Assessing Ecosystem Restoration Alternatives in Eastern Deciduous Forests: The View from Belowground

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Abstract

Both structural and functional approaches to restoration of eastern deciduous forests are becoming more common as recognition of the altered state of these ecosystems grows. In our study, structural restoration involves mechanically modifying the woody plant assemblage to a species composition, density, and community structure specified by the restoration goals. Functional restoration involves reintroducing dormant-season, low-severity fire at intervals consistent with the historical condition. Our approach was to quantify the effects of such restoration treatments on soil organic carbon and soil microbial activity, as these are both conservative ecosystem attributes and not ones explicitly targeted by the restoration treatments, themselves. Fire, mechanical thinning, and their combination all initially resulted in reduced soil organic C content, C:N ratio, and overall microbial activity (measured as acid phosphatase activity) in a study site in the southern Appalachian Mountains of North Carolina, but only the effect on microbial activity persisted into the fourth post-treatment growing season. In contrast, in a similar forest in the central Appalachian Plateau of Ohio, mechanical thinning resulted in increased soil organic C, decreased C:N ratio, and decreased microbial activity, whereas fire and the combination of fire and thinning did not have such effects. In addition, the effects in Ohio had dissipated prior to the fourth post-treatment growing season. Mechanical treatments are attractive in that they require only single entries; however, we see no indication that mechanical–structural restoration actually produced desired belowground changes. A single fire-based/functional treatment also offered little restoration progress, but comparisons with long-term experimental fire studies suggest that repeated entries with prescribed fire at intervals of 3–8 years offer potential for sustainable restoration.

Key words: deciduous forests, fire, microbial activity, restoration alternatives, soil organic carbon.

Introduction

The deciduous forests of the central and southern Appalachians have been managed by humans for at least two millennia (Mann 2005). Pollen and charcoal deposits on the plateaus of the Appalachian Mountains indicate that fire has been common in the forests of the region for at least four millennia (Delcourt & Delcourt 1997). Although the size–frequency distribution of fire changed over that period as human populations and cultures changed, the average fire return interval was relatively stable until the rapid decline of Native American populations after European contact (Delcourt & Delcourt 1997).

Fire, harvesting, and small-holding agriculture remained important in this region through the early 20th century. However, the fire return interval remained relatively unchanged in the Appalachian Mountains and Plateaus through this time, despite rapid Euro-American agricultural intensification in the region. For example, Harmon (1982) chronicled a fire return interval of 10–12 years during 1850–1940 in the Great Smoky Mountains and Sutherland (1997) found a return interval of 7.5 years for extensive fires in mixed-oak forests in the Allegheny Plateau of Ohio over a similar period.

Widespread, effective, government agency–mandated fire suppression began as early as 1930 in Ohio (Sutherland 1997) and 1940 in the Blue Ridge Mountains of North Carolina (Harmon 1982). Fire return intervals increased significantly thereafter; for example, Sutherland (1997) reported a postsuppression interval of 57 years in southeastern Ohio. As a consequence of this policy, the unmanaged forests of the central and southern Appalachians have become denser, have increased detrital mass, and, in some areas, have changed in tree species composition (e.g., Iverson et al. 1997).

It is generally thought that the forests of the Appalachian Mountains and Plateaus were historically N limited

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(Aber et al. 1989), and the historic dominance of tree species dependent on ectomycorrhizae (e.g., oaks, hickories, pines) is also consistent with an ecosystem whose soils are low in available inorganic N and high in relatively recalcitrant organic matter (Vogt et al. 1991).

Since the rapid industrialization of the eastern United States, chronic atmospheric deposition of S and N has been a continuing stress on these ecosystems. Chronic deposition of N from fossil fuel combustion and agricultural practices has increased to the point where additions of inorganic N to the forest soil solution from atmospheric sources now approach the rates at which N is naturally recycled in these ecosystems through the processes of decomposition and mineralization (Morris & Boerner 1998). Indeed, some parts of the Appalachians are now considered to be N saturated, and such areas are now the sources of N to drainage waters rather than the strong sinks of N they were historically (e.g., Peterjohn et al. 1999).

It is in this context of fire suppression and N enrichment that efforts to restore Appalachian ecosystems to structural and functional conditions more indicative of unstressed, well-functioning ecosystems began. The Fire and Fire Surrogate (FFS) Network Study (www.fs.fed.us/ffs) was initiated to test alternative ecosystem restoration and wildfire hazard reduction treatments in forests across the continent. The primary objective of the FFS Network Study is to determine the relative effects of low-severity fire at historical intervals (as a form of functional restoration), mechanical modification of the woody vegetation (i.e., thinning from below) (a form of structural restoration), and the combination of thinning and burning (a combined approach) in comparison with passive management. In this study, we present the results of an assessment of multiple restoration strategies on soil organic carbon and microbial activity, two attributes that will provide insight into the ecosystem consequences of restoration practices. In particular, we sought to determine whether any or all the restoration treatments would result in these ecosystems becoming more like the N-limited ecosystems that preceded fire suppression and heavy atmospheric N deposition: ones characterized by low total ecosystem N and large pools of recalcitrant organic matter.

Methods

Study Sites

This study took place in two of the 13 study sites that comprise the FFS Network study (www.fs.fed.us/ffs): the Ohio Hills (OH) site (representing the Central Appalachian Plateaus), and the Green River (NC) site (representing the southern Appalachian Mountains). Each site consisted of three replicate blocks, with each of the alternative ecosystem restoration treatments applied to a randomly chosen treatment unit within each block.

The Ohio Hills FFS site was located on the unglaciated Allegheny Plateau of southern Ohio (lat 39°20′N, long 82°38′W). The climate of the region was cool, temperate with mean annual precipitation of 1,024 mm and mean annual temperature of 11.3°C (Sutherland et al. 2003). The forests of the region developed between 1850 and 1900, after the cessation of cutting for the charcoal and iron industries (Sutherland et al. 2003). The current canopy composition differed little from that recorded in the original land surveys of the early 1800s. The most abundant species in the current canopy were White oak (*Quercus alba*), Chestnut oak (*Q. prinus*), hickories (*Carya* spp.), and Black oak (*Q. velutina*); however, the midstory and understory were dominated by species that had only in the last few decades become common in this community (e.g., Sugar maple [*Acer saccharum*], Red maple [*A. rubrum*], and Yellow-poplar or Tuliptree [*Liriodendron tulipifera*]) (Yaussy et al. 2003). Analysis of fire scars in stems of trees that were cut as part of the establishment of the Ohio FFS experiment indicated that fires were frequent from 1875 to 1930 (return intervals of 8–15 years). In contrast, few fires occurred after the onset of fire suppression activities in the early 1930s (T. Hutchinson, 2005, USDA Forest Service, personal communication). The soils of the Ohio Hills FFS site were formed in place from sandstone and shale residuum and colluvium and are dominated by Steinsburg and Gilpin series silt loams (typic hapludalfs) (Lemaster & Gilmore 1993).

The Green River FFS site was located in the Green River Game Land in the Blue Ridge Physiographic Province, Polk County, North Carolina (lat 35°29′N, long 82°32′W). The climate of the region was warm continental, with mean annual precipitation of 1,638 mm and mean annual temperature of 17.6°C (Keenan 1998). The forests of the study area were 80–120 years old, and no indication of past agriculture or recent fire was present; however, no detailed land history was available for these sites, as they had been acquired from private sources only recently. The most abundant species in the canopy were Northern red oak (*Q. rubra*), *Q. prinus*, *Q. alba*, Black oak (*Q. velutina*), Pignut hickory (*Carya glabra*), mockernut hickory (*C. tomentosa*), and Shortleaf pine (*Pinus echinata*). A relatively dense evergreen shrub assemblage was present in the understory of a majority of the study site, with Mountain laurel (*Kalmia latifolia*) and Rhododendron (*Rhododendron maximum*) the most common species. The soils of the Green River site were formed in colluvium and residuum from metamorphic parent materials, especially biotite gneiss and sillimanite-mica schist. Most of the study area was occupied by soils of the Evard and Cliffield series (both typic hapludults) (Keenan 1998).

Prior to treatment, the soils at Green River had somewhat greater bulk density and pH than did the soils in the Ohio Hills, whereas available Ca^{2+} and molar Ca:Al ratio differed little between the two study sites (Table 1). The Ohio Hills site had more, but lower quality, soil organic C than did the Green River site (Table 1).

Table 1. Selected soil properties of the Ohio Hills (OH) and Green River (NC) study sites of the FFS Network Study.

Parameter	*Ohio Hills (OH)*	*Green River (NC)*
Texture	Silt loam, sandy loam	Sandy loam, loam
Parent material	Colluvium/residuum from sandstone, shale	Colluvium/residuum from gneiss, mica schist
Soil classification	Alfisols, inceptisols	Ultisols, inceptisols
Bulk density (g/cm^3)	0.86–0.92	1.10–1.25
pH	3.67	4.58
Extractable Ca^{2+} (mg/kg)	130	123
Ca:Al molar ratio	0.47	0.08
Soil organic C (g/kg)	33.8	12.6
Soil C:N ratio	18.9	23.6

All data represent pre-treatment conditions as reported to the national database of the FFS Network (www.fs.fed.us/ffs).

Experimental Design

Each of the three replicate blocks in each site was composed of four treatment units. In the Ohio Hills site, individual treatment units were 19–26 ha, whereas in the Green River site, they were approximately 10 ha. All treatment units were surrounded by buffer zones of 4–10 ha, and both the treatment unit and its corresponding buffer received the experimental treatment. These treatment units were designed to include the prevailing combinations of elevation, aspect, and soil.

A 50 × 50–m grid was established in each treatment unit, and 10 sample plots of 0.10 ha were established randomly on the grid within each treatment unit. The position of each sample plot was established by Geographic Information System (GIS), and the landscape context of each was determined using the GIS-based integrated moisture index developed by Iverson et al. (1997) in the Ohio Hills site and the Landscape Ecosystem Classification System described by Hutto et al. (1999) and Carter et al. (2000) for the Green River site.

Treatments were randomly allocated among treatment units within a site, and all treatments units were sampled through the pre-treatment year: 2000 in the Ohio Hills and 2001 in the Green River. Treatments consisted of prescribed fire, a mechanical thinning treatment, the combination of prescribed fire and thinning, and an untreated control.

In the Ohio Hills, the mechanical thinning treatment involved thinning from below to a basal area comparable to that present prior to Euro-American settlement (approximately 14 m^2/ha). In the Green River, the mechanical treatment involved removing all tree stems >1.8 m height and <10.2 cm diameter at breast height as well as all *K. latifolia* and *R. maximum* stems. In both sites, the mechanical treatments were designed to return forest structure to a condition consistent with what each site would have been like prior to fire suppression and other intensive management activities. Mechanical thinning was accomplished during September 2000–April 2001 in Ohio and December 2001–February 2002 at Green River.

The prescribed fires were applied during March–April 2001 in the Ohio Hills and March 2003 at the Green River. These dormant-season fires were designed to be similar to natural fires in the region. These fires consumed unconsolidated leaf litter and fine woody fuels while leaving the majority of the coarse woody fuels only charred. Tree seedlings, saplings, and shrubs were typically top-killed by these fires, and this was particularly important at Green River where reducing shrub density was an explicit part of the restoration goal. Details on fire behavior are given by Iverson and Hutchinson (2002) and Iverson et al. (2004) for the Ohio Hills and Tomcho (2004) for the Green River site.

Field Methods

For enzyme analysis, soil samples were taken approximately 45–55 m apart, 2–5 m from the opposite corners of each permanently marked 0.10-ha sample plot during mid-summer of the pre-treatment year, the first post-treatment year, and the third or fourth post-treatment year (fourth for all Ohio Hills treatment and the Green River control and mechanical thinning treatment; third for the Green River burn and thin + burn). Geostatistical analysis of the spatial autocorrelation in soil properties in the Ohio Hills site indicated that paired samples taken at such distances constitute spatially uncorrelated, statistically independent samples (Boerner & Brinkman 2004, 2005).

In each of the two sites, 20 samples were taken for enzyme analysis in each treatment unit in each sampling year, yielding for each of the study sites $n = 60$ per restoration treatment and $n = 240$ per study site each year. Additional samples taken at the remaining corners and at the midpoint of the long axis of each sample plot were also taken to increase the sample size for analysis of soil organic C and total N to $n = 360$ per year in the Ohio Hills and $n = 720$ per year at the Green River. The top 10–15 cm of the Oa + A horizon were sampled. To maintain microbial and enzyme activity, all samples were kept refrigerated in field-moist condition until they were analyzed (Speir & Ross 1975).

Laboratory Methods

Each sample was passed through a 2-mm sieve to remove stones, root fragments, and particulate organic materials (i.e., remnants of the Oi, Oe) and then analyzed for soil

organic C; total N; and the activity of phosphomonoesterase (acid phosphatase), chitinase, and phenol oxidase. As all roots were removed prior to analysis, enzyme activities represent only microbial contributions.

Acid phosphatase was chosen as an indicator of overall microbial activity as acid phosphatase activity is strongly correlated with microbial biomass (Clarholm 1993; Kandeler & Eder 1993), fungal hyphal length (Häussling & Marschner 1989), and N mineralization (Decker et al. 1999). Chitinase is a bacterial enzyme that catalyzes the breakdown of chitin, a by-product of the death of both fungi and arthropods, into carbohydrates and inorganic N. As chitin is intermediate in its resistance to microbial metabolism, its synthesis is only induced when other, more labile C and N sources are absent (Handlikova & Jandera 1993). Chitinase is produced only by bacteria; thus, changes in chitinase activity relative to that of other enzymes give an indication of changes both in the relative contribution of chitinolytic bacteria to microbial activity and in organic matter along the gradient from labile to recalcitrant. Phenol oxidase is produced primarily by white rot fungi and is specific for highly recalcitrant organic matter, such as lignin (Carlisle & Watkinson 1994). Increases in phenol oxidase activity relative to other enzymes give another indication of changes in the relative contribution of bacteria and fungi to microbial activity as well as an additional indication of the quality of the organic matter present. Thus, as a group these three enzymes supplied insight into changes in both the microbial community and the organic matter complex.

The enzyme activities were determined on field-moist soil using the methods developed by Tabatabai (1982), as modified by Sinsabaugh (Sinsabaugh et al. 1993; Sinsabaugh & Findlay 1995). Subsamples of approximately 10 g of fresh soil were suspended in 120 mL of 50 mM NaOAc buffer (pH 5.0) and homogenized by rapid mechanical stirring for 90 seconds. To minimize sand sedimentation, stirring was continued while aliquots were withdrawn for analysis.

Acid phosphatase (EC 3.1.3.1) and chitinase (EC 3.2.1.14) activities in soil suspensions were determined using *p*-nitrophenol (*p*NP)-linked substrates: *p*NP-phosphate for acid phosphatase and *p*NP-glucosaminide for chitinase. Samples were incubated for 1 hour (acid phosphatase) or 2 hours (chitinase) at 20–22°C with constant mixing. Following incubation, samples were centrifuged at 3,000 × *g* for 3 minutes to precipitate particulates. An aliquot of 2.0 mL of the supernatant was transferred to a clean, sterile tube, and 0.1 mL of 1.0 M NaOH was added to halt enzymatic activity and to facilitate color development. Prior to spectrophotometric analysis at 410 nm, each sample of the supernatant was diluted with 8.0 mL of distilled, deionized water.

Phenol oxidase (EC 1.14.18.1, 1.10.3.2) activity in soil suspensions was measured by oxidation of L-3,4-dihydroxyphenylalanine (L-DOPA) during 1-hour incubations at 20–22°C. Following incubation, samples were centrifuged as above and analyzed at 460 nm without dilution. Parallel oxidations using standard horseradish peroxidase (Sigma Chemical, St. Louis, MO, USA) were used to calculate the L-DOPA extinction coefficient.

Soil organic C and total soil N were analyzed by micro-Dumas combustion on a Perkin-Elmer 2400 Series II CHNS/O Analyzer (Perkin-Elmer Corporation, Boston, MA, USA). Prior to determination of C and N, soil samples were dried at 70–76°C, then ground to pass an 80 mesh screen.

Data Analysis

This experiment was designed as a randomized complete block, with three blocks per site and four treatments allocated to each block. Responses were either normally distributed (e.g., enzyme activity) or could be normalized by log transformation (e.g., soil C). Differences among treatment units prior to application of the treatments were analyzed by mixed model analysis of variance for a completely randomized design (SAS 1995). Differences among treatments during the first and fourth post-treatment years in each response parameter were analyzed for each site by mixed model analysis of covariance for a completely randomized block design, using the pre-treatment status of that response parameter as a covariate (SAS 1995). Similarly, differences among treatment units during the pre-treatment year were analyzed by mixed model analysis of variance for the completely randomized block design. Mean separations were done by least squares estimation, using the Bonferroni adjustment for multiple comparisons at $p < 0.05$ (SAS 1995). We used nonmetric multidimensional scaling (NMS), a form of ordination, to help visualize the holistic responses of the soils of these treatment units to the four alternative management strategies (McCune & Grace 2002).

Results

Soil Organic C

During the first post-treatment growing season, soil organic C content was affected significantly by restoration treatment in both study sites (Table 2). At the Green River site, all three manipulative treatments resulted in reduced soil organic C content, with an average reduction of 15.6% relative to the control (Fig. 1). At the Ohio Hills site, the only statistically significant difference was between the burn units and the thin + burn units, with soil organic C content was 25.7% greater in the latter than in the former (Fig. 1).

The significant effect of the restoration treatments on soil organic C persisted through the fourth post-treatment growing season at the Ohio Hills site but not at the Green River site (Table 2). Fourth year soil organic C content in the thin treatment in the Ohio Hills site was significantly greater, by an average of 28.5%, than that in the other three treatments (Fig. 1).

Table 2. Analysis of covariance of the effect of four alternative ecosystem restoration treatments on selected soil organic C and microbial activity parameters in the Ohio Hills (OH) and Green River (NC) sites of the FFS Network Study.

		Study Site	
Parameter	*Post-Treatment Year*	*Green River (NC)*	*Ohio Hills (OH)*
Soil Organic C	First	$F = 10.73, p < 0.001$	$F = 2.75, p < 0.044$
	Fourth	$F = 1.95, p < 0.123$	$F = 3.90, p < 0.010$
Soil C:N	First	$F = 8.54, p < 0.001$	$F = 2.97, p < 0.038$
	Fourth	$F = 2.93, p < 0.035$	$F = 1.22, p < 0.307$
Acid phosphatase activity	First	$F = 2.87, p < 0.038$	$F = 4.41, p < 0.005$
	Fourth	$F = 3.85, p < 0.011$	$F = 3.45, p < 0.022$
Chitinase activity	First	$F = 1.58, p < 0.196$	$F = 0.67, p < 0.571$
	Fourth	$F = 1.18, p < 0.317$	$F = 0.85, p < 0.469$
Phenol oxidase activity	First	$F = 3.27, p < 0.022$	$F = 1.80, p < 0.148$
	Fourth	$F = 1.08, p < 0.360$	$F = 0.55, p < 0.647$

The F statistic and associated probability level for the treatment effect are given.

During the first post-treatment year, soil C:N ratio was affected significantly by restoration treatment in both study sites (Table 2). At the Green River site, C:N ratio decreased (and therefore soil organic matter quality increased) in the order: thin > thin + burn = control > burn (Fig. 2). At the Ohio Hills site, the magnitude of the difference among treatments was less than it was at the Green River; however, the thin treatment still had significantly greater soil C:N ratio than did the other three treatments at the Ohio Hills (Fig. 2). The significant effect of the restoration treatments on soil C:N ratio persisted into the fourth post-treatment growing season at Green River but not in the Ohio Hills (Table 2). At Green River, soils from the mechanically thinned plots had significantly greater C:N ratio during the fourth year than did soils from the other treatments (Fig. 2).

Microbial Activity

Soil acid phosphatase activity was greater overall in the Ohio Hills site than in the Green River site. Activities in the control units in the Ohio Hills site were 50 and 63% greater than those at the Green River during year 1 and year 4, respectively (Fig. 3). Acid phosphatase activity was affected by restoration treatments in both study sites during both sampling years (Table 2). At the Green River, fire either with or without mechanical thinning resulted in significantly greater acid phosphatase activity than the control during year 1, and either fire or thinning alone resulted in greater acid phosphatase activity than was present in the control in year 4 (Fig. 3). At the Ohio Hills site, the situation was somewhat reversed. The combination of burning and thinning reduced acid phosphatase activity relative to the control during year 1, and burning with or without thinning resulted in reduced acid phosphatase activity during year 4.

There were no significant differences among restoration treatments in soil chitinase activity in either site during either sampling year (Table 2; Fig. 4). In contrast, phenol oxidase activity was enhanced by burning, either alone or in combination with thinning, in the Green River site during year 1 (Table 2; Fig. 5). However, this enhancement did not persist, and no significant effects of restoration treatments on phenol oxidase activity were observed in the Ohio Hills site (Table 2; Fig. 5).

Ordination

NMS ordination arrayed the site–treatment–year combinations along two ordination axes that together accounted for 98.5% of the variance (Fig. 6). The greatest degree of separation was along the first NMS axis, which was positively correlated with microbial activity and negatively correlated with organic matter quality (C:N ratio) (Fig. 6). There was less separation along NMS axis 1 among the four treatments for either site in any of the three sample years than that among the three sample years, and the Ohio Hills points were generally arrayed to the right of the Green River points. The latter indicated greater microbial activity and greater organic matter quality (as indicated by C:N ratio) in the Ohio Hills than at Green River, regardless of restoration treatment applied. NMS axis 2 separated the Ohio Hills points but not the Green River points by year (Fig. 6). Axis 2 was positively correlated with acid phosphatase activity and negatively correlated with soil organic C content.

The primary goal of this study was to determine the degree to which these restoration treatments would restore these ecosystems to a suite of conditions that included greater content of relatively recalcitrant organic matter coupled with lowered microbial activity. The inset in Figure 6 describes the vectors in ordination space that would correspond to changes in that direction. There was no indication that any of the three treatments in either site resulted in changes in soil properties indicative of significant restoration progress.

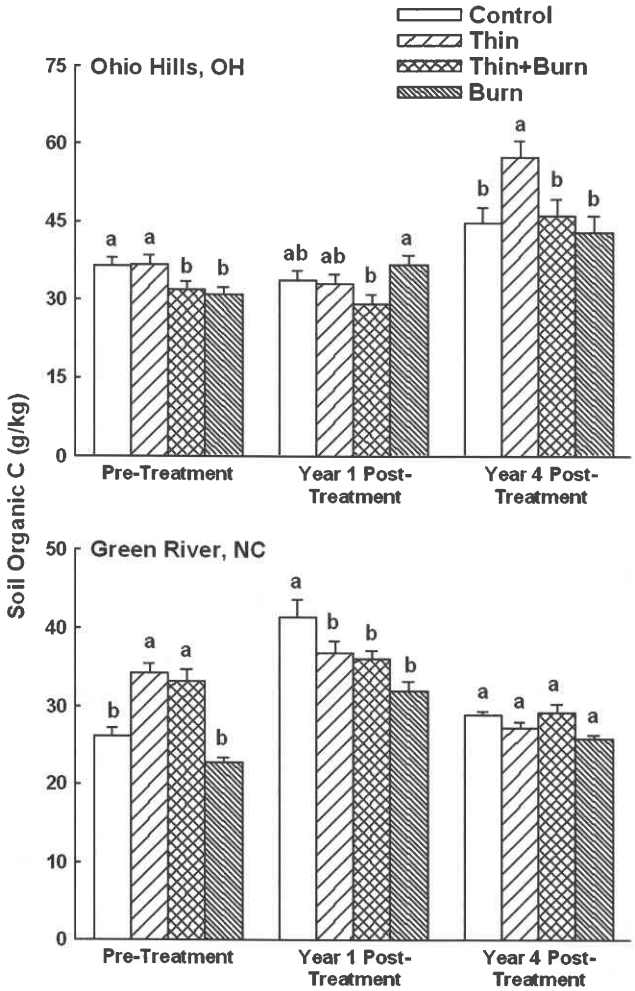

Figure 1. Changes in soil organic C content (g C/kg) in relation to forest restoration alternatives in two forests of eastern North America. Histogram bars represent means of $n = 60$, with standard errors of the means indicated. For site–year combinations in which there were significant treatment effects, histogram bars indicated by the same lowercase letter were not significantly different at $p < 0.05$ following analysis of variance for pre-treatment conditions and analysis of covariance with pre-treatment conditions as the covariate for post-treatment conditions.

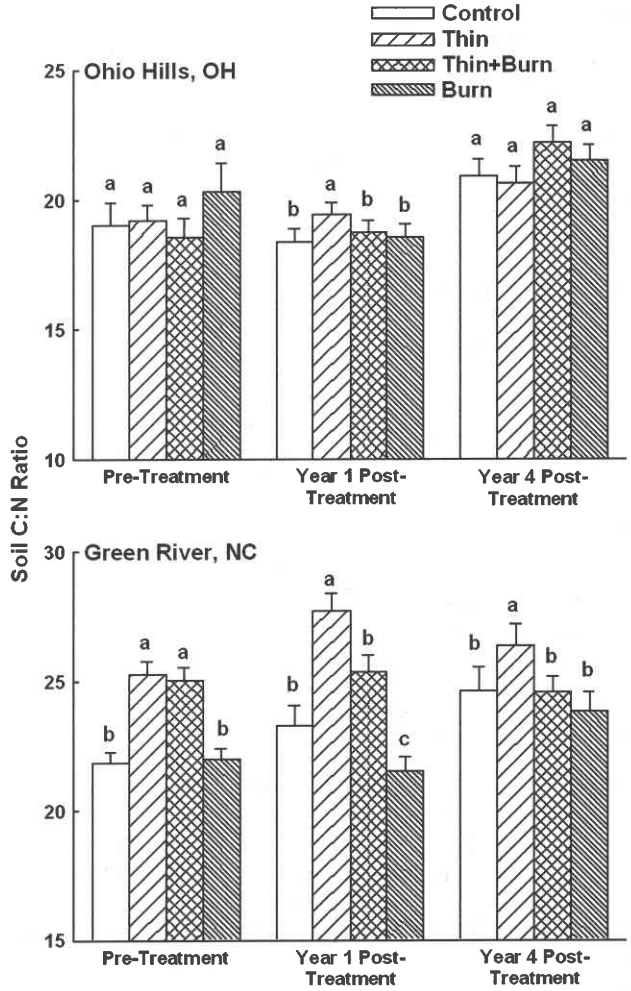

Figure 2. Changes in soil organic matter C:N ratio in relation to forest restoration alternatives in two forests of eastern North America. Format follows Figure 1.

Discussion

The restoration treatments used in this study were designed primarily to shift woody plant community structure, species composition, and spatial pattern, and detrital accumulation in a direction toward what was present at the time of Euro-American settlement. The underlying basis for this restoration goal was that the pre-settlement forests would likely have supported greater species diversity, a larger and more diverse game assemblage, and would have presented a significantly lower hazard of wildfire during adverse fire weather.

Our understanding of historical plant–soil–climate interactions is incomplete for eastern deciduous forests because the history of Euro-American manipulation predates scientific approaches to ecosystem and soil science. The belowground portions of our restoration prescriptions must, therefore, be derived from historical references (reviews by Whitney 1994; Boerner 2006), comparisons among forests with differing properties or degree of alteration (e.g., Vogt et al. 1991), and information from old-growth forest remnants (e.g., Daniels et al. 1987*a*,*b*). Such an approach leads us to postulate that the restoration goal for eastern forests would be soil subsystems that are lower in available nutrients (especially inorganic N), higher in soil organic matter, especially more recalcitrant organic matter, and lower in microbial (especially bacterial) activity than are the current forest soils.

The immediate response of the organic matter complex to the restoration treatments was a reduction in soil organic matter quantity by all three treatments in the Green River site and by the combination of thinning and burning in the Ohio Hills site. This was accompanied by

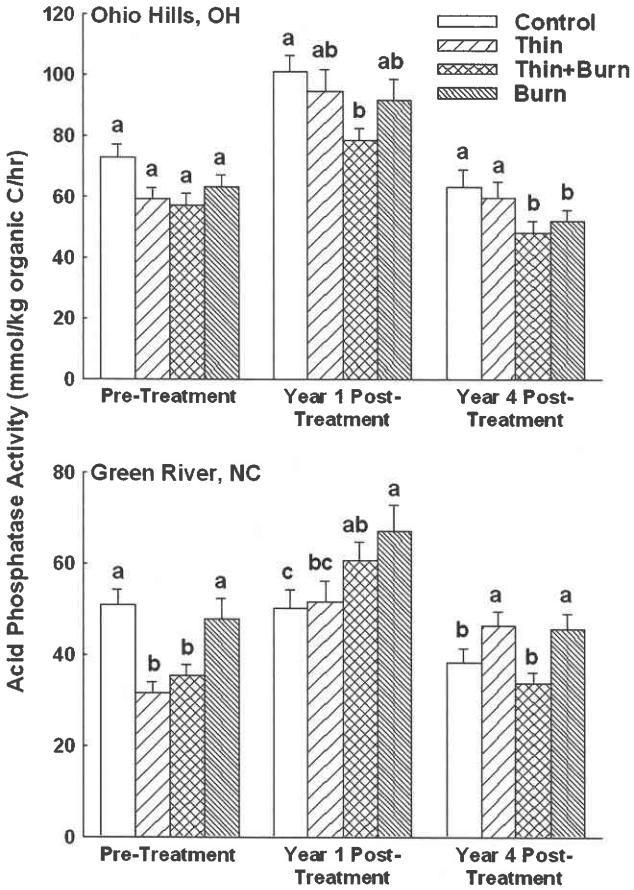

Figure 3. Changes in acid phosphatase activity (mmol kg soil organic C^{-1} hr^{-1}) in relation to forest restoration alternatives in two forests of eastern North America. Format follows Figure 1.

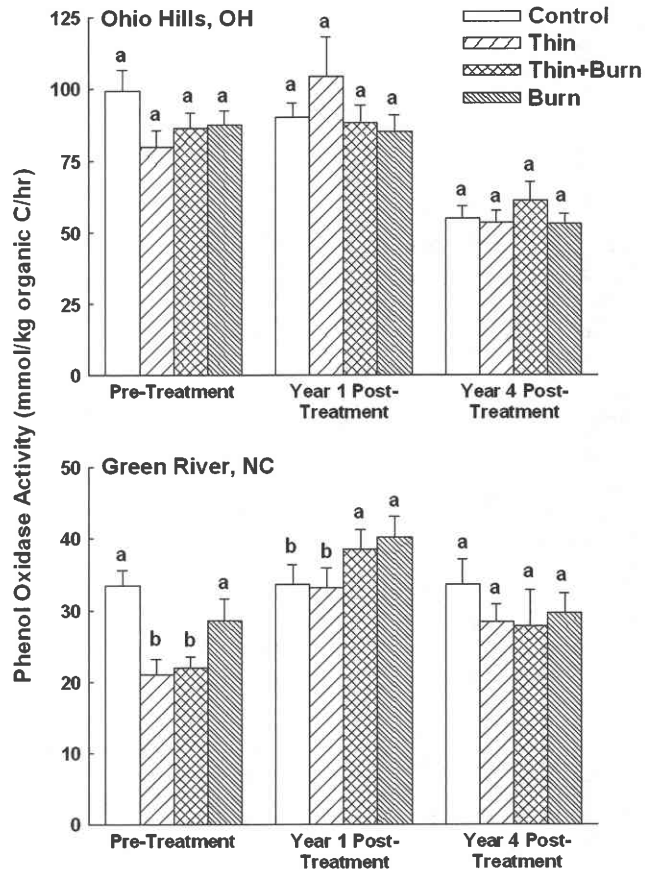

Figure 4. Changes in chitinase activity (mmol kg soil organic C^{-1} hr^{-1}) in relation to forest restoration alternatives in two forests of eastern North America. Format follows Figure 1.

a reduction in soil organic matter quality (as indicated by an increase in soil C:N ratio) in response to mechanical thinning in both sites and an improvement in soil organic matter quality as a result of fire alone at Green River. By the third or fourth growing season after treatment, however, these effects had begun to dissipate and were limited to an elevation in soil organic matter content in the Green River and a reduction in soil organic matter quality in the Ohio Hills site, both of which were induced by the mechanical thinning treatment.

Despite a rich literature from coniferous ecosystems that demonstrate significant losses of soil organic matter during and after fire, few studies have demonstrated major changes in soil organic matter content following fire in eastern oak ecosystems. Knighton (1977) and Knoepp et al. (2004) observed no significant changes in soil organic C as the result of one to three fires in Wisconsin oak forests and oak–pine stands in North Carolina, respectively. Only slight changes in soil organic carbon were observed in other Ohio oak–hickory sites subjected to one to four prescribed fires (Boerner et al. 2000; Boerner & Brinkman 2004).

The responses of the microbial assemblage to our experiment restoration treatments were complex. In the first growing season after treatment, overall microbial activity (measured as acid phosphatase activity) and the activity of wood-rooting fungi (measured as phenol oxidase activity) were stimulated by fire at the Green River site, with or without mechanical treatment. In contrast, in the Ohio Hills site, acid phosphatase activity was not significantly affected by fire alone and was inhibited by the combination of thinning and burning. In addition, phenol oxidase activity in the Ohio Hills soils did not respond significantly to any of the restoration treatments. Thus, the immediate, short-term effect of treatments that included fire was a stimulation of microbial (especially fungal) activity in the Green River but not in the Ohio Hills.

By the fourth year after treatment, there was little indication that the microbial assemblage was still being affected by treatments. There were no significant differences between the untreated controls and the three restoration treatments in the activity of any of the three enzymes during the fourth post-treatment year

Considerably less is known about the responses of the soil microbial assemblage to fire, thinning, and other modes of canopy disturbance. Studies of bacterial

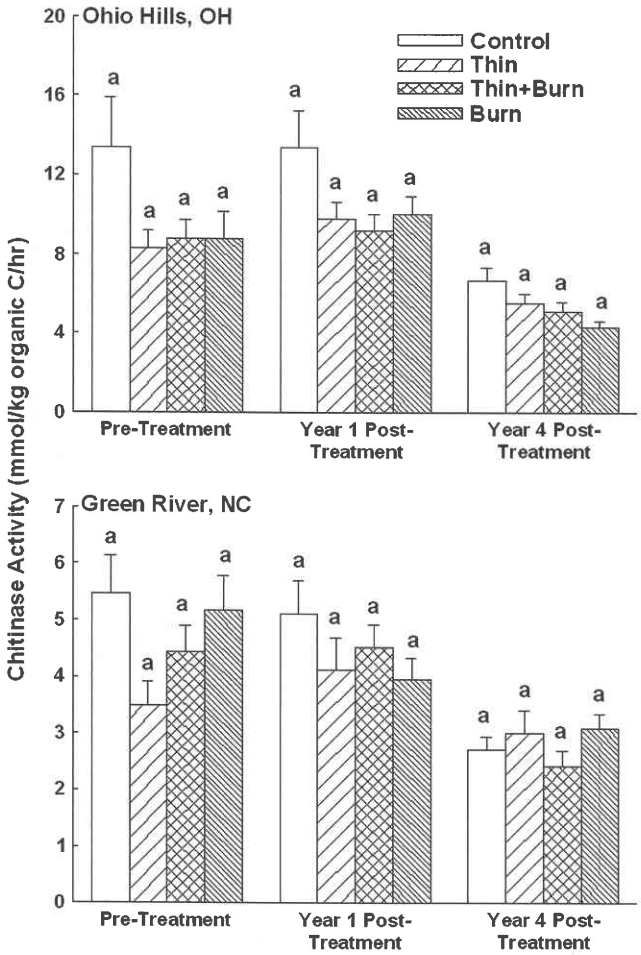

Figure 5. Changes in phenol oxidase activity (mmol kg soil organic C^{-1} hr^{-1}) in relation to forest restoration alternatives in two forests of eastern North America. Format follows Figure 1.

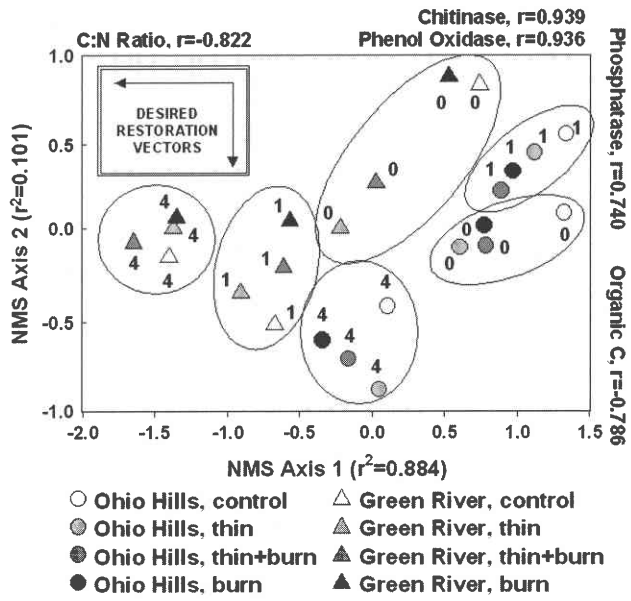

Figure 6. NMS ordination of the effects of restoration alternatives on soil properties in two forested areas of eastern North America. Numbers represent treatment years: 0 = pre-treatment, 1 = initial post-treatment year, 4 = fourth post-treatment year. Factors that were correlated with the ordination axes at $p < 0.01$ are indicated. Inset shows directions of change in ordination space that would be consistent with the stated restoration goals.

abundance after fire have demonstrated positive effects in a Kentucky oak–pine ecosystem (Blankenship & Arthur 1999), mixed effects in a South Carolina pine plantation (Jorgensen & Hodges 1971), and no effect in a pine forest in Spain (Fonturbel et al. 1995). Fungal abundance in the mineral soil is typically changed little by low-severity fire (Jorgensen & Hodges 1971; Fonturbel et al. 1995; Blankenship & Arthur 1999).

Studies of changes in microbial function due to fire and thinning are more common than direct studies of microbial abundance. Fires in Ohio mixed-oak forests (Boerner et al. 2000, Boerner & Brinkman 2003) and pine forests in Spain (Saa et al. 1993) resulted in reduced acid phosphatase activity, and increased phenol oxidase activity was also reported in those Ohio studies (Boerner et al. 2000, Boerner & Brinkman 2003). In the only long-term study of the effects of dormant-season fire on enzyme activity and microbial biomass in a hardwood forest, Eivasi and Bayan (1996) reported that 40 years of either annual or periodic fire reduced acid phosphatase activity, activity of other microbial enzymes, and microbial biomass. They attributed these effects to a long-term reduction in organic matter quality but not quantity (Eivasi & Bayan 1996). Parallel studies on the effects of mechanical thinning on soil microbial assemblages are lacking.

Our results from the Green River site included increases in acid phosphatase and phenol oxidase activities in response to all restoration treatments, and these results are consistent with the earlier Ohio studies (Boerner et al. 2000, Boerner & Brinkman 2003). The greater microbial response in the Green River site may have been the result, to some degree, of the presence of the dense *Kalmia latifolia* and *Rhododendron maximum* shrub layer in this site. In forests with dense ericaceous understories, it is common to observe lower decomposition and soil organic matter consumption rates (DeLuca et al. 2002). The mechanism of this inhibition may be the accumulation of recalcitrant complexes composed of N-containing soil organic matter and tannins (and other polyphenolics) derived from ericaceous litter. Some microbes, especially certain fungi, are capable of exploiting these tannin–organic N complexes as a source of both C and N (Bending & Read 1997). Thus, cutting the ericaceous shrubs at the Green River would result in a sudden input of litter with high concentrations of polyphenolics. As a result, one would expect to see greater phenol oxidase activity in the thin-only treatment but not in the thin and burn or burn only where those compounds would have been combusted, or in the Ohio Hills site where little ericaceous understory exists.

Ordination methods were used to visualize the holistic response of the organic matter and microbial subsystem to the restoration treatments. We found that the patterns of variation were dominated by temporal shifts and by differences between the two study sites. The ordination analysis did not suggest that the restoration treatments were responsible for a measurable proportion of change in soil properties over space and time.

Conclusions

Both structural and functional approaches to restoration of eastern deciduous forests are becoming more common as recognition of the altered state of these ecosystems grows. Structural restoration involves mechanically modifying the woody plant assemblage to shift it to a species composition, density, and community structure more consistent with restoration goals. Functional restoration involves reintroducing dormant-season, low-severity fire at intervals consistent with the historical condition. Our approach was to quantify the effects of alternative restoration treatments on soil organic matter pools and soil microbial activity, as these are both conservative ecosystem attributes and not ones explicitly affected by the restoration treatments. We then compared the trajectory of change to that we believe would provide quantitative evidence of progress toward the stated restoration goals. The effects of the three treatment alternatives on soil organic matter and microbial activity were modest, and none produced unequivocal evidence of significant restoration progress. Mechanical treatments are attractive in that they require only a single entry (or repeated entries only at long time intervals) and may, in some cases, produce wood products that can help offset restoration costs. However, we observe no indication that mechanical–structural restoration actually produced changes in the desired direction, at least from the belowground point of view. A single fire-based/functional treatment also offered little prospect of restoration progress. Comparisons with the sparse long-term experimental fire database suggest that repeated entries at intervals of 3–8 years might offer a more significant chance for sustainable restoration. However, repeated entries with fire have economic, political, and social implications that may make this strategy less suitable for real-world use. Our results indicate that restoration of eastern hardwood forests is likely to be a complex, lengthy, and costly process.

Implications for Practice

- Reintroduction of dormant-season, low-severity fire and mechanical restoration of woody plant species composition and community structure (and their combination) are alternatives for restoring aboveground components of eastern oak-dominated forests that have been impacted by fire suppression and atmospheric N deposition.
- In mixed-oak forest sites in North Carolina and Ohio, the impact of fire, mechanical thinning, and their combination was assessed over 4 years using belowground ecosystem properties.
- Effects of restoration treatments on soil organic matter and microbial activity were modest and short lived, with mechanical thinning of the canopy generally having the greatest (though still modest) effect among the three alternatives tested.
- None of the three treatments shifted the belowground ecosystem components in the desired restoration direction in either site to any great extent. Thus, from the belowground perspective, single entries with any of these treatments are ineffective as restoration tools. However, none of the treatments had adverse effects on either proximate soil fertility or prospects for longer-term restoration; therefore, belowground consequences of a single application of these three treatments are not sufficient to rule them out as viable restoration alternatives.

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