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Prescribed burning effects on soil enzyme activity in a southern Ohio hardwood forest: a landscape-scale analysis

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Abstract

We assessed the effect of a single, dormant season prescribed fire on soil enzyme activity in oak-hickory (*Quercus-Carya*) forests in southern Ohio, USA. Four enzymes specific for different C sources were chosen for monitoring: acid phosphatase, β-glucosidase, chitinase and phenol oxidase. Postfire acid phosphatase activity was generally reduced by burning and decreased with increasing longterm soil water potential. Postfire β-glucosidase differed little between control and burned plots. Chitinase activity increased after fire in proportion to fire intensity. Phenol oxidase activity was highly variable and did not correlate well with either fire or soil water potential. Enzyme activities tended to vary more between samples taken upslope vs. downslope of a given tree than as the result of fire or landscape position. Overall enzymes whose activities are controlled by microclimatic or edaphic factors were affected more than those controlled primarily by substrate availability. Single, dormant season fires may consume a large proportion of the forest floor and change the apparent character of the surface organic matter complex without having major effects on soil enzyme activity.

Keywords: Fire; Landscape; Acid phosphatase; β-Glucosidase; Chitinase; Phenol oxidase

1. Introduction

There exists a history of almost half a century of modern use of prescribed fire for tree plantation management and wildfire fuel reduction (Riebold, 1971). More recently, prescribed fire has become a tool for restoration and conservation ecologists, first in grasslands and more recently in forested ecosystems. In intensively managed ecosystems, such as pine plantations in the southern USA, the efficacy of prescribed fire as a management technique can be assessed in a straightforward manner through assessment of tree mortality, growth, radial increment, yield and rotation time. In contrast, in unmanaged (or less intensively managed) ecosystems, determining the degree to which the less clear-cut goals of longer term conservation projects have been achieved is more difficult. Therefore, the development of metrics with which to assess efficacy of management activities in quasi-natural ecosystems, such as the use of prescribing burning for ecosystem restoration, becomes a higher priority. To this end, we have instituted a monitoring program to determine the effects of prescribed fires on the activity of a suite of soil enzymes as part of a larger, long term assessment of the use of prescribed fire at various frequencies for the restoration of oak-hickory ecosystems in southern Ohio (see Sutherland, 1999).

For some years, agricultural scientists have considered soil biological and biochemical parameters to have great potential as early and sensitive indicators of stress on agroecosystems and on the efficacy of attempts to restore degraded agroecosystems (Dick, 1994; Dick and Tabatabai, 1992). In unmanaged ecosystems, there is a strong correlation between soil

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enzyme activity and plant biomass production (Skujins, 1978) and an equally strong correlation between enzyme activity and microbial biomass (Eivazi and Bayan, 1996). However, in intensively managed or disturbed ecosystems, the relationship can be altered (Bolton et al., 1993; Dick, 1994).

Because forests of eastern North America have been historically N-limited and dependent on detrital pathways for mineralization of N and P (Aber et al., 1989), we chose four enzymes which are specific for a wide range of substrates. These included enzymes involved in the release of N and P and enzymes involved in the degradation of both labile and recalcitrant C forms:

1. Phosphomonoesterase (hereafter acid phosphatase), an enzyme whose activity is strongly correlated with the rate of release of both inorganic N and P to the soil solution;
2. β-glucosidase, the third enzyme in a chain of three which break down labile cellulose and other carbohydrate polymers;
3. Chitobiase = *N*-acetylglucosaminidase (hereafter chitinase), the second enzyme in the chain of three which degrade chitin and release low molecular weight C- and N-rich compounds; and
4. Phenol oxidase, one of a suite of enzymes involved in degradation of lignin, along with laccases and peroxidases.

Thus, this suite of four enzymes should represent the responses of a diverse microbial assemblage to a wide range of substrate types, and more importantly for ecosystem analysis, a range of soils from high to low organic matter quality and nutrient availability.

2. Materials and methods

2.1. Study sites and sampling design

The two forest sites chosen for study were located in Vinton and Lawrence Counties on the unglaciated Allegheny Plateau of southern Ohio. The sites were contiguous blocks of 90–120 ha occupied by oak-dominated forests which had developed following clearcutting for charcoal production 100–150 y ago. The Vinton County study site, Arch Rock (lat. 39°11′N, long. 82°22′W), and the Lawrence County study site, Young's Branch (lat. 38°43′N, long. 82°41′N) were separated by approximately 55 km. The study areas were chosen on the basis of the following criteria:

1. they met the age and land use history criteria listed above
2. the three watersheds within each study area were as uniform as possible in topography and geology and
3. there were no indications of significant anthropogenic disturbance since the clearcutting in the mid-to-late 1800s.

The parent materials underlying the study sites were sandstones and shales of Pennsylvanian age. The soils were dominated by silt loams formed from colluvium and residuum, and were predominantly Alfisols (Boerner and Sutherland, 1999). The climate of the region is cool, temperate and continental, with mean annual temperature and precipitation of 11.3°C and 1024 mm for the Vinton County sites and 12.9°C and 1059 mm for the Lawrence County sites (Sutherland and Yaussy, 1999). Microclimatic gradients generated by the steep, dissected topography of the region included the tendency for south, southwest and west facing slopes to be drier and warmer than northwest, north and east facing slopes due to the strong relief in this region (Wolfe et al., 1949).

Each study site was composed of three contiguous watersheds (or treatment units) of 30–80 ha. One of the watersheds within each study area was randomly assigned to be an unburned control. Each watershed was stratified using a GIS-based integrated moisture index (IMI) developed by Iverson et al. (1997) for this region. The IMI stratification was achieved through integration of elevation, aspect, hill shade profile, solar radiation potential, accumulation of water downslope, total water holding capacity of the soil and curvature profile of the landscape (Iverson et al., 1997). Each component was weighted and standardized on a 0–100 scale. Three IMI classes were delimited as: xeric, intermediate, and mesic.

Within each of the watersheds, three sample plots of 0.125 ha were established in each of the three IMI classes, for a total of nine sample plots per watershed and 27 sample plots per study site. In each sample plot, a single canopy northern red oak (*Quercus rubra* L.) tree with diameter at breast height (dbh) of 40–60 cm was chosen for sampling at the individual tree scale, and soil samples were taken 1.0 m upslope and downslope of that tree.

The positions of the sample plots were determined from a digital elevation model overlain with an IMI class map in an ARC/INFO environment, and the overall experiment was designed to be a balanced, randomized block design with study areas as blocks (Sutherland, 1999). However, subsequent GPS analysis of the sample plot locations determined that approximately 15% of the sample plots were not actually located at points within the IMI classes they were designed to represent. This resulted in an unbalanced design.

Previous analysis of the soils of these study areas indicated that soil chemical properties varied significantly among sites and among IMI classes, but not

among watersheds within sites (Boerner et al., 1999). The soils at Young's Branch had greater inorganic N content, Ca, Mg and molar Ca-to-Al ratio and higher pH than the soils at Arch/Rock. Similarly, soils from plots located in the xeric IMI class had lower inorganic N, lower extractable PO_4, Ca and Ca-to-Al ratio than soils in the mesic IMI class plots (Boerner et al., 1999).

In addition to differences in soil chemistry, our previous studies of these sites have also demonstrated that N mineralization and net nitrification increase significantly from xeric to mesic IMI classes, whereas chitinase and acid phosphatase activities are greatest in xeric IMI class soils (Decker et al., 1999; Boerner et al., 2000). In addition, organic matter content and acid phosphatase activity are greater in samples taken 1 m upslope from a given tree than in those taken 1 m downslope, whereas β-glucosidase activity was greater downslope (Decker et al., 1999).

The two treatment watersheds in each of the study sites were burned on 18–19 April 1996. The fires at Young's Branch were of low intensity, with mean temperature at 10 cm above the forest floor of 157°C (±12°C) (Boerner et al., 2000). An average of 35% (±4%) of the unconsolidated leaf litter was consumed by the fire, and there was no significant variation in either fire temperature or litter consumption with IMI class (Boerner et al., 2000). Only six of 36 sample plots at Young's Branch experienced fire temperatures >200°C, the critical minimum for significant loss of N to volatilization (Boerner, 1982).

The fires at Arch Rock were both hotter and more heterogeneous (Boerner et al., 2000). Mean temperature at 10 cm above the forest floor was 210°C (±11°C), and approximately 40% (±5%) of the unconsolidated litter was consumed. More importantly, fire temperature and litter consumption decreased with increasing long term moisture potential (measured as IMI), and 28 of the 36 sample plots at Arch Rock experienced temperatures >200°C.

2.2. Soil sampling and laboratory analysis

In late August and early September 1995 (prefire) and 1996 (postfire), samples of approximately 150 g of A-horizon soil were taken to a 15 cm depth with a sterile soil corer. The corer was sterilized between samples with 95% EtOH. Three samples were taken each at a point 1.0 m upslope of and a point 1.0 m downslope of one red oak (*Q. rubra*) tree identified adjacent to each sample plot. This yielded a total of six samples per IMI plot, for a total of 18 samples per watershed and 54 samples per study site. All samples were brought to the laboratory under refrigeration and analyzed within 24 h of removal from the field.

Approximately 5 g of fresh soil from each sample was diluted with 120 ml of 50 mM NaOAc buffer (pH 5.0) and homogenized by rapid stirring for 90 s. To minimize sand sedimentation, stirring was continued while aliquots were withdrawn for analysis. For each of the enzymes, we analyzed four analytical replicates of each sample using 2.0 ml of soil slurry and 2.0 ml of enzyme substrate for each analytical replicate. In addition, soil-free blanks consisting of 2.0 ml of buffer and 2.0 ml of enzyme substrate were analyzed to correct for non-enzymatic hydrolysis of substrates. All enzyme nomenclature follows IUB (1978).

Acid phosphatase (EC 3.1.3.1), β-glucosidase (EC 3.2.1.21), and chitinase (EC 3.2.1.14) activities were assayed using *p*-nitrophenol (*p*NP) linked substrates: *p*NP-phosphate for phosphatase, *p*NP-glucopyranoside for β-glucosidase, and *p*NP-glucosaminide for chitinase. Acid phosphatase and β-glucosidase samples were incubated for 1 h and chitinase samples were incubated for 2 h, both at 20°C with constant mixing on a platelet mixer. Following incubation, samples were centrifuged to remove soil particles, and 0.1 ml of 1.0 M NaOH was added to the soil-free supernatant to halt enzymatic activity and facilitate color development. Prior to spectrophotometric analysis, the sample was diluted with 8.0 ml of distilled, deionized water. Phenol oxidase (EC 1.14.18.1 and 1.10.3.2) activity was measured by oxidation of ℓ-DOPA (ℓ-3,4-dihydroxyphenylalanine) following 1 h incubation at 20°C. Parallel oxidations utilizing standard Horseradish Peroxidase (Sigma Chemical) were used to calculate the ℓ-DOPA extinction coefficient. Absorbances were determined spectrophotometrically at 410 nm for the *p*NP assays and 460 nm for phenol oxidase. To minimize errors due to hydrolysis of the *p*NP-linked substrates by the NaOH, all absorbances were determined within 30 min after the addition of NaOH. All enzyme analyses followed methods described by Sinsabaugh et al. (1993) and Sinsabaugh and Findlay (1995).

The initial soil moisture and fresh-to-dry weight ratio of each soil sample was determined by drying 8–10 g of fresh soil at 65°C to constant weight. Organic matter content was determined by dry ashing 2 g samples at 600°C for 4 h. We chose to express enzyme activity both in relation to soil mass and in relation to soil organic matter content. Expressing enzyme activity on a mass basis gives an estimate of the rate at which the product of the enzymatic activity is being made available to microbes and plants; as such it is a quantity measure. In contrast, expressing activity on an organic matter basis gives an estimate of how suitable the organic matter complex is to degradation by those specific enzymes; thus this is an organic matter quality measure.

We also calculated the change in enzyme activity between the prefire and postfire sampling dates in two ways. First, we substracted directly the activity from

the prefire sample (data given by Decker et al., 1999) from the activity of the corresponding postfire sample to generate an absolute rate of change. To further explore the potential for direct fire effects, we subtracted the absolute change in activity for each site × treatment watershed × IMI class × position sample in the control watershed from that of the comparable site × treatment watershed × IMI class × position sample from each of the burned watersheds to estimate the change from prefire to postfire sampling that could be attributed to the effects of fire alone.

2.3. Data analysis

All response variables except the proportional activities were found to be normally distributed (PROC univariate of SAS, 1995); the proportional activities were arcsine transformed prior to analysis. As the fire behavior and site characteristics differed somewhat between the two study areas, we analyzed postfire and temporal changes in enzyme activity by mixed model analysis of variance using a nested, unbalanced design (PROC mixed; SAS, 1995) using fire temperature as a covariate. Where main effects were significant, least squares means were used to test differences among sites, watersheds within sites, and IMI classes.

3. Results

3.1. Postfire enzyme activity

At Arch Rock there was a significant interactive effect of IMI class and fire on acid phosphatase activity after the fire (Table 1). On a soil mass basis, acid phosphatase activity was greater in intermediate (but not xeric or mesic) IMI class soils from the unburned control watershed than in soils from the two burned watersheds (Fig. 1). On an organic matter basis, acid phosphatase activity was greater in the control soils than the burned soils in both the xeric and intermediate IMI class plots (Fig. 1).

There was also a significant interactive effect of fire and IMI class on acid phosphatase activity on a soil mass basis at Young's Branch (Table 1). Activity was significantly greater in soils from the control than in soils from the burned watersheds in both xeric and intermediate IMI class plots, while the opposite was the case in soils from mesic IMI class plots (Fig. 1). There were no significant effects of either fire or IMI class on acid phosphatase on an organic matter basis at Young's Branch (Table 1, Fig. 1).

There were no significant effects of fire or IMI class in postfire β-glucosidase activity at either study site or in postfire chitinase activity at Arch Rock (Table 1). At Young's Branch, there was a significant interactive

Table 1
Analysis of variance of postfire acid phosphatase, β-glucosidase, chitinase, and phenol oxidase activities in two forest sites in relation to burn treatment, long term moisture potential (IMI class) and position relative to a single red oak tree (upslope vs. downslope). $N = 54$ for each enzyme in each forest site. For ANOVAs in which the full model was significant at $P \leq 0.05$, F and P are given for all variance components (ns = variance component not significant); ANOVAs in which the full model was not significant at $P \leq 0.05$ are indicated by: model ns

Variance component	Soil mass basis (μmol g^{-1} soil h^{-1})		Organic matter basis (μmol g^{-1} OM h^{-1})	
	Arch Rock	Young's Branch	Arch Rock	Young's Branch
Acid phosphatase				
Fire	$F = 9.86$, $P < 0.003$	$F = 5.72$, $P < 0.021$	$F = 26.23$, $P < 0.001$	$F = 0.35$, ns
IMI class	$F = 2.28$, ns	$F = 6.14$, $P < 0.005$	$F = 5.17$, $P < 0.028$	$F = 10.47$, $P < 0.002$
Fire × IMI class	$F = 6.06$, $P < 0.005$	$F = 6.28$, $P < 0.004$	$F = 3.78$, $P < 0.031$	$F = 2.27$, ns
Position	$F = 1.84$, ns	$F = 0.75$, ns	$F = 1.43$, ns	$F = 0.15$, ns
β-glucosidase				
Fire	$F = 0.35$, ns	model ns	$F = 0.30$, ns	model ns
IMI class	$F = 0.76$, ns	model ns	$F = 1.20$, ns	model ns
Fire × IMI class	$F = 1.25$, ns	model ns	$F = 1.46$, ns	model ns
Position	$F = 5.56$, $P < 0.023$	model ns	$F = 5.54$, $P < 0.023$	model ns
Chitinase				
Fire	$F = 2.44$, ns	$F = 4.73$, $P < 0.037$	$F = 0.76$, ns	model ns
IMI Class	$F = 0.11$, ns	$F = 3.21$, $P < 0.050$	$F = 0.24$, ns	model ns
Fire × IMI Class	$F = 0.28$, ns	$F = 7.28$, $P < 0.002$	$F = 1.09$, ns	model ns
Position	$F = 10.56$, $P < 0.002$	$F = 0.01$, ns	$F = 8.46$, $P < 0.006$	model ns
Phenol oxidase				
Fire	$F = 9.35$, $P < 0.004$	$F = 1.45$, ns	$F = 5.36$, $P < 0.026$	$F = 0.17$, ns
IMI Class	$F = 1.13$, ns	$F = 3.69$, $P < 0.033$	$F = 1.89$, ns	$F = 0.08$, ns
Fire × IMI Class	$F = 0.85$, ns	$F = 9.32$, $P < 0.004$	$F = 0.36$, ns	$F = 3.56$, $P < 0.036$
Position	$F = 0.05$, ns	$F = 4.69$, $P < 0.036$	$F = 0.01$, ns	$F = 5.67$, $P < 0.022$

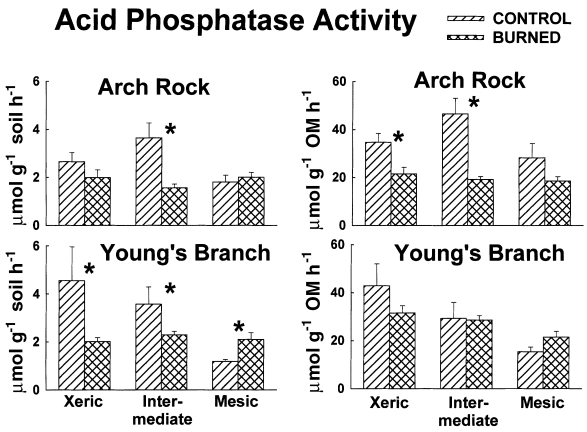

Fig. 1. Acid phosphatase activity expressed per unit soil mass (μmol g^{-1} soil h^{-1}) and per unit organic matter (μmol g^{-1} OM h^{-1}) in two southern Ohio forest sites in relation to integrated moisture index classes and fire treatment. Histogram bars represent means with standard deviations of the means of $N = 18$ for controls and $N = 36$ for burned sites; significant differences between means are indicated by *.

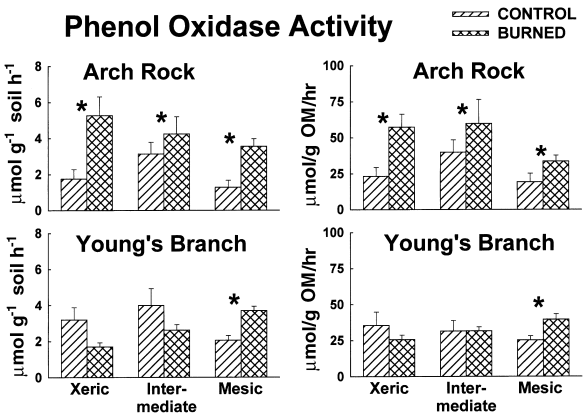

Fig. 3. Phenol oxidase activity expressed per unit soil mass (μmol g^{-1} soil h^{-1}) and per unit organic matter (μmol g^{-1} OM h^{-1}) in two southern Ohio forest sites in relation to integrated moisture index classes and fire treatment. Histogram bars represent means of $N = 18$ for controls and $N = 36$ for burned plots, with standard deviations of the means indicated; significant differences between means are indicated by *.

effect of fire and IMI class on postfire chitinase activity on a soil mass basis (Table 1). Chitinase activity was greater in control than burned plots in soils from xeric IMI class plots, while the opposite was the case in soils from mesic IMI class plots (Fig. 2)

There was a significant effect of fire on phenol oxidase activity in soils from Arch Rock on both organic matter and soil mass bases (Table 1) with activity consistently greater in soils from burned watersheds than in soils from the unburned control (Fig. 3). At Young's Branch, phenol oxidase activity was greater in burned watersheds only in soils from mesic IMI class plots (Table 1, Fig. 3).

3.2. Relative carbon source utilization

To gain insight into the relative importance of chitin and the labile vs. recalcitrant lignocellulose fractions as carbon sources in these soils, we calculated the relative proportion of phenol oxidase, β-glucosidase and chitinase activity contributed by each of the three enzymes to the sum of the three. At Arch Rock the soils from unburned control had significantly greater proportional β-glucosidase activity ($F = 5.53$, $P < 0.008$) and significantly lower phenol oxidase activity ($F = 5.23$, $P < 0.010$) than did soils from the two burned plots (Fig. 4). There were no significant differ-

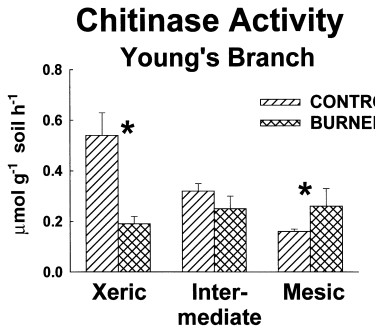

Fig. 2. Chitinase activity in soils from Young's Branch, an oak-hickory forest site in southern Ohio, in relation to integrated moisture index classes and fire treatment. Histogram bars represent means of $N = 18$ for controls and $N = 36$ for burned plots, with standard deviations of the means indicated; significant differences between means are indicated by *.

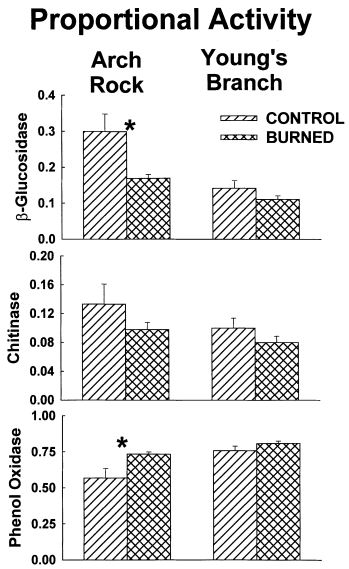

Fig. 4. Proportional activity of β-glucosidase, chitinase and phenol oxidase as a percentage of their summed activity in relation to prescribed fire in two southern Ohio forest sites. Histogram bars represent means of $N = 18$ for controls and $N = 36$ for burned plots, with standard deviations of the means indicated; significant differences between means are indicated by *.

Table 2
Listing of response variables which indicated a significant effect at $P \leq 0.05$ of sampling position relative to a single red oak tree (1 m upslope vs. 1 m downslope. Units are soil mass basis: μmol g^{-1} soil h^{-1} and organic matter basis: μmol g^{-1} OM h^{-1}. Means and standard errors are given

Site	Enzyme/temporal context	Estimation basis	Upslope	Downslope
Arch Rock	change in phosphatase	soil mass	−1.43 (0.41)	0.98 (0.30)
Arch Rock	change in phosphatase	organic matter	−17.39 (3.80)	−1.08 (3.46)
Young's Branch	change in phosphatase	soil mass	−1.62 (0.28)	−0.87 (0.32)
Young's Branch	change in phosphatase	organic matter	−14.16 (3.79)	−5.27 (1.82)
Arch Rock	β-glucosidase, postfire	soil mass	0.94 (0.09)	0.69 (0.06)
Young's Branch	β-glucosidase, postfire	soil mass	0.46 (0.04)	0.34 (0.03)
Young's Branch	change in β-glucosidase	organic matter	6.59 (1.37)	2.02 (0.66)
Arch Rock	chitinase, postfire	soil mass	0.57 (0.08)	0.30 (0.03)
Arch Rock	chitinase, postfire	organic matter	6.96 (1.16)	3.46 (0.26)
Young's Branch	phenol oxidase, postfire	soil mass	3.15 (0.31)	2.46 (0.22)
Young's Branch	change in phenol oxidase	organic matter	−12.78 (10.78)	−8.12 (4.44)

ences in proportional activity among watersheds at Young's Branch, nor among IMI classes at either site.

3.3. Fine-scale spatial variations

To determine what effect tree bases would have on postfire heterogeneity on these steep slopes, we analyzed differences in samples taken 1 m above and below individual trees (Table 1). Although there were no significant differences in absolute acid phosphatase activity between soils taken upslope and downslope, the rate of change in phosphatase activity between prefire and postfire samples was significantly greater in soils taken upslope than downslope in both study sites (Table 2). Postfire β-glucosidase activity was significantly greater in soils collected upslope from the tree base than in those taken downslope (Table 2) as was the magnitude of the change in activity between prefire and postfire (Table 2).

Variations in chitinase activity at this spatial scale were present at Arch Rock both on soil mass and organic matter bases (Table 2). Postfire chitinase activity on soil mass and organic matter bases were 90 and 101% greater, respectively, in upslope than downslope soils (Table 2). Similarly, phenol oxidase activity on a soil mass basis was 28% greater in upslope than downslope soils after the fire and activity in upslope soils changed more between prefire and postfire samplings than did that in downslope soils, at least at Young's Branch (Table 2).

3.4. Net fire effects

To estimate the net effect of the prescribed burning, we first estimated the change in each response parameter from prefire (using data presented by Decker et al., 1999) to postfire in each combination of site, IMI class, and position in the control watershed. We then subtracted the net temporal change in the control plots from the changes in the corresponding samples from the two burned watersheds.

There were significant effects of fire on the change in phosphatase activity in both sites (Table 3). Activity decreased significantly in the burned plots but not in the control plots on both soil mass and organic matter bases at Young's Branch and on a soil mass basis at Arch Rock (Fig. 5). In contrast, at Arch Rock chitinase activity decreased significant from prefire to postfire in control soils but not in soils from burned plots (Table 3, Fig. 5). The changes in the acid phosphatase and chitinase in soils from Arch Rock were also affected significantly by IMI class (Table 3), with the magnitudes of the decreases in activity decreasing with increasing soil water potential (Fig. 6). There were no significant fire or IMI class related changes in the activity of β-glucosidase or chitinase from prefire to postfire (Table 3).

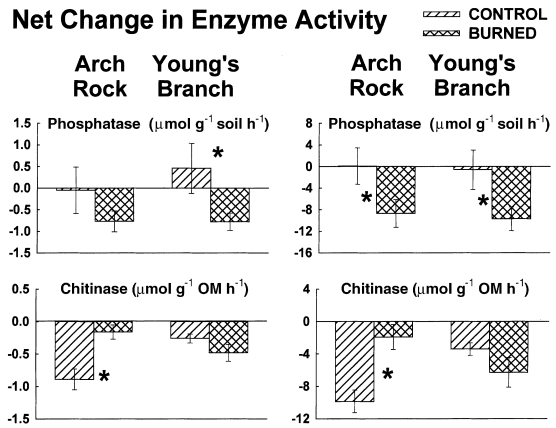

Fig. 5. Net change in acid phosphatase and chitinase activity attributable to the effects of prescribed burning in two southern Ohio forest sites. Histogram bars represent means of $N = 18$ for controls and $N = 36$ for burned plots, with standard deviations of the means indicated; significant differences between means are indicated by *.

Table 3
Analysis of variance of the net, fire-related change in phosphatase, β-glucosidase, chitinase and phenol oxidase activities in two forest sites in relation to burning treatment, long term moisture potential (IMI Class) and position relative to a single red oak tree (upslope vs. downslope). $N = 54$ for each enzyme in each forest site. For ANOVAs in which the full model was significant at $P \leq 0.05$, F and P are given for all variance components (ns = variance component not significant); ANOVAs in which the full model was not significant at $P \leq 0.05$ are indicated by: model ns

Variance component	Soil mass basis (μmol g^{-1} soil h^{-1})		Organic matter basis (μmol g^{-1} OM h^{-1})	
	Arch Rock	Young's Branch	Arch Rock	Young's Branch
Change in phosphatase				
Fire	$F = 0.06$, ns	$F = 7.51$, $P < 0.009$	$F = 3.03$, $P < 0.045$	$F = 5.85$, $P < 0.020$
IMI class	$F = 3.39$, $P < 0.043$	$F = 1.22$, ns	$F = 3.24$, $P < 0.048$	$F = 1.91$, ns
Fire × IMI Class	$F = 0.08$, ns	$F = 1.10$, ns	$F = 0.61$, ns	$F = 0.06$, ns
Position	$F = 8.39$, $P < 0.006$	$F = 10.33$, $P < 0.003$	$F = 3.80$, $P < 0.048$	$F = 7.89$, $P < 0.008$
Change in β-glucosidase				
Fire	model ns	model ns	model ns	$F = 0.97$, ns
IMI Class	model ns	model ns	model ns	$F = 0.44$, ns
Fire × IMI Class	model ns	model ns	model ns	$F = 3.27$, ns
Position	model ns	model ns	model ns	$F = 5.98$, $P < 0.019$
Change in chitinase				
Fire	$F = 17.10$, $P < 0.001$	model ns	$F = 11.08$, $P < 0.002$	model ns
IMI Class	$F = 3.36$, $P < 0.044$	model ns	$F = 1.44$, ns	model ns
Fire × IMI Class	$F = 1.46$, ns	model ns	$F = 0.90$, ns	model ns
Position	$F = 1.03$, ns	model ns	$F = 0.06$, ns	model ns
Change in phenol oxidase				
Fire	model ns	model ns	model ns	model ns
IMI Class	model ns	model ns	model ns	model ns
Fire × IMI Class	model ns	model ns	model ns	model ns
Position	model ns	model ns	model ns	model ns

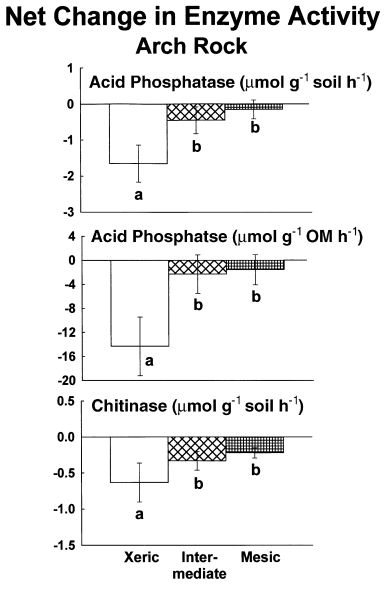

Fig. 6. Net change in acid phosphatase and chitinase activity attributable to the effects of prescribed burning in two southern Ohio forest sites in relation to long term soil moisture potential (as measured by integrated moisture index/IMI class). Histogram bars represent means of $N = 18$ for controls and $N = 36$ for burned plots, with standard deviations of the means indicated; significant differences between means are indicated by *.

4. Discussion

The activity of acid phosphatase we observed was similar to or greater than that reported in other ecosystems: woodlands in England (1–6 μmol g^{-1} soil h^{-1}: Harrison, 1979), pine plantations in Spain (2–8 μmol g^{-1} soil h^{-1}: Saa et al., 1993), young oak and pine forests in eastern Europe (4–12 μmol g^{-1} soil h^{-1}: Kuprevich and Shcherbakova, 1971) and semi arid steppe (2–6 μmol g^{-1} soil h^{-1}: Bolton et al., 1993). However, our estimates of both acid phosphatase and β-glucosidase activities were 3–5 fold greater than those reported for oak forests in Missouri similar to ours in soils and vegetation (0.5–1.6 μmol g^{-1} soil h^{-1}: Eivazi and Bayan, 1996).

We observed a significant, fire-related decrease in acid phosphatase activity on both soil mass and organic matter bases in soils from Young's Branch and on an organic matter basis in soils from Arch Rock. These results were consistent with those of Saa et al. (1993), who reported 80–90% decreases in acid phosphatase activity as a result of wildfire in pine plantations and gorse shrublands in Spain, and Eivazi and Bayan (1996) who reported 60–70% decreases in acid phosphatase activity in oak forests in Missouri that were burned annually or periodically for 30+ y. It should be noted, however, that Saa et al. (1993) also

reported no significant change in acid phosphatase activity following low intensity prescribed fire in gorse (*Ulex europaea*) shrublands.

The fires also reduced spatial heterogeneity in acid phosphatase activity in the burned watersheds. After the fire, there was considerably less effect of topography (as measured by IMI class) on activity than was present either in prefire sampling (Decker et al., 1999) or in the control watersheds during the postfire sampling. This suggests that disturbance by fire (if, indeed, fire should be considered a disturbance in this ecosystem type) might serve to homogenize resources. Such a pattern has also been reported for semiarid shrublands and grasslands in the western US by Bolton et al. (1993). They found strongly heterogeneous patterns of soil phosphatase activity, dehydrogenase activity, and microbial biomass in undisturbed shrublands and more homogeneous spatial distributions in grasslands that had resulted from disturbance of the native shrubland vegetation.

We observed little impact of fire on β-glucosidase activity at the landscape scale. In contrast, Eivazi and Bayan (1996) reported reductions of 50–65% in β-glucosidase activity after 30+ y of annual or periodic prescribed burning in oak woodlands. This, again, points out the potential for the effects of a single fire to differ dramatically from those of repeated fires (see Vance and Henderson, 1984).

We observed significantly larger fire-related changes in chitinase activity than in β-glucosidase activity. At Arch Rock, chitinase activity decreased significantly from the prefire to postfire sampling in soils from the unburned control but not in those from the burned watersheds. Thus, soils from burned plots experienced an increase in activity relative to what would have been expected in the absence of fire. Several factors may have contributed to this fire-induced increase in chitinase activity. First, there could have been a strong stimulation of fungal growth and turnover in the upper soil and forest floor as a result of the fire, thus increasing the availability of chitin as a substrate. However, prior studies of the impact of low intensity fire on fungi have indicated either the lack of significant effect on fungal growth or modest reductions in biomass (Wright and Tarrant, 1957; Jorgenson and Hodges, 1971). Second, it may have reflected an increase in chitinolytic bacteria or actinomycetes, the organisms that dominate chitinase production in the soil. Both Wright and Tarrant (1957) and Jorgenson and Hodges (1971) report that periodic prescribed burns affected bacteria and actinomycetes less than they did fungi; thus, a preferential effect of fire on fungi could have increased the availability of chitin as a substrate for the relatively unaffected bacterial and actinomycete populations. In a grassland soil with high N availability (C-to-N of 9.9), additions of chitin produce increases in both chitinase activity and the abundance of chitinolytic organisms (Hanzlikova and Jandera, 1993); in contrast addition of chitin + glucose resulted in a depression of chitinase activity, demonstrating that chitin is not a favored substrate for carbon utilization at high N availability (Hanzlikova and Jandera, 1993). Our observation of significant and positive changes in chitinase activity after fire support both the notion that fungal abundance would be affected more than bacterial abundance and that these sites remained N-enriched despite volatilization of N during the fires.

There was considerable spatial variability in phenol oxidase activity, both prior to the fire (Decker et al., 1999) and after the fire, and we saw no clear indication of a significant effect of a single prescribed burn on the activity of this enzyme. In a study of wood decomposition in a range of ecosystem types, Sinsabaugh et al. (1992, 1993) found lignocellulose degrading enzymes (such as phenol oxidase) to be controlled primarily by substrate availability, whereas chitinase and phosphatases were controlled more by microclimate and edaphic factors. That we observed significant effects of fire on both chitinase and acid phosphastase, but not on phenol oxidase, suggests that the ecological impact of this fire was primarily a modifaction of the microclimate and structure of the forest floor surface rather than on the composition of the organic matter complex within the soil.

In our earlier studies of a larger suite of hardwood forest watersheds in southern Ohio (Morris and Boerner, 1998, 1999; Decker et al., 1999) we observed large and significant variations in organic matter and microbial biomass between samples taken 1 m upslope and 1 m downslope of an individual red oak in each sample plot. The data we report here demonstrates that acid phosphatase activity was significantly greater downslope of a given tree than upslope, and the magnitude of this difference was increased by the effects of fire. Phenol oxidase activity was also greater downslope than upslope, at least on a soil mass basis. β-glucosidase activity was greater in upslope than downslope both before and after the fire; however, fire reduced the magnitude of this difference. Finally, chitinase activity was greater upslope than downslope after the fire, primarily because of a greater change upslope than downslope as a result of the fire. The concept of single tree influence circles has been well established in the literature for some time (e.g. Zinke, 1962; Crozier and Boerner, 1984; Boerner and Koslowski, 1988; Boettcher and Kalisz, 1990). However, this study and the others we have done in these sites have demonstrated for the first time a directional asymmetry to single tree influence circles in steep lands (cf. Boettcher and Kalisz, 1990).

A single, dormant season prescribed fire can con-

sume the majority of the unconsolidated leaf litter on the forest floor, and produce what appear to be major changes in the quantity, quality and character of the organic matter complex of the forest floor. Such changes often result in rapid and significant changes in microbial activity and net N mineralization (Boerner et al., 2000). However, the data presented here indicate that such changes do not lead to significant and widespread changes in microbial community structure or metabolic profiles, at least to the degree that soil enzyme activity mirrors those attributes. Thus in this ecosystem type, at the least, application of single prescribed fires for management or restoration purposes may be conducted without the concern that major effects on the microbial community will result.

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