. Downs, and R. Hallett. 1995. Forest biogeochemistry and primary production altered by nitrogen saturation. *Water Air and Soil Pollution* **85**:1665-1670.
- Aber, J., K. Nadelhoffer, P. Steudler, and J. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. *Bioscience* **39**:378-386.
- Alban, D. H., and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on 2 sites in Minnesota. *Canadian Journal of Forest Research* **23**:1744-1749.
- Allen, C., M. Savage, D. Falk, K. Suckling, T. Swetnam, T. Schulke, P. Stacey, P. Morgan, M. Hoffman, and J. Klingel. 2002. Ecological restoration of Southwestern ponderosa pine systems: A broad perspective. *Ecological Applications* **12**:1418-1433.
- Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science* **9**:593-602.
- Atlegrim, O., and K. Sjojberg. 2004. Selective felling as a potential tool for maintaining biodiversity in managed forests. *Biodiversity and Conservation* **13**:1123-1133.
- Attwill, P. 1994. The disturbance of forest ecosystems- The ecological basis for conservative management. *Forest Ecology and Management* **63**:247-300.
- Berg, B., and C. McClaugherty. 2008. *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*. Springer-Verlag, Berlin, Heidelberg.
- Brais, S., D. Pare, and C. Lierman. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. *Canadian Journal of Forest Research* **36**:2331-2340.
- Busby, P., G. Motzkin, and D. Foster. 2008. Multiple and interacting disturbances lead to *Fagus grandifolia* dominance in coastal New England. *Journal of the Torrey Botanical Society* **135**:346-359.
- Campbell, J., J. Hornbeck, M. Mitchell, M. Adams, M. Castro, C. Driscoll, J. Kahl, J. Kochenderfer, G. Likens, J. Lynch, P. Murdoch, S. Nelson, and J. Shanley. 2004. Input-output budgets of inorganic nitrogen for 24 forest watersheds in the northeastern United States: A review. *Water Air and Soil Pollution* **151**:373-396.
- Carey, A., and M. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* **5**:336-352.
- Carroll, C. 1993. Coarse woody debris in forest ecosystems: An overview of biodiversity issues and concepts. Page 146 *in* Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. DIANE Publishing, Athens, GA.
- Coleman, D., and W. Whitman. 2005. Linking species richness, biodiversity and ecosystem function in soil systems. *Pedobiologia* **49**:479-497.

- Currie, W., and K. Nadelhoffer. 2002. The imprint of land-use history: Patterns of carbon and nitrogen in downed woody debris at the Harvard Forest. *Ecosystems* **5**:446-460.
- D'Amato, A., D. Orwig, and D. Foster. 2006. New estimates of Massachusetts old-growth forests: useful data for regional conservation and forest reserve planning. *Northeastern Naturalist* **13**:495-506.
- D'Amato, A., D. Orwig, and D. Foster. 2008. The influence of successional processes and disturbance on the structure of *Tsuga canadensis* forests. *Ecological Applications* **18**:1182-1199.
- D'Amato, A., D. Orwig, and D. Foster. 2009. Understory vegetation in old-growth and second-growth *Tsuga canadensis* forests in western Massachusetts. *Forest Ecology and Management* **257**:1043-1052.
- del Rio, C. 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. *Canadian Journal of Forest Research* **36**:2943-2954.
- Driscoll, C., D. Whittall, J. Aber, E. Boyer, M. Castro, C. Cronan, C. Goodale, P. Groffman, C. Hopkinson, K. Lambert, G. Lawrence, and S. Ollinger. 2003. Nitrogen pollution in the northeastern United States: Sources, effects, and management options.
- Duffy, D., and A. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology* **6**:196-201.
- Fahey, T. J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecological Monographs* **53**:51-72.
- Foster, D. 1988. Disturbance History, Community Organization and Vegetation Dynamics of the Old-Growth Pisgah Forest, South-Western New Hampshire, U.S.A. *Journal of Ecology* **76**:105-134.
- Foster, D., D. Orwig, and J. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution* **11**:419-424.
- Foster, J. R., and G. E. Lang. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Canadian Journal of Forest Research* **12**:617-626.
- Franklin, J. F., T. Spies, R. Van Pelt, A. Carey, D. Thornburgh, D. Berg, D. Lindenmayer, M. E. Harmon, W. Keeton, D. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* **155**:399-423.
- Fraver, S., R. Wagner, and M. Day. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. *Canadian Journal of Forest Research* **32**:2094-2105.
- Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, S. Flemming, G. Forbes, J. Gerrow, G. Johnson, and S. Woodley. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environment Reviews* **4**:238-265.
- Ganjugunte, G. K., L. M. Condron, P. W. Clinton, M. R. Davis, and N. Mahieu. 2004. Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management* **187**:197-211.
- Gilliam, F., N. Turrell, and M. Adams. 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. *Ecological Applications* **5**:947-955.
- Gough, C., C. Vogel, C. Kazanski, L. Nagel, C. Flower, and P. Curtis. 2007. Coarse woody debris and the carbon balance of a north temperate forest. *Forest Ecology and Management* **244**:60-67.
- Guo, L. B., E. Bek, and R. M. Gifford. 2006. Woody debris in a 16-year old *Pinus radiata* plantation in Australia: Mass, carbon and nitrogen stocks, and turnover. *Forest Ecology and Management* **228**:145-151.
- Halpern, C. 1989. Early successional patterns of forest species- Interactions of life-history traits and disturbance. *Ecology* **70**:704-720.
- Halpern, C., and T. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* **5**:913-934.
- Hansen, A., W. McComb, R. Vega, M. Raphael, and M. Hunter. 1995. Bird habitat relationships in natural and managed forests in the west Cascades of Oregon. *Ecological Applications* **5**:555-569.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986.

- Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**:133-302.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for Measurements of Woody Detritus in Forest Ecosystems. Page 73 Publication No. 20. U.S. LTER Network, University of Washington, Seattle, WA
- Hart, S. 1999. Nitrogen transformations in fallen tree boles and mineral soil of an old-growth forest. *Ecology* **80**:1385-1394.
- Henry, J., and J. Swan. 1974. Reconstructing forest history from live and dead plant material- an approach to the study of forest succession in southwest New Hampshire. *Ecology* **55**:772-783.
- Hobbie, S. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution* **7**:336-339.
- Holub, S., J. Spears, and K. Lajtha. 2001. A reanalysis of nutrient dynamics in coniferous coarse woody debris. *Canadian Journal of Forest Research* **31**:1894-1902.
- Hooper, D., and P. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302-1305.
- Laiho, R., and C. E. Prescott. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Canadian Journal of Forest Research* **34**:763-777.
- Lang, G. E., and R. Forman. 1978. Detrital dynamics in a mature oak forest: Hutcheson Memorial Forest, New Jersey. *Ecology* **59**:580-595.
- Lang, G. E., and D. H. Knight. 1979. Decay rates for boles of tropical trees in Panama. *Biotropica* **11**:316-317.
- Lindenmayer, D., and R. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology* **20**:949-958.
- Magill, A., J. Aber, W. Currie, K. Nadelhoffer, M. Martin, W. McDowell, J. Melillo, and P. Steudler. 2004. Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management* **196**:7-28.
- Maguire, D., S. Canavan, C. Halpern, and K. Aubry. 2004. Fate of taxa after variable-retention harvesting in Douglas-fir forests of the northwestern United States. Pages 271-279 in C. E. Peterson and D. Maguire, editors. *Balancing Ecosystem Values: Innovative Experiments for Sustainable Forestry*.
- Marshall, V. 2000. Impacts of forest harvesting on biological processes in northern forest soils. *Forest Ecology and Management* **133**:43-60.
- McClaugherty, C., J. Pastor, J. Aber, and J. Melillo. 1985. Forest litter decomposition in relation to soil-nitrogen dynamics and litter quality. *Ecology* **66**:266-275.
- McClure, M. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). *Environmental Entomology* **19**:36-43.
- McGee, G., D. Leopold, and R. Nyland. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecological Applications* **9**:1316-1329.
- McLachlan, J., D. Foster, and F. Menalled. 2000. Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. *Ecology* **81**:717-733.
- Micks, P., M. Downs, A. Magill, K. Nadelhoffer, and J. Aber. 2004. Decomposing litter as a sink for N-15-enriched additions to an oak forest and a red pine plantation. *Forest Ecology and Management* **196**:71-87.
- Minteer, B., and J. Collins. 2005. Why we need an "ecological ethics". *Frontiers in Ecology and the Environment* **3**:332-337.
- Mladendoff, D., M. White, J. Pastor, and T. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* **3**:294-306.
- Moola, F., and L. Vasseur. 2004. Recovery of late-seral vascular plants in a chronosequence of post-clearcut forest stands in coastal Nova Scotia, Canada. *Plant Ecology* **172**:183-197.
- Nadelhoffer, K., B. Emmett, P. Gundersen, O. Kjonaas, C. Koopmans, P. Schleppi, A. Tietema, and R. Wright. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* **398**:145-148.

- Nordén, B., M. Ryberg, F. Götmark, and B. Olausson. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biological Conservation* **117**:1-10.
- Olson, J. S. 1963. Energy-storage and balance of producers and decomposers in ecological-systems. *Ecology* **44**:322-331.
- Orwig, D., C. Cogbill, D. Foster, and J. O'Keefe. 2001. Variations in old-growth structure and definitions: Forest dynamics on Wachusett Mountain, Massachusetts. *Ecological Applications* **11**:437-452.
- Orwig, D., and D. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England. *Journal of the Torrey Botanical Society* **125**:60-73.
- Petranka, J., M. Brannon, M. Hopey, and C. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecology and Management* **67**:135-147.
- Poore, M. 1955. The use of phytosociological methods in ecological investigations: I. the Braun-Blanquet system. *Journal of Ecology* **43**:226-244.
- R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Schimmel, J. P., and M. Firestone. 1989. Nitrogen incorporation and flow through a coniferous forest soil-profile. *Soil Science Society of America Journal* **53**:779-784.
- Schoonmaker, P. 1992. Long-term vegetation dynamics in southwestern New Hampshire. Harvard University, Cambridge, Massachusetts, USA.
- Siitonen, J., P. Martikainen, P. Punttila, and J. Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* **128**:211-225.
- Sollins, P., S. P. Cline, T. Verhoeven, D. Sachs, and G. Spycher. 1987. Patterns of log decay in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* **17**:1585-1595.
- Spears, J., S. Holub, M. E. Harmon, and K. Lajtha. 2003. The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, USA. *Canadian Journal of Forest Research* **33**:2193-2201.
- Sturtevant, B., J. Bissonette, J. Long, and D. Roberts. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecological Applications* **7**:702-712.
- Thomas, S., C. Halpern, D. Falk, D. Liguori, and K. Austin. 1999. Plant diversity in managed forests: Understory responses to thinning and fertilization. *Ecological Applications* **9**:864-879.
- Tyrell, L., and T. Crow. 1994. Dynamics of dead wood in old-growth hemlock hardwood forests of northern Wisconsin and northern Michigan. *Canadian Journal of Forest Research* **24**:1672-1683.
- U.S.D.A. 1941. *Climate and Man. Yearbook of Agriculture.* in U. S. D. o. Agriculture, editor., Washington, D.C.
- Uhl, C., and J. Kauffman. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* **71**:437-449.
- Vitousek, P., J. Aber, R. Howarth, G. Likens, P. Matson, D. Schindler, W. Schlesinger, and G. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* **7**:737-750.
- Ziegler, S. 2000. A comparison of structural characteristics between old-growth and postfire second-growth hemlock-hardwood forests in Adirondack Park, New York, U.S.A. *Global Ecology and Biogeography* **9**:373-389.