SOIL, FIRE, WATER, AND WIND: HOW THE ELEMENTS CONSPIRE IN THE FOREST CONTEXT

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Abstract.—Reviews our current understanding of the impact of fires typical of eastern oak forests on soil properties, soil organisms, and water quality. Most oak ecosystem fires are dormant-season fires whose intensity falls at the low end of the range of wildland fires. Direct heating of the mineral soil generally is minor except where accumulations of woody debris smolder for lengthy periods. Considerable proportions of nitrogen, phosphorus, and cations may be lost during fire through a combination of volatilization and ash convection. Post-fire precipitation events govern the return of nutrients in ash to the mineral soil, and the interaction of the soil exchange capacity, geomorphology, and weather control the proportion of nutrients from ash that will be retained for later plant use. Exposure of mineral soil by fire may lead to increased sheet erosion, but soil hydrophobicity does not seem to be important in oak ecosystems. Nitrogen availability and organic carbon content of soils may increase after fire, though both appear to be lesser in magnitude and duration than in other ecosystems. Impacts on fungi, bacteria, and microarthropods in the mineral soil are small, whereas those in the forest floor are proportional to the degree of consumption and the extent of heating due to smoldering woody fuels. Microbial activity and microarthropod populations recover quickly except after repeated annual burning. Little is known of effects of fire on other groups of soil organisms (e.g., nematodes and earthworms). The geomorphology of much of the eastern oak region is complex and heterogeneous. In such terrain, the difficulties inherent in scaling up plot-based studies to land areas of management scale are considered in the context of demonstrated landscape-scale variations in belowground effects of fire. GIS-derived landscape-scale metrics can be used to help generate management-scale recommendations from smaller scale research studies.

INTRODUCTION

Analysis of pollen and charcoal deposits taken from water bodies along the plateaus of the Appalachian Mountains demonstrates that fire has been a frequent and consistent part of the forests, savannas, and grasslands of Eastern North America for at least the last 4,000 years (Delcourt and Delcourt 1997). Further, evidence from macrofossils and pollen indicates that forests dominated by fire-dependent trees such as oak (*Quercus*) and pine *(Pinus)* have covered much of Eastern North America for at least 10,000 years (Delcourt and Delcourt 1987). Thus, the history of fire in eastern forests precedes the development of significant human populations in the region.

During and after European settlement, many observers noted the use of fire by Native Americans. Whitney (1994) summarized more than 20 historical references to the use of fire by Native Americans in oak forests and savannas, from Massachusetts to Missouri, and from the early 1600's to the early 1800's. Some of these early observers even commented on the positive (Lorain 1825) or negative (Coxe 1794; Lorain 1825) effects of fire on forest soil productivity.

The key role that fire plays in the ecology of oak-dominated forests was recognized by ecologists as early as the 1920's and 1930's (e.g., Daubenmire 1936; Cottam 1949). Ironically, this is the same time period in which organized fire suppression policies came into force and became effective, at least in Ohio (Sutherland and others 2003).

Quantitative studies of the effects of fire on the soils of oak forests, and on the waters draining such forests, did not become common until after World War II. Thus, current and recent studies of the effects of fire on forest soil and water have taken place not in the context of the long, continuous history of fire that preceded the 20th century but in the artificial context of forests already affected by many decades of fire suppression.

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FIRES IN OAK FORESTS

The term "forest fire" conjures images of fires in western pine forests, with flames rising 30 meters or more, trees exploding, and fire storms carrying burning brands for miles. Although such intense fires can occur in our region, especially during lengthy droughts in forest types with a significant pine component (Forman and Boerner 1981), such intense, stand-replacing fires are uncommon in oak forests. Most fires in the oak forests of the central hardwoods occur during the dormant seasons (spring and autumn). Such fires typically move along the forest understory without climbing into the canopy (Sutherland and others 2003).

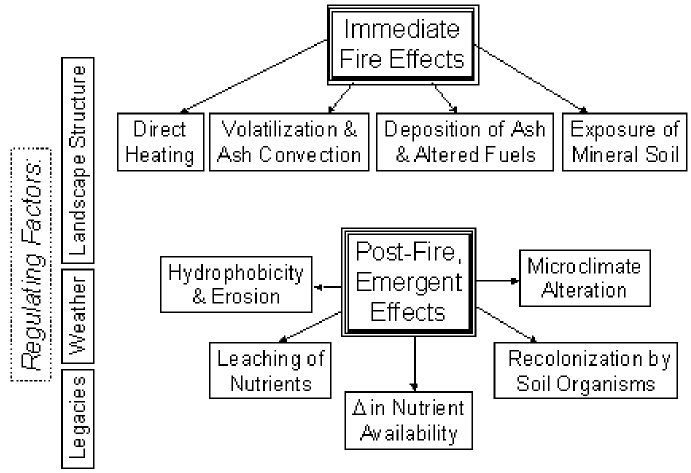

Figure 1.—Schematic of immediate fire effects and post-fire emergent effects on soil physical, chemical, and biological properties, with regulating factors indicated at left.

Fire has both immediate, direct effects as well as delayed effects on soil, soil organisms, and water that emerge in the days, weeks, and months after fire (Fig. 1). The degree to which those effects are felt is, in turn, regulated by weather, by the structure of the landscape, and by the legacies of past management, fire history, and land use (Fig. 1). In reviewing the available information on these topics I will rely where possible on studies from eastern oak forest ecosystems, and will supplement with studies from other temperate ecosystems (particularly pine forests and shrublands) only where there is insufficient direct evidence from eastern oak forests. Those interested in reviews of fire effects on ecosystems in general may consult recent, broadly based reviews, such as those of Neary and others (1999), Ice and others (2004) and Certini (2005).

SOIL HEATING

As a generalization, surface fires moving across the floor of a forest do not present a strong potential for severe soil heating because only a small percentage of the heat generated by the fire is partitioned downward into the soil. Further, mineral soil is a poor conductor of heat, especially when the soil is relatively dry (Raison 1979).

How much the temperature of the mineral soil increases during fires is the key to understanding the impact of the fire on soil organisms. Temperatures of 70°C for as little at 10 minutes will kill almost all fungi and soil microfauna, and also a significant proportion of soil bacteria (Lawrence 1956). Temperatures of 60°C are considered lethal to plant roots (Steward and others 1990) and temperatures above 60 °C denature enzyme systems of metabolically active cells of most microorganisms.

In areas where a distinct humus layer is absent or where that forest floor layer does not begin to smolder, insufficient heat is transferred downward into the mineral soil for temperatures to rise above ~60°C at depths below several centimeters (Anson and Gill 1976; Steward and others 1990). Saa and others (1993) measured soil temperatures at a depth of 5 cm in the mineral soil during surface fires in pine forests and shrublands in Spain. They did not record soil temperatures ≥ 50°C either during or after fire. Similarly, Hayward (1938) recorded soil temperatures during a fire in a longleaf pine (*Pinus palustris* Mill.) forest in North Carolina and found that temperatures at 2.5 cm into the mineral soil did not exceed 40°C at any time during or after the fire. Thus, fires moving across the forest floor are unlikely to produce increases in mineral soil temperatures sufficient to cause significant soil organism mortality.

One situation in which temperatures may rise sufficiently to induce considerable mortality is when localized concentrations of organic materials, either as woody debris (Miller and others 1955; Busse and others 2004) or as a particularly thick, dry humus layer (Miyanishi 2001), smolder in place for an extended period. Miller and others (1955) monitored surface and mineral soil temperatures during and after a fire in a New Zealand shrubland. aThere was no significant change in temperature at a depth of 5 or 10 cm in the mineral soil under this fire as it moved across the site. However, in areas where localized wood heaps burned for several hours, sensors recorded maximum temperatures of 100°C at 5 cm and 60°C at 10 cm into the mineral soil. Similarly, temperatures of 100 to 200°C have been recorded under smoldering *Arctostaphylos* residues at a depth of of 7.5 to 12.5 cm in a mixed-conifer forest in California (Busse and others 2004). Thus, localized heavy fuel accumulations such as slash piles from harvesting or detrital accumulations from storm damage present a situation in which direct heating effects may have significant negative effects on soil biota, including plant roots.

VOLATILIZATION AND ASH CONVECTION

Two pathways by which nutrients may be lost from an oak forest during and shortly after fire are direct volatilization (conversion of elements in fuel to gas phase) and ash convection (conversion of elements to solid, inorganic ash subject to wind action). Which nutrients are subject to being volatilized depends on the element's chemical properties, the properties of the compound in which that element is found, and the behavior of the fire. Similarly, losses via ash convection depend on the local weather conditions, the behavior of the fire, and the characteristics of the fuels being combusted.

Under controlled laboratory conditions, organic compounds containing nitrogen (N), phosphorus (P), and sulfur (S) often begin to volatilize when temperatures approach or exceed 200°C (Table 1). The temperatures reached in the fuelbed (~650°C) during flaming or smoldering after the flames have passed are considerably higher than that critical temperature. This helps explain why the amount N lost by volatilization is so closely dependent on the amount of fuel consumed (e.g., Raison and others 1985).

One of the few estimates of the loss of N via this pathway in oak forests is the report of Hubbard and others (2003) of losses of 55 kg N/ha from litter + wood and 6 kg N/ha from humus as the result of prescribed fires in oak-pine stands in Georgia and Tennessee. They indicated that losses of this magnitude could be replaced by atmospheric deposition of N in a relatively short time.

One also can gain perspective on the potential importance of this pathway of N loss from estimates generated in other temperate ecosystems dominated by woody plants. Losses of N from vegetation and detritus to the atmosphere have been estimated at 70 percent in a North Carolina longleaf pine savanna (Christensen 1977), 33 percent in a mixed pine plantation in South Carolina (Wells 1971), 39 percent in a mixed conifer forest in Washington (Grier 1975), and 39 percent in a chaparral shrubland in California (DeBano and Conrad 1978). In general, losses of N to the atmosphere are proportional to fuel mass loss during fire (Raison and others 1985).

Compared to N, base cations such as calcium (Ca), magnesium (Mg), and potassium (K) and inorganic forms of P have considerably higher laboratory volatilization temperatures (Table 1). Nonetheless, losses of cations and P from vegetation and detritus during a fire can be significant. Estimates of Ca loss range from 11 percent in a Washington mixed conifer forest (Grier 1975) to 15 percent in a longleaf pine savanna (Christensen 1977), to 17 percent in a mixed-eucalypt forest (Harwood and Jackson 1975). The same three studies report losses of K ranging from 9 to 46 percent and losses of Mg ranging from 13 to 17 percent. Similarly, estimates of the loss of P through this pathway range from 10 percent in a mixed-eucalypt forest in Tasmania (Harwood and Jackson 1975) to 46 percent in the longleaf pine site described by Christensen (1977).

The degree of combustion of the fuels and the resultant nature of the particulate materials available for transport can influence the relative importance of volatilization and ash convection as pathways for nutrient export. Raison and others (1985) determined that low intensity fires in three subalpine *Eucalyptus* forests resulted a ratio

Table 1.—Estimates of temperatures at which various elements/compounds of ecological importance volatilize under laboratory conditions; elements/compounds are listed in order of increasing minimum volatilization temperature

Element	Form	Volatilization
		°C
N	organic forms	175-200[a]
N	fumaric acid dinitrile	189[b]
N	alanine	<200[b]
N	adenine	<200[b]
P	phosphoric acid	203[b]
P	phosphobenzoic acid	249[b]
N	aminobenzoic acid	249[b]
P	organic forms	340-360[a]
S	organic forms	375[a]
K	inorganic forms	550[a]
P	inorganic forms	770[a]
K	base metal	774[b]
Ca	$CaCO_3$	825-898[b]
Mg	$MgCO_3$	900[b]
Mg	base metal	1107[b]
P	potassium hexametaphosphate	1320[b]
Ca	base metal	1487[b]

[a]Agee (1993).
[b]Weast (1969).

of 57 percent particulate to 43 percent nonparticulate loss of P when combustion produced black ash, and a ratio of 73 percent particulate to 27 percent nonparticulate loss when combustion proceeded all the way to very fine grey ash.

Although small losses of cations via direct volatilization may occur even in low intensity fires (e.g., Raison and others 1985), losses from the ecosystem of P and cations of the magnitudes listed also must represent exports of ash and other particulate combustion products due to the action of either ambient wind or air drawn (entrained) into the combustion zone because of the buoyancy of hot flame gases. Fire intensity (the rate of heat release from flaming per unit length of fire line, kW/m) determines both flame length and the velocities of air entrainment. Thus, it would be expected that losses of nutrients by ash convection would increase with fire intensity, a pattern suggested by Raison and others (1985). In addition, fire intensity tends to increase when fires burn in wind, so wind and fire intensity often may act together to increase nutrient losses in ash. Given the strong spatial heterogeneity in fuel consumption and intensity typical of most oak ecosystem fires, there likely are large spatial differences in nutrient losses either from volatilization or ash convection. Thus, one can generalize that losses of nutrients to the atmosphere may result in large losses of nutrients from the ecosystem, what proportion of the ecosystem nutrient capital is lost and via which atmospheric pathway depends on the element of interest, its biochemical context, the local weather conditions, and the behavior of the fire.

ASH DEPOSITION AND SOIL NUTRIENT AVAILABILITY

The material that remains after fire has consumed part or all of the fuel it can access is a combination of patches of uncombusted material, partially combusted woody material, and ash, the end product of complete combustion of the carbon (C) skeleton of the fuel materials. The inorganic materials that comprise the ash/partially combusted materials and whatever soluble organic compounds are present in the latter are all easily dissolved by rainfall. Whether these materials remain in the mineral soil or are lost from the system through leaching or overland runoff depends on several factors, most notably weather patterns, topography, and the properties of the mineral soil at that site.

During the first month after an early spring fire in a South Carolina pine plantation complex, approximately 80 mm of rainfall resulted in ~70 percent of the Ca and K in the ash being dissolved and transported downward into the soil (Lewis 1974). Similarly, in a study of post-fire nutrient dynamics in a mixed conifer forest in Washington, Grier (1975) observed that 90 percent or more of the ~150 kg Ca/ha, 50 kg K/ha, and 85 kg Mg/ha present in ash were dissolved and transported during the first precipitation event after the fire: 67 cm of snowmelt. In both of these cases, there was little actual loss from the ecosystem as the vast majority of the nutrients dissolved from the ash remained in the mineral soil.

The impact of ash deposition and dissolution on soil nutrient status is most obvious when fire has been both frequent and concentrated in space. For example, in their study of an oak forest site in Pennsylvania that had been used as a charcoal hearth from 1771 to 1884, Mikan and Abrams (1995) reported that Ca and Mg availability in the soils under the former hearth were 12.1 and 4.8-fold greater, respectively, than in the surrounding forest. Thus, repeated deposition of concentrated ash caused changes in nutrient status that were still apparent more than a century after the last hearth fire.

A similar example is from the study of the effects of burning concentrated slash piles (i.e., jackpot fires) after logging in an English oak forest (Jalaluddin 1969). In this study, the slash was piled in areas of < 2.0 m in diameter and burned for nearly 3 hours. Samples taken several days after the fires indicated that dissolution of the resulting ash had increased soil pH from 6.0 to 9.0. However, within 6 months, continued leaching of the soil resulted in the pH returning to ~ 6.0. Thus, the effects of fire on nutrient status are sensitive to the amount of ash deposited in a fire, the number of fires on that site, and the intensity/duration of the leaching of the site by precipitation following ash deposition.

After a single fire in a pine-oak ecosystem in Kentucky, Blankenship and Arthur (1999) reported that soil pH had increased by 0.2 to 0.3 unit, demonstrating the effect of a single fire and subsequent ash dissolution on soil base status. After two or four fires in a mixed-oak ecosystems in Ohio, Boerner and others (2004) reported fire-induced, significant and persistent increases in soil pH of 0.2 to 0.6 unit. This study also reported increases in extractable Ca^{2+}, reductions in extractable aluminum (Al^{3+}), and in increased molar Ca:Al ratios, though these differences were statistically significant only in the more nutrient-poor sites (Boerner and others 2004). In sites with significant limestone influence in the soils, changes in base cation status were transitory. Similarly, Knoepp and others (2004) observed increased soil pH, exchangeable Ca, and exchangeable Mg after site preparation (fell-and-burn) burning in western North Carolina.

Although most studies of the effects of fire on nutrient status focus on a single fire or several fires over a decade or less, two longer term experiments in oak forests may help shed light on chronic effects of burning on oak forest soils. Eivasi and Bayan (1996) assessed the nutrient status of soils in oak-hickory flatwoods in Missouri that had been subjected to annual or periodic (~ 4 year interval) burning for 40 years. They found no significant effects of fire at either frequency on soil pH, Ca, K, or Al. They did report that available P was reduced to 24 percent of controls by annual burning and to 35 percent of controls by periodic burning. Thor and Nichols (1973) reported a similar lack of change in pH from eight annual or two periodic burns in oak stands on the Highland Rim region of Tennessee. DeSelm and others (1991) resampled the Thor and Nichols (1973) sites after 27 years of annual or periodic burning, and again reported that burning had no significant effect on soil pH or the availability of K or P. Thus, although the effect of lengthy periods of burning had no effect on base-cation availability in either ecosystem, the long-term effect of low-intensity fire on P availability remains unclear.

No aspect of the belowground responses to fire has been more intensively studied than the availability of N in the soil. This is partially the result of the generally accepted view that most ecosystems are N-limited. Whether eastern oak ecosystems are still N-limited in 2005 given the chronic deposition of N from fossil fuel combustion and agricultural sources is an open question and beyond the scope of this review.

Wan and others (2001) performed a meta-analysis of the effects of fire on soil N availability and concluded that, over all ecosystem types, inorganic N availability is increased by fire. Ammonium (NH_4^+) availability peaks soon after fire but returns to pre-fire levels in less than a year. The pulse of NH_4^+ is due to a combination of liberation from organic matter degraded during the fire, activity of heterotrophic soil biota, and N-fixation by symbionts of newly colonizing plants. Nitrate (NO_3^-) availability peaks some months later (generally 6 to 12 months after fire), and is the result of enhanced NH_4^+ availability and increased activity of nitrifying bacteria.

However, when the results were stratified by fire type or intensity, Wan and others (2001) concluded that high intensity wildfires and slash fires resulted in increased NO_3^- and NH_4^+ whereas prescribed burning did not. As the majority of fires in eastern oak forests may be more like prescribed fires than wildfires or slash fires in grasslands, shrublands, or coniferous forests, one might speculate that the conclusions of Wan and others (2001) would have been different had their analysis been limited to ecosystems with a significant oak component.

Soil organic matter is a key part of a forested ecosystem. This material is an essential store of nutrients (especially N and C), is essential to exchange processes that regulate the availability of Ca, Mg, S, P, and K to plants and microbes, helps stabilize soil structure by cementing soil particles into stable aggregates, and insulates the soil against changes in microclimate. Enhancement of soil organic matter development in forests also is a pathway that is being examined as a possible mechanism for ameliorating the effects of CO_2 released by fossil fuel combustion.

Johnson and Curtis (2001) performed an extensive meta-analysis of the effects of disturbance on soil organic matter in forests. They concluded that ecosystems that had experienced fire approximately 10 years earlier had an average gain in soil organic C of approximately 8 percent. They attributed this change to a combination of factors, including infiltration into the mineral soil of organic matter from partially combusted fuels, conversion of labile (easily decomposed) organic matter into recalcitrant (stable) organic matter, and the effects of the colonization of burned areas by plants which harbor N-fixing symbionts.

Despite a rich literature from coniferous ecosystems that demonstrates significant loss 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) observed no significant change in soil organic C following one to three fires in Wisconsin oak forests, and Knoepp and others (2004) reported no significant change in soil C over 5 years following site preparation burning in oak-pine stands in North Carolina. We observed only slight changes in soil organic matter in Ohio oak-hickory sites subjected to one to four prescribed fires (Boerner and others 2000b; Boerner and Brinkman 2004). It is important to note that the lack of change in soil organic matter after fire may be specific to low-intensity, dormant-season fire regimes. For example, soil organic matter was reduced by as much as 50 percent following intense wildfire in an Israeli pine-oak (*Pinus halepensis* Mill-*Quercus calliprinos* Webb) ecosystem (Kutiel and Naveh 1987).

Results from single fires or from studies of several fires to the longer term are projected with considerable uncertainly. And, this is exacerbated by somewhat conflicting results from the two longer term studies of fire in oak forests that do exist. Eivasi and Bayan (1996) could not detect significant changes in soil organic-matter content in the soils of a Missouri oak flatwoods ecosystem even after more than 40 years of annual or periodic burning. By contrast, Philips and others (2000) reported significant reductions in A horizon organic-matter concentration and content after 35 years of annual fires (but not periodic fires) in a Tennessee oak forest.

Some of the material deposited on the ground surface after a fire is partially combusted, charred woody material. The blackened materials that comprise a considerable portion of this charred fuel have been termed “black carbon,” and have become a focus of research on organic matter changes after fire (Certini 2005). Black carbon can comprise as much as 40 percent of the soil organic matter in ecosystems exposed to frequent fire (Ponomarenko and Anderson 2001), and this material may have sorptive properties that are important in regulating soil solution chemistry and biochemistry for some time after fire (Wardle and others 1998). However, no estimates of the abundance or importance of black carbon in oak forests have been published.

EXPOSURE, EROSION, AND HYDROLOGY

Changes in the soil water and hydrological regimes of an ecosystem typically are proportional to the proportion of the litter, humus, coarse woody debris, and woody stems that are consumed during the fire. Fires that consume most or all of the forest floor and root systems may produce major changes in watershed hydrology. For example, Folliot and Neary (2003) reported an increase of 90 percent in watershed output after a high-intensity fire in a ponderosa pine (*Pinus ponderosa* Laws.) ecosystem in Arizona. By contrast, low-intensity fires that do not consume the entire forest floor and/or fires that affect only part of a watershed may not produce hydrological changes that can be resolved by typical monitoring methods (Bethlalmy 1974).

The volume of water leaving a forested watershed in streamflow and ground water recharge is a function of a range of factors, including interception of precipitation by the canopy and subsequent evaporation, transpiration by plants, evaporation from the ground surface, overland runoff, water storage in the soil, and transport of water through the soil profile to groundwater or surface waters. As low-intensity, dormant-season fires in eastern oak forests typically do not have a major impact on canopy structure and understory vegetation grows/regrows rapidly after fire, neither canopy interception/evaporation nor transpiration likely will be affected strongly by fire. Evaporation from the blackened soil surface may be enhanced after fire but such an effect likely will be limited to the period before the canopy leafout and understory development in the spring (Iverson and Hutchinson 2002).

Fires that consume the entire forest floor also may affect the water-holding capacity of the top several centimeters of the soil through changes in soil texture and structure (Austin and Baisinger 1955). Severe heating may cause clay-size particles to fuse into larger particles, thereby affecting soil texture and porosity; however, the intensity necessary to produce such effects is not typical of oak ecosystem fires. Changes in surface soil permeability or porosity also may occur as the result of the volatilization of organic compounds that had served to cement soil aggregates (Dyrness and Youngberg 1957). This can result in reduced porosity as impacted aggregates crumble and plug large soil pores (Moehring and others 1966). Severe and/or repeated burning also has the potential to increase soil bulk density, though such effects typically are less evident after low intensity, periodic fires (Moehring and others 1966; Agee 1973).

Whether water impacting on the forest floor/soil surface percolates into the soil or runs off over the surface depends not just on the permeability of the soil but also on whether water is free to move downward through the soil. In ecosystems where coarse-textured soils are overlain by resinous forest floor materials, combustion of the forest floor can cause volatilization of hydrophobic organic compounds. If there is significant downward transport of those volatilized materials, they may condense as hydrophobic coatings on soil aggregates, resulting in the development of what has been termed a hydrophobic or water-repellant layer (Agee 1973). Significant hydrophobicity has been observed after fire in coniferous forests and chaparral (e.g., DeBano and others 1970), and once developed can result in significantly increased erosion, as water that would normally percolate vertically through the profile is instead routed downslope through the surface soils along the water-repellant layer (Agee 1973). Although examples of fire producing nonwettable soil layers are common in coniferous ecosystems to the west and north of the oak forest region, I have found no reports of hydrophobicity developing after fires in oak forests.

As regulation of water flow and water quality are among the most important ecosystem services we expect forested watersheds to supply, the issue of the effect of fire on water quality merits consideration. Again, in ecosystems subject to large, intense fires, water quality may be affected greatly by surface runoff and particulate erosion. However, in ecosystems such as the eastern oak forests, fires do not typically produce effects on the watershed that are likely to produce such large or chronic changes in erosion and runoff. Instead, leaching of soluble materials from the ash and partially combusted fuels through the soil profile and into ground water or water bodies is of greater concern.

Knighton (1977) analyzed the effects of zero to three annual burns on the quality of water leaving an oak-hickory forest in central Wisconsin. He reported solution concentrations of Ca^{2+} and Mg^{2+} to be significantly greater in leachate below the burned areas than in leachate from unburned controls. The solution concentrations of NO_3^- and PO_4^{3-} also were greater in leachate from burned sites, and the degree of enrichment was proportional to the number of fires a site had experienced. However, Knighton (1977) pointed out that the increases in N and P concentration with fire frequency were not statistically significant due to high-among sample variability. Similarly, Lewis (1974) noted increases of 50 to 125 percent in concentrations of Ca^{2+} and K^{+} (but little change in NO_3^- and PO_4^{3-}) in soil leachate after fires in South Carolina pine plantations, but great variation among samples resulted in the differences not being statistically significant. Whether water quality is affected by low-intensity, dormant-season fires is likely to be determined by the relationship among ash deposition, post-fire precipitation, and soil nutrient storage capacity. Thus, predictions of fire effects on water quality will be site and situation specific.

SOIL BIOTA AND ECOSYSTEM PROCESSES

The assemblage of animals in the forest floor and soil of a forested ecosystem is both highly diverse and critically important to ecosystem processes. These animals form a complex food web that is responsible for much of the conversion of coarse detritus produced both below- and aboveground into fine organic materials that are suitable for subsequent microbial decay. Without these micro- and mesofauna present, leaf litter decomposition essentially ceases (Edwards and Heath 1963).

Of the many groups of arthropods present in and on the forest floor and soil of forested ecosystems, the *Collembola* (springtails) and *Acari* (mites) are the most important to the decay process (see also Rieske-Kinney, this volume). In southern Ohio mixed-oak forests, three annual burns reduced the numbers of springtails and mites by more than 50 percent, while a single fire resulted in no significant change in abundance in either group (Dress and Boerner 2004). There are even suggestions in that study that conditions after a single fire may have supported greater densities of microarthropods than did those of the unburned controls. Metz and Farrier (1971) reported that mites and springtails in the forest floor decreased in abundance in direct relation to fire frequency in a South Carolina pine plantation. When fires were applied every 4 years, there was sufficient time for recolonization and population growth to return numbers to pre-fire levels, whereas when fire was applied annually, abundances remained depressed over time. By contrast, Metz and Farrier (1971) reported no significant effect of annual or periodic fire on mites and springtails in the mineral soil.

As sparse as the database for microarthropods might be, that for other faunal groups is even more depauperate. Matlack (2001) reported no longterm effect of fire on nematode numbers or diversity in southern pine plantations. Bhadauria and others (2000) observed that annelid earthworm abundance was depressed by fire in a mixed oak-pine forest in northern India. However, they also reported that earthworm abundance returned to pre-fire levels over several months after fire as the result of migration from neighboring, unburned areas. Bhadauria and others (2000) suggested that post-fire conditions in the burned areas might be better suited for annelid growth than conditions present in unburned areas.

The effects of fire on the soil microbial community can be evaluated by examining individual species, species groups, or microbially mediated processes such as the conversion of organic, N-containing compounds to inorganic N as NH_4^+ (N mineralization). In a South Carolina pine plantation, Jorgensen and Hodges (1971) found that both fungal and bacterial abundance in the forest floor were reduced by annual fire, but abundances of both groups in the forest floor of plots burned on a 4-year cycle were greater than those of unburned controls (Fig. 2). The same pattern was apparent for bacteria in the upper 5 cm of the mineral soil, whereas

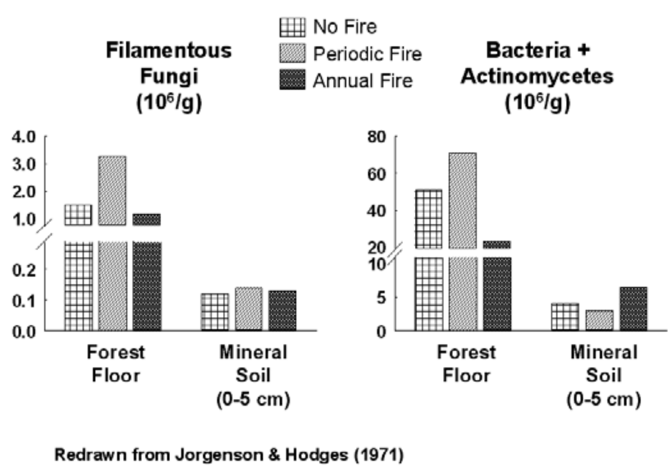

Figure 2.—Effects of fire on soil and forest floor microorganisms, redrawn from Jergensen and Hodges (1971).

fungal abundance in the mineral soil was not affected by fire treatment (Jorgensen and Hodges 1971). The notion expressed in this study that periodic fire produces conditions for soil microbes superior to those present in unburned sites parallels those from the studies of soil invertebrates described earlier (Bhadauria and others 2000; Dress and Boerner 2004.

Blankenship and Arthur (1999) demonstrated a significant, positive effect of a single winter fire in an eastern Kentucky oak-pine ecosystem on bacterial biomass, and this was accompanied by an increase in the bacteria:fungi biomass ratio in this ecosystem. A similar shift in the bacteria:fungi ratio after a low-intensity slash fire was reported by Perry and others (1984) in a northwestern coniferous forest. As the fungi in those coniferous systems are responsible for producing the compounds that make Fe available for plant uptake (hydroxymate siderophores), Perry and others (1984) believed that there was a potential for iron deficiency of tree seedlings after fire, especially where pH has been increased. Whether such short-term effects on the microbial community occur broadly in oak ecosystems and for how long such effects might persist is unknown. Fonturbel and others (1995) found no chronic or lasting effect of prescribed fire on heterotrophic bacteria or filamentous fungi in a pine ecosystem in Spain, but the applicability of this finding to eastern oaks is uncertain. Eivasi and Bayan (1996) found that 40 years of annual or periodic burning reduced microbial biomass in a Missouri oak forest by 32 and 21 percent, respectively.

Mycorrhizal fungi are key symbionts for virtually all forest plants. There are two major groups of mycorrhizal fungi found in the eastern oak regions (as well as several more limited groups of mycorrhizae *sensu latu* that are not considered here). Ectomycorrhizal fungi (ECM) are a group of higher fungi (basiodiomycetes and ascomycetes) that form symbioses with many conifers (e.g. *Pinus, Picea, Abies*), oaks (*Quercus* spp.), hickories (*Carya* spp.), and beech (*Fagus grandifolia* Ehrh.). Arbuscular mycorrhizal fungi (AMF), also referred to as endomycorrhizae, vesicular-arbuscular mycorrhizae and (VAM), are a much smaller and less diverse group of lower fungi that form symbioses with herbaceous plants and with woody plants that do not form ECM symbioses. Both AMF and ECM are critical to plants for the acquisition of P, as P is relatively immobile in most forest soils. In addition, ECM can be important in N uptake and pathogen resistance.

The colonization of roots by arbuscular mycorrhizal fungi is sensitive to soil heating, at least under laboratory conditions. Colonization of plant roots by AMF was reduced by ~50 percent when soil temperatures exceeded 50 to 60°C, and was reduced by 95 percent when soil temperature reached 90°C (Klopatek and others 1988). Whether this is important under field conditions is uncertain, as Knorr and others (2003) reported no significant effect of one to four fires on the abundance of the AMF-specific glycoprotein glomalin in oak forest soils in Ohio.

Severe fires can alter ECM community structure in bishop pine (*Pinus muricata* D.Don.) stands on the Pacific coast (Baar and others 1999). The decrease in ECM abundance and diversity that takes place after fire in western conifer forests may occur because the bulk of the fungal mycelium in those ecosystems is located in the humus layer of the forest floor, and that layer often is completely lost in severe wildfires (Harvey and others 1986). However, the applicability of this work to eastern oak ecosystems is uncertain. First, not all eastern oak forests exhibit a strongly developed humus horizon in the forest floor. Second, two studies in oak ecosystems suggest that fungi present in the mineral soil can rapidly recolonize the forest floor in the months after fire.

Tresner and others (1950) found that the species composition of fungi in a Wisconsin oak forest did not change with depth from the forest floor down through the upper mineral soil. They concluded that colonization of disturbed surface layers from deeper soil is possible without changing fungal community structure. Jalaluddin (1969) examined fungal dynamics in soils of small plots on which concentrated piles of slash had been burned. Fungal abundance in the center of those intensely burned plots was only 3, 6, and 11 percent of control levels at 1 week, 3 months, and 6 months after fire. However, at the edges of the burned plots, where recolonization from neighboring, unburned soils could occur, abundances were 17, 31, and 43 percent of control levels at those same points in time. Thus, even when intense fire effectively sterilizes the mineral soil, thus precluding recolonization from below (*sensu* Tresner and others 1950), mycelial ingrowth from surrounding areas can facilitate reestablishment of the fungal assemblage relatively quickly (Jalaluddin 1969).

Studies of changes in microbial function due to fire are more common than direct studies of community structure or abundance. In western conifer systems, a significant proportion of the N lost during fire may be offset by N_2 fixation by leguminous plants and their *Rhizobium* symbionts (Agee 1996). Among N-fixing woody species, black locust (*Robinia pseudoacacia* L.) has the most potential to contribute to the post-fire N economy in this way. Although black locust and its bacterial symbionts fix considerable amounts of N_2 and may have been common in burned areas historically, this species is now most common in postagricultural old fields in the southern portion of the oak forest region (Boring and Swank 1984); thus, there are few data with which to assess its impact after fire.

In Georgia loblolly pine forests, considerable amounts of N may be fixed by herbaceous perennials (e.g., *Desmodium* spp. and *Lespedeza* spp.) using the same symbiosis (Hendricks and Boring 1999). As both of these genera are widespread in the Eastern United States, the potential exists for this pathway to be important in oak ecosystems. Determining whether this potential is achieved awaits specific studies in oak forests.

In contrast to the sparse database on N_2 fixation in oak forests, many studies have demonstrated increases in N mineralization after single fires (reviews by Raison 1979; Boerner 1982; Wan and others 2001). These increases often are attributed to the alteration of organic matter by fire in such a manner as to render it more susceptible to microbial attack, to increases in microbial activity, and to changes in microclimate. Boerner and others (2000b, 2004) quantified soil organic matter, N mineralization rate and nitrification rate in four southern Ohio mixed-oak forests subjected to annual or periodic burning. At the full watershed scale, there was no consistent or persistent change in any index of microbially mediated N mineralization. In that study, pre-fire conditions and landscape characteristics were more important than fire behavior in explaining changes in C and N dynamics (Boerner and others 2000b). In a subsequent study of thinning+burning in a neighboring site, Boerner and Brinkman (2004) found no significant effect of a single fire on N mineralization in Ohio mixed oak-forests; a similar lack of fire effect on N mineralization has been reported for oak-pine forests in Georgia and Tennessee (Hubbard and others 2003) and oak-pine stands in North Carolina (Knoepp and others 2004).

It is important to note that the results of single fires or relatively short-term studies may not scale across longer time periods accurately. Vance and Henderson (1984) measured rates of N mineralization in the same long term Missouri stand used by Eivasi and Bayan (1996) a decade later. They found that N mineralization was reduced by longterm burning (30 years) and concluded that this change was a consequence of a change in organic matter quality rather than quantity. This is consistent with what one would expect if long-term burning results in an accumulation of black carbon over time (Ponomarenko and Anderson 2001).

Yet another approach to examining the impact of fire on the soil microbial assemblage is measuring the activity of the enzymes that microbes secrete into the soil to perform digestion processes. The activity of acid phosphatase is commonly used as a measure of overall microbial activity and as a surrogate measure for the rate at which N and P are mineralized from organic matter by microbes. Single fires in Ohio mixed-oak forests (Boerner and others 2000a) and pine forests in Spain (Saa and others 1993) and two to four fires over 5 years in Ohio mixed-oak forests (Boerner and Brinkman 2003) demonstrated reductions in acid phosphatase after fire, indicating an overall reduction in microbial metabolism. However, in the Ohio studies there were significant increases in phenol oxidase activity (Boerner and others 2000a; Boerner and Brinkman 2003). Phenol oxidase is an enzyme produced by fungi for the breakdown of recalcitrant organic compounds such as those that are likely to be left behind after the more labile organics are volatilized during fire or consumed shortly after fire.

Again, these short-term effects may not reflect what might happen over a long period of fire. Eivasi and Bayan (1996) reported significantly lower microbial biomass, acid phosphatase activity, and β-glucosidase activity in soils of Missouri oak-hickory sites exposed to annual or periodic fire for four decades.

Our overall understanding of the impact of fire in oak ecosystems on the soil microbial assemblage is growing but is not yet to the stage where a synthesis is achievable. Studies of community composition suggest that effects of one or several fires are rapidly ameliorated. Most functional studies suggest that the effects of fire are too modest to resolve analytically or are ones related primarily to changes in the relative proportions of labile and recalcitrant organic matter. However, long-term studies suggest that microbial activity and abundance may be significantly reduced if fire occurs frequently over many decades.

LANDSCAPE AND SCALE ISSUES

Forests with a significant oak component occur in a variety of landscape contexts in Eastern North America, from sandy coastal plains to Appalachian Piedmont and plateaus to the slopes of the Appalachian Mountains. Some of the oak region is recently glaciated, whereas other parts have not experienced glaciation for more than 10^6 years. Much of the eastern oak region consists of terrain that is dissected into ridges, hills, and valleys within which are strong gradients of microclimate (e.g., Wolfe and others 1949). In such complex landscapes, the behavior and effects of fire may vary so much among landscape positions within a watershed that considering only whole-watershed average effects may obscure important ecological patterns at the landscape scale.

To illustrate how fire behavior varies across the landscape, I present an example from the Ohio Hills Fire and Fire Surrogate (FFS) research sites in southern Ohio. The individual treatment units for the FFS project are areas of 20 to 30 ha in southern Ohio on which 50-m grids have been superimposed. Although the majority of studies that report fire behavior do so in terms of the

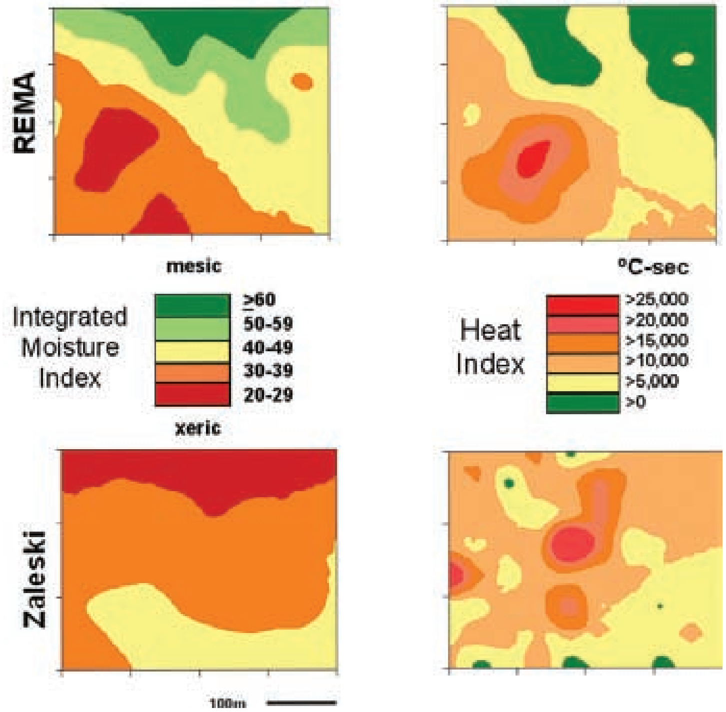

Figure 3.—Interpolated maps (semivariance analysis + kriging) of Integrated Moisture Index (IMI) and heat index in the forest floor based on 50-m grid points in two southern Ohio watersheds. The IMI data were supplied by L. Iverson and fire behavior data by M. Dickinson.

maximum temperature experienced by thermocouple probes, this may not be the most useful metric for understanding fire effects. The potential impact of fire is better described by the integration of thermocouple probe temperature over the time a fire is actually present at a point. When expressed at a single point (above a single sensor) this metric is referred to as the heat index (Bova and Dickinson 2005) and is expressed in units such as °C-sec.

Figure 3 presents interpolated maps of two of the Ohio FFS treatment units, with a metric of landscape position and long-term soil moisture potential (Iverson and others 1997) on the left and a map of heat index on the right. The heat index map clearly portrays both the variations in fire behavior across this landscape as well as the strong patchiness or spatial heterogeneity typical of fire in these forests. Unfortunately, the time and expense involved in instrumenting a site for measurements of heat index and the unpredictability of wildfire occurrence combine to make measurements of actual fire intensity in oak forests uncommon.

The recent development of integrative, GIS derived metrics designed to represent within-watershed scale gradients of elevation, aspect, slope shape, soil type/depth, and other aspects of microclimate have made available tools to allow us to begin to understand the landscape ecology of fire in a quantitatively rigorous manner. For southern Ohio, Iverson and others (1997) developed an Integrated Moisture Index (IMI) that integrates a large number of microclimate and soil parameters into a single metric. By stratifying sampling designs based on this integrated measure, we have been able to resolve within-watershed variations in fire effects on the soil.

In Ohio mixed-oak forests where fire has been effectively suppressed, soil pH, inorganic N, extractable Ca^{2+}, Mg^{2+}, and Al^{3+}, and molar Ca:Al ratio commonly vary among landscape positions, with relatively xeric ridgetops and upper, south-to-west-facing slopes having lower pH, cation availability, and molar Ca:Al ratio than other landscape positions (Table 2). N mineralization rate, and nitrification, and inorganic N in the soil solution tend to increase with increasing long-term soil moisture potential, or from xeric through median to mesic IMI classes Table 2).

By contrast, glomalin content tends to be greatest in the most xeric landscape positions (Table 2). As the content of this AM fungal-specific compound is thought to be directly proportional to AM fungal activity and inversely proportional to P availability, this suggests that the latter varies across the landscape in a manner parallel to that of N, This has been supported by direct analyses of P availability among landscape positions (Boerner and others 2003).

In some studies, relatively xeric landscape positions tend to have greater soil organic C content than more mesic positions, though others demonstrate no significant within-watershed scale variations in organic matter (Table 2). Soil enzyme activities, as indices of microbial activity, parallel total soil organic C closely, as do the abundances of various soil arthropod groups (Table 2). Thus, variations in soil biological and chemical properties among landscape positions within the small watersheds of the Appalachian plateaus are so diverse and significant as to cast doubt on the utility of watershed-scale averages, and point out the need for sampling designed to detect treatment effects to be stratified by landscape position.

This is illustrated by comparing responses to fire at the whole watershed-scale treatment unit level to those in the various landscape positions within that treatment unit (Table 3). In some cases, watershed-wide responses parallel (at least in direction) those in the individual landscape positions, e.g., phenol oxidase activity at Arch Rock (Boerner and others 2000a, Table 3) and both soil organic matter and N availability at Arch Rock (Boerner and others 2000b, Table 3). Far more common are situations in which there are significant effects of fire in one or more landscape positions that are not reflected in the overall, watershed-scale, treatment unit effect (Table 3), and even some where the effects at different landscape positions are opposite in direction, e.g., acid phosphatase and chitinase at Young's Branch (Boerner and others 2000a, Table 3).

On level terrain with relatively small variations in topography and soils over fairly large areas (e.g., till plains and some coastal plains), extrapolating manipulative experimental studies on plots in the m^2 size range to the km^2 scale at which management decisions are made and applied is a straightforward process of multiplication. By contrast, on the complex and dynamic landscapes of the Appalachian plateaus, such scaling up is more complex. GIS-based, integrative tools such as the IMI make the conversion from small plot-based studies to broad-scale prediction possible in a way that is only now being realized by ecologists and forest managers.

Table 2.—Variations in soil properties among landscape positions within Ohio mixed-oak forests in the absence of fire (except Boerner and others (2000b) in which fire had no significant effect on soil properties). The Integrated Moisture Index (IMI) classes of Iverson and others (1997) are used to denote landscape positions. Upper case letters reflect relative ranks, with A=highest and C=lowest; landscape positions with different upper case letters were significantly different, based on the anova or ancova used in the indicated source.

Sources/site(s)	Parameter	Integrated Moisture Index Class		
		Xeric	Median	Mesic
Boerner *and others* (2003)	Soil pH	B	A	A
Four southern Ohio	Inorganic N	C	B	A
sites pooled	PO_4^{3-}	B	A	A
	extractable Ca^{2+}	B	A	A
	extractable Mg^{2+}	B	A	A
	extractable Al^{3+}	A	B	C
	Ca:Al molar ratio	B	A	A
Morris and Boerner (1998)	Soil pH	B	A	A
Watch Rock	Organic C	A	B	B
	N mineralization	B	B	A
	Nitrification	B	B	A
Decker *and others* (1999)	Acid phosphatase	A	B	C
Arch Rock and Young's	Chitinase	A	B	B
Branch pooled	Phenol oxidase	A	A	A
	β-glucosidase	A	A	A
	Organic C	A	A	A
Dress and Boerner (2001)	Live root mass	A	A	A
Arch Rock	Dead root mass	A	A	A
	Root production	A	B	B
Boerner *and others* (2000b)	Organic C	A	C	B
Arch Rock	N mineralization	C	B	A
	Nitrification	B	B	A
Boerner *and others* (2000b)	Organic C	A	A	A
Young's Branch	N mineralization	C	B	A
	Nitrification	B	A	A
Knorr *and others* (2003)	Glomalin content	C	B	A
Arch Rock				
Dress and Boerner (2004)	Oribatid Mites	A	B	B
Arch Rock	Collembola	A	A	A

Table 3.—Fire-induced variations in soil properties at the watershed scale and among landscape positions within Ohio mixed-oak forests. The Integrated Moisture Index (IMI) classes of Iverson and others (1997) are used to denote landscape positions, and the column labeled "Pooled" represents the full watershed. Effects of fire are indicated as 0=no significant effect, ↓=significant decrease, and ↑=significant increase, based on the anova or ancova used in the indicated source.

Sources/site(s)	Parameter	Integrated Moisture Index Class			
		Pooled	Xeric	Median	Mesic
Boerner *and others* (2000b)	Organic C	0	0	0	0
Arch Rock	Total Inorganic N	0	0	0	0
Boerner *and others* (2000b)	Organic C	0	↑	↑	0
Young's Branch	Total Inorganic N	0	0	↑	0
Boerner *and others* (2000a)	Acid phosphatase	↓	0	↓	0
Arch Rock	Chitinase	0	0	0	0
	Phenol oxidase	↑	↑	↑	↑
Boerner *and others* (2000a)	Acid phosphatase	↓	↓	↓	↑
Young's Branch	Chitinase	↓	↓	0	↑
	Phenol oxidase	↑	0	0	↑
Dress and Boerner (2001)	April Root Mass	↓	0	0	↓
Arch Rock	May Root Mass	0	0	↑	0
	June Root Mass	↓	0	0	↓

CONCLUSIONS

The last century has seen literally thousands of individual studies of the effects of fire on the forest floor and soils of American forests, shrublands, and grasslands. Despite this rich literature, the available database for the eastern oak forest ecosystems is surprisingly sparse, particularly in studies that have continued past the first post-fire year.

Most fires in oak ecosystems for which there are data generally have intensities that fall in the lower end of the range for North American ecosystem fires, though occasional higher intensity, stand-replacing fires have been reported. Most of the unconsolidated litter and a portion of the humus layer are combusted during typical oak forest fires, yet significant heating of the mineral soil is limited to areas where accumulations of fuel smolder for extended periods. As a result, direct mortality of organisms in the soil is low, and mortality in the forest floor is proportional to the extent of consumption.

A considerable portion of the N in detritus and vegetation may be lost to a combination of direct volatilization and ash convection. Ash convection also can result in significant losses of P and base cations. Fire behavior, intensity, and weather are important regulators of these processes. The nutrients contained in ash typically are dissolved by the first several precipitation events following fire, and the proportion of those solubilized nutrients that remain in the soil for subsequent plant use depends on the exchange capacity of the soil, landscape geomorphology, and weather. In shrublands and coniferous forests, development of hydrophobicity in soil during and just after fire is often an important factor in determining how much of the post-fire precipitation and solubilized nutrient load are lost to runoff. However, the literature does not suggest that this is an important process in eastern oak forests.

The availability of N, a potentially limiting nutrient for post-fire plant growth, and the total amount of organic matter in the soil are typically greater after fire, though this may be a more transient phenomenon in oak forests than in coniferous forests and shrublands where fire intensities are considerably greater. The possible importance of the charcoal (black carbon) remaining after partial combustion of woody material to post-fire biological activity is anl area of current fire research in coniferous forests and grasslands, though little information on black carbon in oak forests is available.

Microbial activity, biomass, and community structure in the forest floor often is affected in proportion to the consumption of this organic-rich layer. By contrast, short-term effects on microbes in the mineral soil seem to be primarily the result of progressive soil heating under accumulations of organic materials that smolder for longer periods. Recovery of the microbial assemblage from fire is relatively rapid and is the result both of propagules in situ and colonization from surrounding, unburned areas. Similar spatial and temporal patterns have been reported for microarthropods in the forest floor and soil, but the database on other soil invertebrates groups is so sparse as to warrant no generalization.

Much of the oak forest region of Eastern North America is complex in geomorphology, and this complexity is a challenge when experimental studies must be scaled up to land areas as large as those for which management decisions are made. The use of GIS-derived measures of landscape structure and heterogeneity to stratify sampling designs, inform statistical analyses, and integrate plot results to the landscape scale has emerged as a viable tool for generating management-scale information.

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