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The influence of current year fire on leaf litter decomposition rates and microbial enzyme activity in forests undergoing ecological restoration

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THE INFLUENCE OF CURRENT YEAR FIRE ON LEAF LITTER DECOMPOSITION RATES AND MICROBIAL ENZYME ACTIVITY IN FORESTS UNDERGOING ECOLOGICAL RESTORATION

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ABSTRACT

As a result of fire suppression, open oak woodlands, once characteristic of the interior of the southern USA, are being lost to mesophication. This process leads to changes in the plant community and has the potential to change rates of decomposition and nutrient cycling through changes in environmental conditions or leaf litter composition. Restoration projects to reduce the effects of mesophication include thinning the canopy to remove mesophytic species and prescribed burn regimens to return the plant community to a fire tolerant and dependent one. However it is unclear what effects restoration (or mesophication) has on the decomposition of leaf litter, nutrient cycling, and microbial activity. This study compared leaf litter decomposition rates of six tree species (*Quercus stellata, Quercus falcata, Quercus alba, Carya tomentosa, Liquidambar styraciflua,* and *Ulmus alata*) ranging from those characteristic of historical open oak woodland to those that are mesophytic, and determined how these decomposition rates differed between restored and unrestored and burned and unburned portions of an upland oak forest. Decomposition rates were related to microbial extracellular enzyme activity in decomposing litter to examine potential mechanisms for different decay rates. Enzymatic efficiency of decomposition was generally higher in restored sites, but prescribed fire in a given year was important and significantly reduced decomposition rates and enzymatic efficiency. Reductions in decomposition rates due to fire were more evident in mesophytic species than in upland oak species. This combination of results suggests that while restoration increases enzymatic efficiency in years between burns, a fire in a given year can override any effect of past restoration treatment on the enzymatic efficiency of decomposition in these woodlands.

Furthermore, decreases in litter abundance following fire, coupled with increased decomposition in years between fires and decreased litter inputs from the thinned canopy should increase solar penetration to the understory and soil layers and promote regeneration of shade-intolerant species that once dominated these ecosystems.

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I. INTRODUCTION

Decomposition of leaf litter is a critical process in the cycling of nutrients and carbon through an ecosystem. Microorganisms degrade components of leaf litter such as lignin and cellulose through the production of extracellular enzymes (Skujins, 1976; Sinsabaugh et al., 1994; Kirchman, 2012). In addition to providing carbon to the microbial community, this degradation can also release organically bound nutrients (N, P) to the soil. Leaf litter is the most important input of nutrients to forests, contributing 69-87% of the nutrients needed each year (Waring & Schlesinger, 1985). However, changes in biotic factors such as dominant vegetation type and litter quality, as well as in abiotic factors such as moisture availability, solar penetration, salinity, pH, and nutrient status can affect microbial enzyme activity, and thus impact decomposition rates (Elliot et al., 1993; Sinsabaugh et al., 2008; Jackson & Vallaire, 2009). At a broader scale, climate is also important, and warmer and wetter environments typically have a higher rate of decomposition than cooler and drier environments (Moore, 1986; Dilly & Munch, 1996).

Open oak woodlands, once characteristic of much of the interior of the southern USA, are rapidly being lost to mesophication. Mesophication leads to changes in plant community composition (Abrams & Downs, 1990; Cain & Shelton, 1994; Brewer, 2001), and the process also has the potential to change rates of decomposition and nutrient cycling in these forests (Giai & Boerner, 2007; Rietl & Jackson, 2012). When fire is suppressed, mesophytic shade-tolerant and fire-intolerant seedlings are allowed to thrive and these species can become dominant

components of the plant community (Abrams & Downs, 1990; Platt, 2007; Nowacki & Abrams, 2008). Mesophytic species such as sweetgum (*Liquidambar styraciflua)*, winged elm (*Ulmus alata)*, and red maple (*Acer rubrum*) are now common in what were historically oak uplands, even though these species were once limited to lowland areas near fire breaks and other moist environments (Abrams, 1998; Nowacki & Abrams, 2008; Surrette et al., 2008; Kreye et al. 2013). As fire suppression continues and the prevalence of these mesophytic species increases, the canopy becomes more closed, preventing sunlight from reaching the forest floor. These increasingly shady conditions further promote the growth and recruitment of mesophytic species, resulting in positive feedback that continues the closing of the canopy (Nowacki & Abrams, 2008).

Tree species can alter local environmental conditions and rates of nutrient cycling to positively influence their resource use strategies (Mitchell et al., 2007; Ayers et al., 2009; Miki et al., 2010; Aponte et al., 2013). Tree litter characteristics (size, shape, flammability) can also alter the fire regime and fire behavior (Engber & Varner, 2012). Thus, prior to mesophication, rates of nutrient cycling and fire frequency in upland oak forests were likely at levels that selected for the existing plant community (e.g. fire occurring every 2-5 year; Fowler & Konopik, 2007). However, fire suppression changed these systems and resulted in the continuing transition from upland oak species to mesophytic species, with positive feedback furthering the dominance of mesophytic species. Restoration projects attempt to ameliorate the effects of almost a century of fire suppression, and include the removal of mesophytic species to thin the canopy, along with a prescribed burn regimen to shift the plant community to a fire tolerant and dependent one (Higgs, 1997; Ryan et al., 2013). Despite the growing popularity of these restoration projects, and their marked success in restoring oak regeneration and plant communities (Laatsch & Anderson,

2000; Brewer & Menzel, 2009; Arthur et al., 2012; Brose et al., 2013; Kinkead et al., 2013; Brewer et al., 2015), it is unclear what effect restoration (or, for that matter, mesophication) has on the decomposition of leaf litter, nutrient cycling, and soil microbial activity. This is despite the fact that impacts of restoration on decomposition rates can be significant at the ecosystem level (Hernández & Hobbie, 2008).

This study compared leaf litter decomposition rates between upland and mesophytic tree species, and determined how these decomposition rates differed in restored and unrestored portions of an upland oak forest. Four primary questions were investigated:

1. How does restoration treatment (burning) affect decomposition rates of litter?

It is hypothesized that a current year prescribed burn will affect microbial communities primarily through mortality (Pietikäinen & Fritze, 1995; Neary et al., 1999), which will decrease decomposition because of overall reduced activity of decomposer microorganisms. Prescribed fire may also affect the decomposition of litter through the flush of nutrients added to the forest floor after a burn, thus affecting activity of microbial decomposers, or by the addition of charcoal to the soil (Wardle et al., 2008; Rietl & Jackson, 2012).

2. How does decomposition differ in litter from different tree species (oak vs. mesophytic)?

The chemical composition of leaf litter varies by tree species which influences litter decomposition rate, and presumably associated microbial enzyme activity. Oak tree species are often considered to have low-quality litter, and contain high concentrations of recalcitrant materials such as lignin and tannins, and has a high C:N ratio (White, 1987; Carreiro et al., 2000). Several mesophytic species are known to produce more high-quality litter, which is more

nutrient rich (lower C:N ratio), and has a lower concentration of lignin and more easily degraded materials (White, 1987; Carreiro et al., 2000). High-quality litter decomposes more quickly than low-quality litter (Strickland et al., 2009), thus it is hypothesized that mesophytic leaf litter will decompose at a higher rate than upland oak leaf litter.

3. How does history of restoration affect the decomposition rates of litter?

In upland oak systems, restoration activities have led to greater canopy openness and greater sunlight penetration to the understory, and decreases in the amount of litter fall due to fewer canopy trees. Thus, it is hypothesized that the effects of restoration on decomposition will be consistent regardless of how old the restoration treatment is. Alternatively, there could be cumulative effects of prescribed fire that mount to alter nutrient availability or shape decomposer microbial communities over longer periods of time that will affect decomposition rates differently in younger restoration plots than in older ones.

4. Can differences in decomposition rates be related to enzyme activity?

Assays of the activity of extracellular enzymes are an established method to gain a better understanding of the microbial community, their metabolic activity, and the type of nutrients and substrates that are present or limiting in an environment (Burns, 1982). Potential extracellular enzyme activity has also been related to decomposition rates (Sinsabaugh et al., 1994; Jackson et al., 1995; Carreiro et al., 2000, Jackson & Vallaire, 2007), has been used as a way to describe the quality and health of an ecosystem (Jordan et al., 1995; Dick, 1997), and is known to vary depending on ecosystem type and management of an area (Bandick & Dick, 1999). In this study, it is hypothesized that enzyme activity will reflect site nutrient availability (which is potentially

altered by fire and restoration history), as well as by litter quality (which is an effect of tree species).

II. METHODS

Study Area

The study was conducted at Strawberry Plains Audubon Center in Holly Springs, Mississippi, USA. The Center is characterized by rolling hills with mesic silt and sandy loamy soils (Brewer, 2001). Two sites (Site 1: 34°49'60"N, 89°28'32"W and Site 2: 34°49'52"N, 89°27'17"W), approximately 1 km apart, were established at this site in 2004 for an experimental restoration project that aimed to reduce mesophytic tree density, to increase the abundance of open woodland plant species, and to restore natural regeneration and recruitment of upland oak tree species (Surrette et al., 2008; Brewer & Menzel, 2009). Neither site had experienced prior anthropogenic disturbance, although cotton was once grown in a low lying area adjacent to both sites, up until the 1950's. Both sites are historically upland oak dominated forests and contain mature oak trees over 100 years old. However, when the restoration project was implemented the sites were characterized by a closed canopy deciduous forest of both mature oaks and mesophytic tree species, with very little understory vegetation (Surrette et al., 2008).

Restoration treatments have occurred in a chronosequence of treatment history within each site. At Site 1, thinning treatment began in 2004 at the southern end of the site followed by prescribed burns in 2004 and 2006. In 2008, the section to the north was thinned, and the entire thinned area was burned. Additional thinning to the north end followed by burning of the entire area occurred again in 2010 and continued with fire only in 2012 and 2014. Site 2 was treated in the same manner as Site 1, with treatment starting in 2008 at the western edge of the site and continuing to the east in 2010 and 2012. Thus, both sites contain sections at different stages of

the restoration process, with the initially treated sections having received three or more burn treatments. We refer to these sections as the “old” section (thinned and three or more burns), the “new” section (the most recently thinned and having one or more burn), and the “control” section (no prior restoration treatment). Site restoration continues at both sites by prescribed burning every 2-4 years.

During this study, the prescribed burn on April 10, 2014 at Site 1 escaped containment and burned the control plot, in addition to the old and new portions of the treated plot. For this reason, the treated plot at Site 2 was not burned in April 2014 as initially scheduled. Not burning the treated plot at Site 2 provided an opportunity to examine the differences between the effects of past restoration treatments (thinning and repeated burning) and the effect of a single current year fire in 2014.

Determination of Leaf Litter Decomposition Rates

Leaves of six tree species (*Quercus stellata, Q. falcata, Q. alba, C. tomentosa, L. styraciflua,* and *U. alata*) were collected from both study sites in September through November 2013, using elevated litter traps to ensure that all leaf litter was from the current year. These species were selected based on being characteristic of upland oak woodlands (*Q. stellata, Q. falcata*), mesophytic areas (*U. alata, L. styraciflua*), or intermediate between these two extremes (*Q. alba, C. tomentosa*; Fralish et al., 2007; Brewer, 2001). Litter was air dried at room temperature for 10 d to equilibrate moisture content of leaves collected on different days from different sites. After that time, approximately 2 g leaves of each species was weighed and placed into a series of 25 x 25cm litterbags constructed of 2 mm fiberglass mesh. A larger sample of each species’ air dried leaves were weighed, oven-dried (75 ºC, 48 h) and reweighed to convert

air-dried mass to actual (oven-dried) mass. This ratio was used to calculate the initial dry mass in each litterbag.

Litterbags were placed in the old, new, and control sections of each site in December 2013. 120 litterbags (20 bags per species) were placed in each section for a total of 720 litterbags (120 bags x 3 sections x 2 sites). Placement and subsequent collection of the litterbags at the two sites were staggered 2 d apart to facilitate sampling and laboratory analyses. On each collection date, two litterbags for each tree species were collected from each section. Collections occurred on days 0 (in December 2013), 5, 28, 56, 105, 126, 154, 210, 280, and 343 (in November 2014), with the day 0 collections being used to correct for any losses from handling and litterbag placement. Litterbags were returned to the laboratory, and the contents weighed to determine field mass. A known mass of subsample (0.2-0.4 g) was removed for assays of microbial extracellular enzyme activity and the remaining leaf material weighed, oven dried (70 ºC, 48 h) and reweighed to determine dry mass remaining. Because Site 1 was scheduled to undergo a burn during the study, all litterbags at that site were transferred to an adjacent area prior to this event and then replaced 7 d after the fire. A set of bags (the 126 d sample, April 2014) were then collected and processed to account for potential effects of this procedure. While Site 2 was not burned, the procedure used at Site 1 was repeated there for experimental consistency.

Assays of Extracellular Enzyme Activity

The potential activity of hydrolytic enzymes related to the acquisition of carbon (β-glucosidase, *N*-acetyl-β-D-glucosaminidase (NAGase, through degradation of chitin), cellobiohydrolase (CBH)), nitrogen (NAGase), or phosphorus (phosphatase) was assayed using *p*-nitrophenyl (*p*NP)-linked substrates following the procedures of Jackson et al. (2013). In

addition, the activity of oxidative enzymes related to lignin degradation (phenol oxidase, peroxidase) was measured using 3,4-dihydroxyl-L-phenylalanine (L-DOPA) (Jackson & Vallaire, 2007). 0.2-0.4 g of recovered litter was coarsely chopped with sterile scissors, and then homogenized in 0.5 M pH 5.0 sodium acetate buffer to form a slurry. 150 µl aliquots of each slurry were used in assays of activity (three replicates per sample) or controls (two replicates per sample). Assay reactions received slurry plus 150 µl of the respective substrate, with the peroxidase assay plate also receiving 15 µl of 0.3% H_2O_2. Control reactions received 150 µl acetate buffer instead of substrate. Reactions were incubated at room temperature for 0.5-4 h, and then centrifuged (5,000 x g, 10 min). 100 µl of supernatant was transferred to microplate wells containing 10 µl of 1M NaOH and 190 µl H_2O for *p*NP-linked substrates or 200 µl of H_2O for L-DOPA substrates. Activity was determined from absorbance at 410 nm (*p*NP-linked substrates) or 460nm (L-DOPA) using a BioTek Synergy HT microplate spectrophotometer. Final potential activity was expressed as µmoles substrate consumed h^{-1} g^{-1} dry weight of sample.

Comparisons to In Situ Leaf Litter

To assess the amount of leaf litter at each site, and to determine if microbial enzyme activity on leaf litter in litterbags was representative of that associated with unconfined litter material, leaf litter was collected from each site in April, June, and September 2014. On each date, five 0.5 x 0.5 m quadrats were placed in each experimental section. Average litter depth was measured with a ruler. All of the leaf litter in each quadrat was then collected and weighed using a digital hanging scale. After weighing, litter from three of these quadrats in each section was placed back in their original location (to minimize disturbance to the system), while the litter from the two quadrats with the greatest litter mass was collected. Leaves were sorted to tree

species and the total weight for each species recorded. For the April and September *in situ* collections, a subsample of leaves from each of the six tree species of interest was assayed for extracellular enzyme activity as described above. The remaining litter material was oven dried (70 ºC, 48 h) and reweighed to convert field determined mass to dry mass.

Data Analysis

Decomposition rates of leaf litter were determined using linear regressions of the percent of initial dry mass remaining against time. Linear models provided as good or better fits than exponential or second order polynomial models. Differences in decomposition rates and enzyme activities between the two sites were analyzed using analysis of variance (ANOVA) with site, treatment history, and litter species as factors along with all interactions between these factors. Site was the dominant significant factor, so following analyses were conducted on each site separately. Since Site 1 was burned and Site 2 was not, site was also used to describe the effect of current year fire on decomposition rates and enzyme activities.

Potential activity for each enzyme over days in the field was plotted to obtain enzyme activity trends over the course of the study. Cumulative enzymatic activity for each enzyme was calculated as the mean activity between sample points, summed over all previous sample intervals (Sinsabaugh et al., 1994; Jackson et al., 1995; Rietl & Jackson, 2012). All enzymes were then combined into a model depicting an integrated index of microbial activity. Activity of each enzyme was standardized to a scale of 0-1 by dividing the activity for a specific enzyme on a sample date by the maximum activity of that enzyme over the course of the entire study (Sinsabaugh et al., 1994; Jackson et al., 1995; Rietl and Jackson, 2012). An average activity was obtained from the standardized values of the six enzymes on a particular date. Simple linear

regressions were used to relate % mass loss as a function of total cumulative activity for each species, site, and treatment history. This relationship of decomposition rate to enzyme activity is a measure of the apparent enzymatic efficiency (AEE) of those enzymes in the decomposition process (Sinsabaugh et al., 1994). Planned contrasts were used to determine significant differences in decomposition rate and AEE between the predicted groups of upland oak species' litter (*Q. stellata* and *Q. falcata*) and mesophytic species' litter (*U. alata* and *L. styraciflua*), followed by one-way ANOVA comparisons between the two species in each group. Contrasts were again employed using site treatment history as a factor comparing "control" vs. "treated" (new and old plots) followed by one-way ANOVA between the decomposition rates and AEE of new and the old plots.

Enzyme activity associated with *in situ* litter was compared to that of litter in litterbags assayed on the nearest sampling date using ANOVA with site, species, and *in situ*/litterbag as factors in addition to the interactions between these factors. The wet/dry ratio was applied to all field weights. Litter volume was calculated as litter depth (cm) x 50cm x 50cm and used to calculate litter layer density as dry g volume^{-1}.

III. RESULTS

Leaf Litter Decomposition Rates

Mass loss of leaf litter was generally linear over the course of the study, and thus the decomposition rate constant (k) could be expressed as % mass loss d^{-1} (illustrated in Appendix 1). A few dates yielded mass remaining ≥100% of the initial mass (largely because of bound inorganic material) and these dates were considered erroneous and not included in rate calculations. While factors of treatment history ($F_{2,46} = 5.04$, $p = 0.010$) and litter species ($F_{5,46} = 4.03$, $p = 0.004$) were significant, site was by far the most significant ($F_{1,46} = 46.37$, $p < 0.001$) and was significant in site x treatment history ($F_{2,46} = 3.98$, $p = 0.025$) and site x species ($F_{5,46} = 4.19$, $p = 0.003$) interactions (Appendix 2). This suggested site to be the primary factor in determining decomposition rate and that sites could be analyzed separately. To determine if site differences were due to the prescribed burn or pre-existing site differences, decomposition rates were calculated for both the entire time period of the study (through d 343, November 2014), and for up to the burn event (through d 126, April 2014). Decomposition rates up to the prescribed burn were significantly greater at Site 1 than Site 2 ($k = 0.091$ and 0.066, respectively; three-way ANOVA, $F_{1,63} = 9.46$, $p = 0.003$, Fig. 1). However, when calculated over the entirety of the study this pattern was reversed, and decomposition rates at Site 1 were lower than those at Site 2 as previously stated (ANOVA, $p < 0.001$, Fig. 1). Because of these differences, subsequent analyses examined the sites separately.

Within each site, leaf species was a significant factor influencing decomposition rate (two-way ANOVA, Site 1 $F_{5,28} = 4.03$, $p = 0.007$, Site 2 $F_{5,28} = 3.98$, $p = 0.007$). Paired

contrasts were used to compare the upland oak species *Q. stellata* and *Q. falcata* against the mesophytic species *U. alata* and *L. styraciflua*. At Site 1, the upland oak species decomposed faster than the mesophytic species (k = 0.093±0.007 and 0.068±0.005, respectively; p = 0.006, Fig. 2a). Within these pairs, *U. alata* and *L. styraciflua* did not differ from each other in decomposition rate (p = 0.853). However, *Q. falcata* decomposed at a higher rate than *Q. stellata* (k = 0.109±0.007 vs. 0.078±0.007, p = 0.014, Fig. 2a). At Site 2 there was no difference in k between upland oak species and mesophytic species (k = 0.106±0.007 and 0.099±0.014, respectively; p = 0.241), although there was a difference in decomposition rates between the two mesophytic species, with *U. alata* (k = 0.089±0.007) decomposing slower than *L. styraciflua* (0.109±0.007; p = 0.018). *Q. falcata* had lower decomposition rates than *Q. stellata* at this site, although this difference was not quite significant (k=0.098±0.003 and 0.112±0.007, p=0.089, Fig. 2b). In terms of restoration treatment history, at Site 1 leaves in the new and old treated plots did not have different decomposition rates in a contrast against the control plot (p = 0.367), although the old plot did have higher decomposition rates than those in the new plot (k = 0.094±0.005 and 0.072±0.006, respectively; p = 0.017). Restoration treatment history had no effect on the decomposition rate of leaves at Site 2 (old plot k = 0.108±0.006, new plot k = 0.111±0.003, control plot k = 0.099±0.005, p = 0.158).

Assays of Extracellular Enzyme Activity

Patterns in enzyme activity generally corresponded to changes in season rather than site, treatment history, or leaf litter species. Activity increased initially from December through January or February, followed by a decrease in activity to a low point in May or July, before again increasing through the end of the study in November (Appendix 3).

Phosphatase activity was higher at Site 2 than at Site 1 (ANOVA, $F_{1,46} = 46.89$, $p < 0.001$), although factors of species and treatment history were also significant ($F = 14.19$ and 17.35, $p < 0.001$ and 0.001 respectively), as was the site x treatment history interaction ($F_{2,46} = 10.37$, $p < 0.001$). Cumulative phosphatase activity tended to be highest in the control plots for all species' litter, though this trend was most apparent at Site 2. Cumulative phosphatase activity was positively correlated with cumulative phenol oxidase activity ($r^2 = 0.717$) which showed a similar pattern of higher activity in the control plot (Appendix 4). Activities of β-glucosidase, CBH, and NAGase were all positively correlated ($r^2 = 0.72$-0.92 for pairwise comparisons) and showed higher cumulative activity at Site 1 than at Site 2; these differences being either significant or near significant (β-glucosidase $p = 0.052$, CBH $p = 0.046$, NAGase $p = 0.062$). Cumulative peroxidase activity was not correlated with any other enzyme ($r^2 < 0.55$ for all comparisons), but litter decomposing at Site 1 had substantially higher peroxidase activity than Site 2 (ANOVA, $p < 0.001$).

Relationships between Enzyme Activity and Decomposition Rate

Linear regressions were calculated to relate cumulative activity of each enzyme to decomposition of each litter species at each site and level of restoration (Appendix 4). Other than peroxidase, all regressions were at least a good fit ($r^2>0.70$). The slope of these regressions of mass remaining vs. cumulative enzyme activity is the effective AEE of an enzyme in the decomposition process, and sites 1 and 2 were significantly different from each other in AEE for every enzyme ($p < 0.001$) with the exception of phenol oxidase, which was almost significant ($p < 0.057$). Activities of the four hydrolytic enzymes were all highly correlated with k (phosphatase $r^2 = 0.69$, β-glucosidase $r^2 = 0.77$, CBH $r^2 = 0.78$, NAGase $r^2 = 0.76$), while

cumulative activities of the oxidative enzymes (phenol oxidase, peroxidase) explained less of the variation in *k* (r^2 = 0.45 and 0.56, respectively).

Combined AEE for all species of leaf litter was higher at Site 2 than at Site 1 (0.40 ±0.018 vs. 0.30±0.014, $p < 0.001$). Leaf species ($p < 0.001$) had a significant effect on AEE at Site 1 while treatment history did not ($p = 0.94$). AEE was not significantly different between mesophytic and upland oak species at this site ($p = 0.289$, Fig. 3a), although there were differences between individual tree species within these classifications, with higher AEE for *Q. falcata* litter compared to that of *Q. stellata* ($p = 0.045$), and for *L. styraciflua* than *U. alata* ($p = 0.009$). Restoration history was not a significant effect on AEE at Site 1 (ANOVA, $p = 0.175$). Cumulative AEE for upland oak species and mesophytic species at Site 2 was also similar ($p = 0.974$), but as with Site 1 there were differences between individual species in each category, with *L. styraciflua* litter having higher AEE than that of *U. alata* ($p < 0.001$) and the AEE on *Q. stellata* litter being almost significantly higher than that of *Q. falcata* ($p = 0.080$). More importantly, treatment history was a significant factor at Site 2, with the new and old plots having higher overall AEE compared to the control ($p = 0.006$).

In Situ Leaf Litter Abundance

Pre-burn litter depth was greater at Site 1 than Site 2 (mean depth = 6.6±0.3 cm vs. 5.3±0.6 cm, respectively; $p < 0.001$, Fig. 4a and 4b). Treatment history differences were only apparent at Site 2, where the litter layer was deeper in the control plot compared to the new or old restoration plots (depths = 7.2±0.2, 4.3±0.3 and 3.0±1.0 cm, respectively; $p < 0.001$). This trend of deeper litter in the control vs. the other two treatments continued for all three *in situ* collections (Fig. 4b). While Site 1 did not show any differences in litter depth between treatment

history plots, there were differences in litter density (dry g volume^{-1}), which was highest in the control plot and lowest in the new and old restored plots (density = 0.017±0.001, 0.012±0.001, and 0.008±0.001 g cm^{-3}, respectively; $p < 0.05$, Fig. 4c). Although litter depth at this site decreased drastically after the prescribed burn, litter density actually increased (Fig. 4a and 4c). Litter density at Site 2 was greatest in the control and new plots, and lower in the old plot (density = 0.018±0.002, 0.020±0.004, and 0.006±0.002 g cm^{-3}, respectively; $p = 0.021$, Fig. 4d).

Enzyme Activities on In Situ Leaf Litter

Pre-burn *in situ* samples of leaf litter showed higher enzymatic activity than litter bag samples for all six enzymes at Site 1. At Site 2, enzyme activity was higher in *in situ* than in litter bag litter for some species and some enzymes, but lower than in litter bag litter for others.

During the final *in situ* sampling, activity of phosphatase, β-glucosidase, NAGase, and phenol oxidase did not differ between litter *in situ* and litter in decomposition bags at Site 1 (two-way ANOVA, $p = 0.52$, 0.74, 0.78, 0.44, respectively). However CBH activity was higher in bagged litter than *in situ* litter (activity = 6.70±0.44 and 3.92±0.41 μmoles h^{-1} g^{-1}, respectively; two-way ANOVA $p < 0.001$), as was the activity of peroxidase (activity = 4.03±0.46 and 1.48±0.42 μmoles h^{-1} g^{-1}, respectively; two-way ANOVA $p < 0.001$). At Site 2, enzyme activity was higher in litter bags than in *in situ* litter for phosphatase (though only in *Q. falcata* and *Q. stellata* litter), β-glucosidase (activity of 48.15±2.18 and 33.65±2.76 μmoles h^{-1} g^{-1}, respectively; two-way ANOVA $p < 0.001$), CBH (10.78±0.48 and 7.70±0.77, μmoles h^{-1} g^{-1}, respectively; two-way ANOVA $p = 0.007$), and peroxidase (1.21±0.22 and 0.36±0.14 μmoles h^{-1} g^{-1}, respectively; two-way ANOVA $p = 0.001$). Activity did not differ between litter bags and *in situ* litter for NAGase or phenol oxidase (two-way ANOVA, $p = 0.76$ and 0.79).

IV. FIGURES

Fig. 1. Mean decomposition rates for leaf litter of six tree species (*Ulmus alata*, *Liquidambar styraciflua*, *Carya tomentosa*, *Quercus alba*, *Quercus falcata*, *Quercus stellata*) in two upland oak woodland sites (Site 1, 2) undergoing ecological restoration. Pre-Burn indicates mass loss data from December 2013 through April 2014, when Site 1 (shaded bars) was burned, while Site 2 (open bars) was not. Post-Burn indicates mass loss data from April 2014 through November 2014. Whole Study includes mass loss data from December 2013 through November 2014. Decomposition rate is expressed as % original mass lost per day and bars represent mean (±SE) decomposition rate across all species and replicates (n = 36).

Fig. 1.

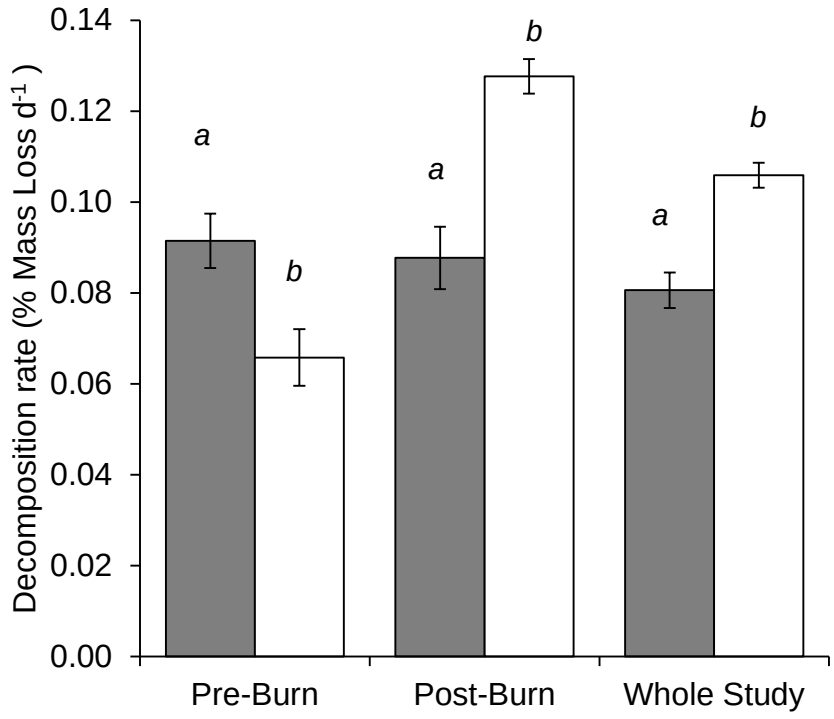


Fig. 2. Species-specific decomposition rates (in % original mass lost per day) for leaf litter of six tree species (*Ulmus alata, Liquidambar styraciflua, Carya tomentosa, Quercus alba, Quercus falcata, Quercus stellata*) in two upland oak woodland sites (Site 1, 2) undergoing ecological restoration. Each site consisted of "control" plots (open bars) that had no restoration, "new" plots (gray bars) that had experienced more recent mechanical thinning and 1-2 prescribed burns, and "old" plots (black bars) that had experienced mechanical thinning and 3+ prescribed burns. Site 1 (a) was treated with a prescribed burn during the study, while Site 2 (b) last experienced a prescribed burn four years prior and had higher overall decomposition rates ($p < 0.001$). Within each site, lower case letters indicate the results of paired contrasts to examine differences between decomposition rates of the upland oak species (*Q. falcata, Q. stellata*) vs. mesophytic species (*U. alata, L. styraciflua*) which were $p = 0.006$ for Site 1, and $p = 0.241$ for Site 2 ($n = 24$ for each comparison), followed by contrasts within those two groups (*Q. falcata* vs. *Q. stellata* Site 1 $p = 0.014$, Site 2 $p = 0.089$; *U. alata* vs. *L. styraciflua* Site 1 $p = 0.853$, Site 2 $p = 0.018$, $n = 12$ for each). There was no consistent difference in decomposition rates between the treated and control plots ($p = 0.488$).

Fig. 2.

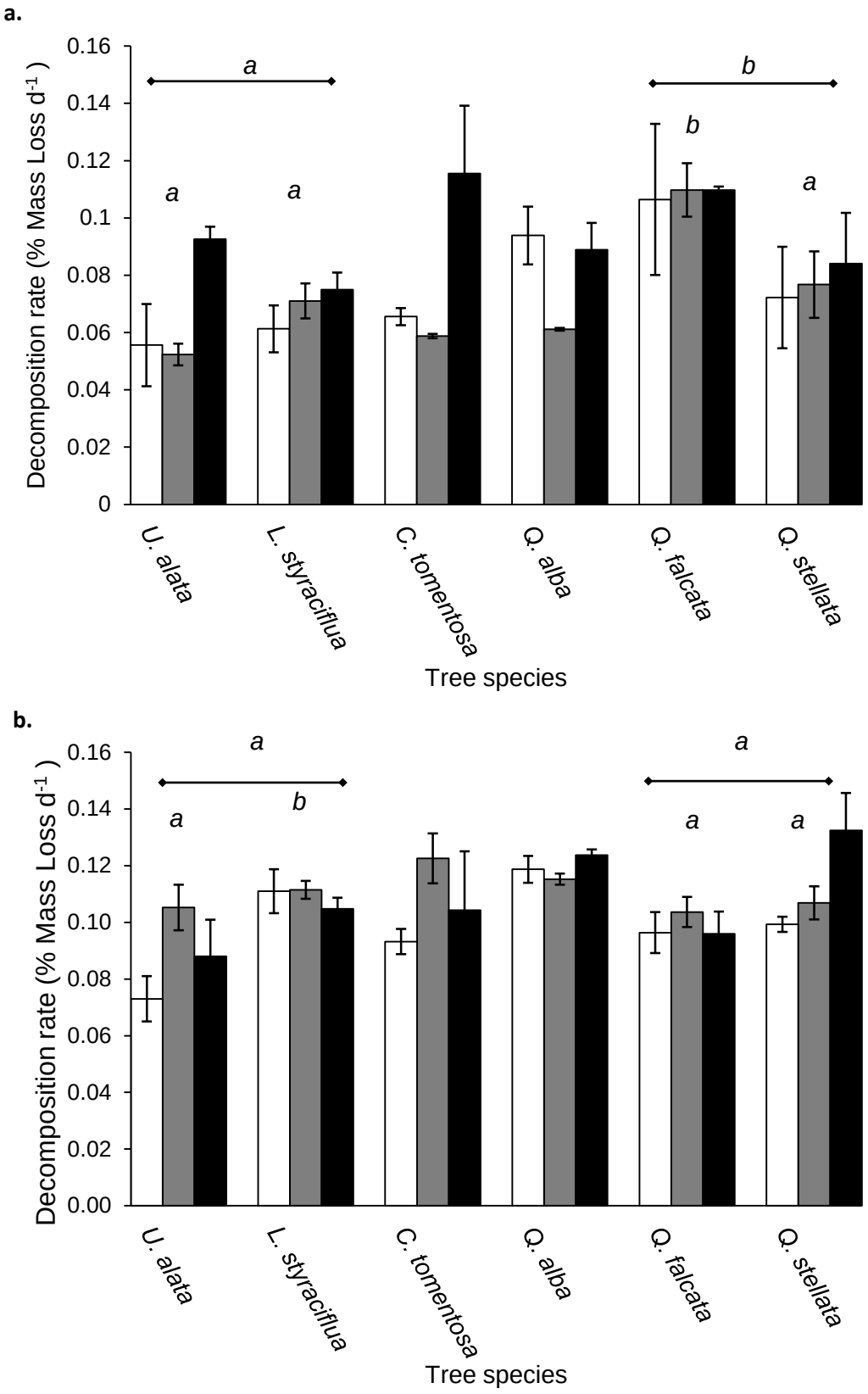
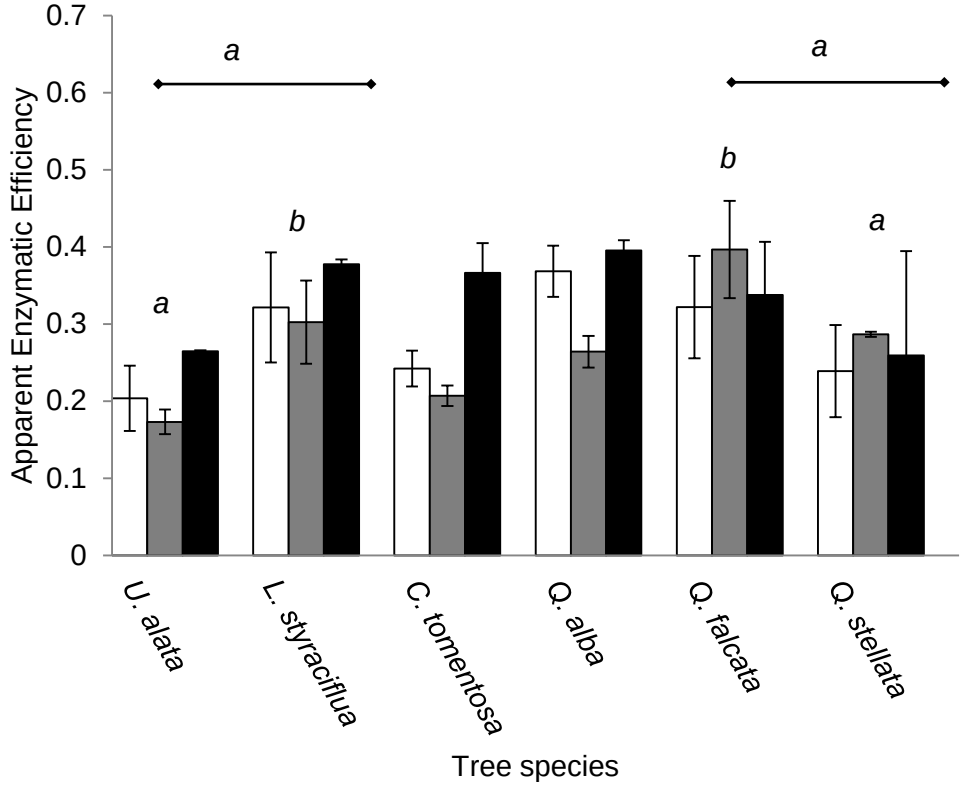

a.
Decomposition rate (% Mass Loss d-1)
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
a
b
a
a
b
a
U. alata
L. styraciflua
C. tomentosa
Q. alba
Q. falcata
Q. stellata
Tree species
b.
Decomposition rate (% Mass Loss d-1)
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0.00
a
a
b
a
a
a
U. alata
L. styraciflua
C. tomentosa
Q. alba
Q. falcata
Q. stellata
Tree species

Fig. 3. Cumulative apparent enzymatic efficiency (AEE, expressed as mass loss per unit enzyme activity) for six species of leaf litter (*Ulmus alata, Liquidambar styraciflua, Carya tomentosa, Quercus alba, Quercus falcata, Quercus stellata*) decomposing in two upland oak woodland sites undergoing ecological restoration. Each site consisted of "control" plots (open bars) that had no restoration, "new" plots (gray bars) that had experienced mechanical thinning and 1-2 prescribed burns, and "old" plots (black bars) that had experienced mechanical thinning and 3+ prescribed burns. Site 1 (a) was treated with a prescribed burn during the study, and had lower AEE ($p < 0.001$) than Site 2 (b) which last experienced a prescribed burn four years prior. For each site, lower case letters indicate the results of paired contrasts to examine differences in AEE between the upland oak species (*Q. falcata, Q. stellata*) vs. mesophytic species (*U. alata, L. styraciflua*) which were $p = 0.289$ for Site 1 and $p = 0974$ for Site 2 ($n = 24$ for each comparison), followed by contrasts within those two groups (*Q. falcata* vs. *Q. stellata* Site 1 $p = 0.045$, Site 2 $p = 0.080$; *U. alata* vs. *L. styraciflua* Site 1 $p = 0.009$, Site 2 $p < 0.001$, $n = 12$ for each). Control plots had lower AEE than the new or the old plots at Site 2 ($p = 0.006$).

Fig. 3.

a.


Apparent Enzymatic Efficiency
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
a
a
a
b
b
a
U. alata
L. styraciflua
C. tomentosa
Q. alba
Q. falcata
Q. stellata
Tree species

b.

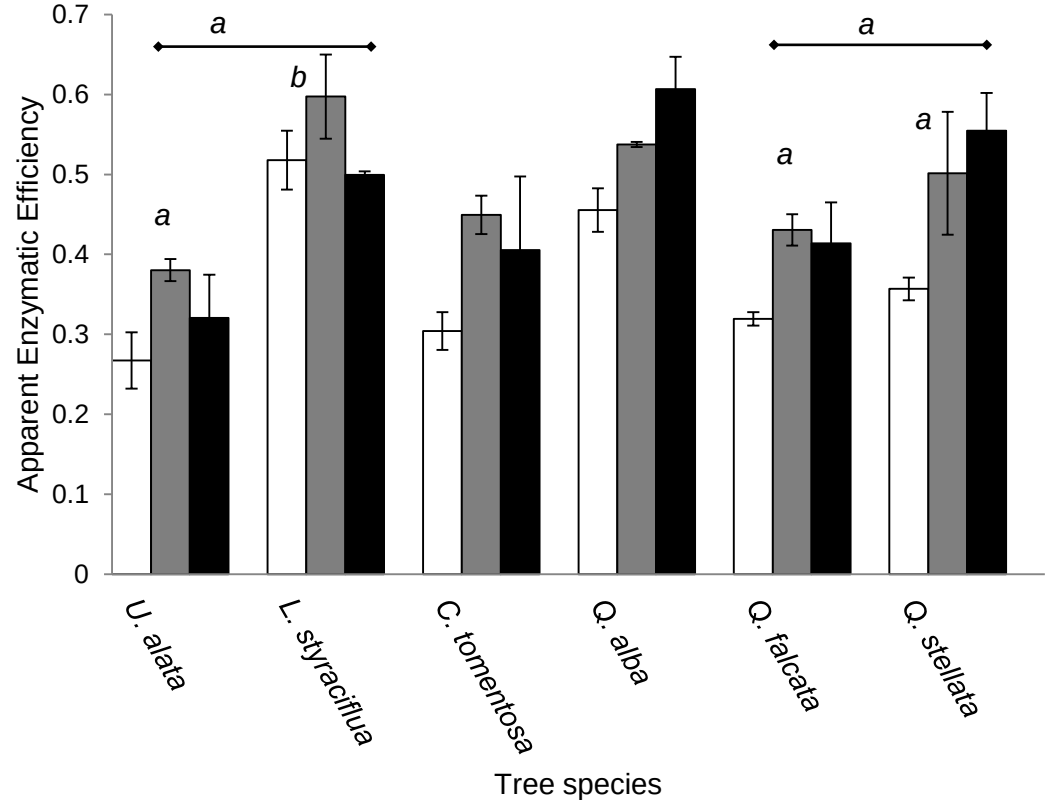
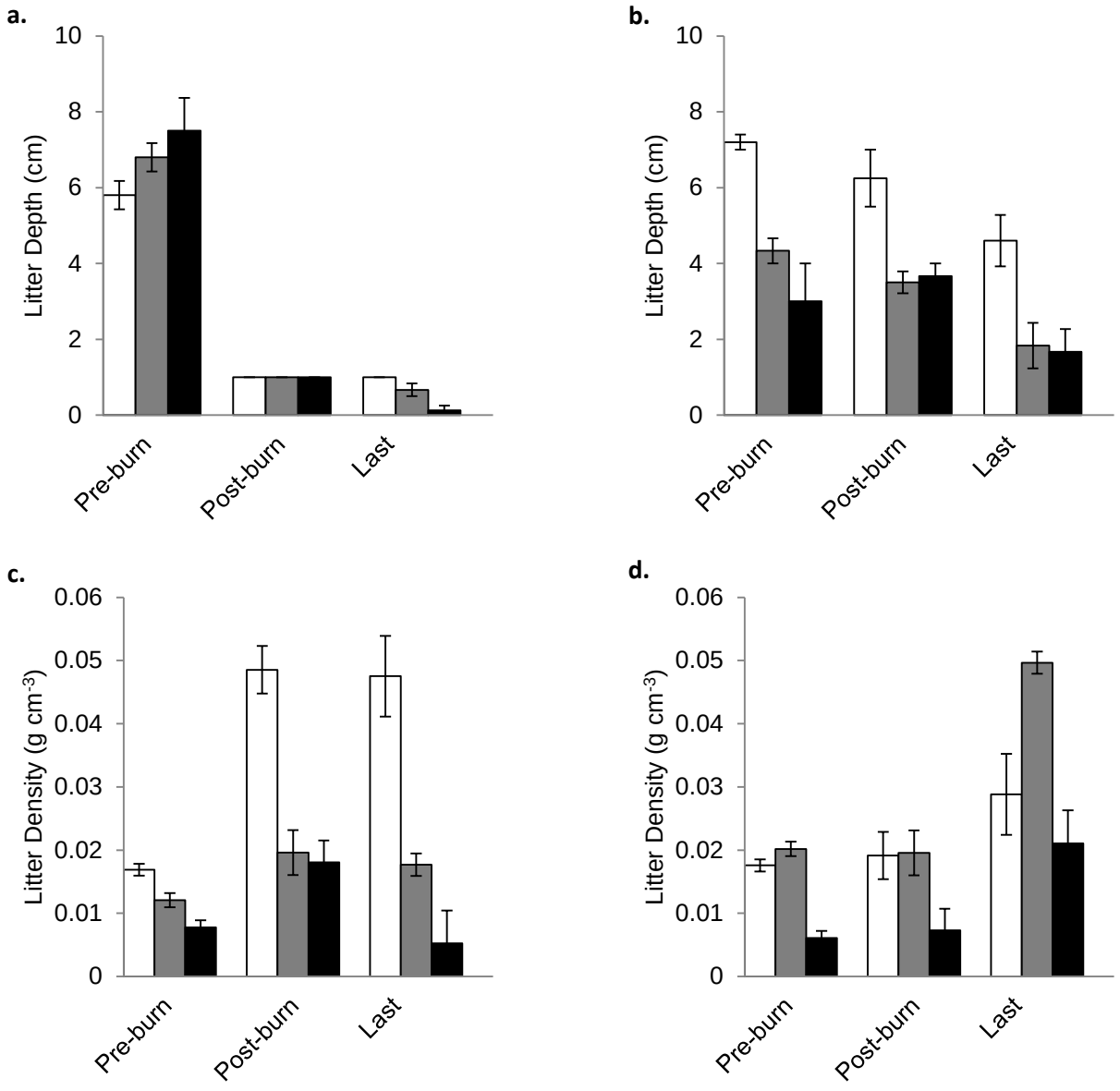

Apparent Enzymatic Efficiency
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
a
a
a
b
a
a
U. alata
L. styraciflua
C. tomentosa
Q. alba
Q. falcata
Q. stellata
Tree species

Fig. 4. Leaf litter depth (a, b) and litter layer density (c, d) at two sites (Site 1, 2) in an upland oak woodland undergoing ecological restoration. Each site consisted of "control" plots (open bars) that had no restoration, "new" plots (gray bars) that had experienced mechanical thinning and 1-2 prescribed burns, and "old" plots (black bars) that had experienced mechanical thinning and 3+ prescribed burns. Site 1 (a, c) was treated with a prescribed burn during the study (April 2014), while Site 2 (b, d) last experienced a burn four years prior. In each case, Pre-burn indicates litter depth in March 2014, Post-burn in June 2014, and Last in September 2014.

Fig. 4.


a.
b.
c.
d.
Litter Depth (cm)
Litter Density (g cm-3)
0
2
4
6
8
10
0.01
0.02
0.03
0.04
0.05
0.06
Pre-burn
Post-burn
Last

V. DISCUSSION

In this study I compared decomposition rates and enzyme activities between mesophytic and upland oak tree litter in woodlands treated with a prescribed burn as well as in woodlands that were not burned. I aimed to answer four primary questions:

1. How does fire affect decomposition rates of litter?

Before the prescribed burn, mean leaf litter decomposition rates were 28% higher at the woodland to be burned (Site 1) than at the unburned woodland (Site 2). However, after the burn this pattern was reversed with mean decomposition rates at Site 1 being 31% lower than those at Site 2. This pattern suggests that the prescribed fire substantially reduced the rate of decomposition for remaining litter. A potential explanation for this observation could be microbial decomposer mortality from fire (DeBano et al., 1998), especially fungi. Fungi are critically important in the degradation of leaf litter, and are more susceptible to heat mortality than bacteria (Pietikäinen & Fritze, 1995; Hart et al., 2005). A decrease in microbial (and especially fungal) abundance following fire would presumably lead to decreases in microbial activity and therefore decomposition rates. The conversion of leaf litter to ash following fire also alters the physical and chemical characteristics surrounding the remaining leaf litter (Ryu et al., 2009), which could also impact decomposition rates. Litter remaining after burning was clearly affected by the fire event that occurred during the study at Site 1, especially in the control plot. While the depth of litter was reduced, the density of leaf litter increased dramatically post-burn.

Remaining leaves were often charred and partially consumed by fire, reducing their size, degree of curling, and the formation of air spaces in the litter layer. There were also decreases in litter depth and increases in litter density at Site 2, although these changes were less dramatic than those associated with burning, and likely arose from the reduction of leaf size and structure over the decay process.

2. *How does decomposition differ in litter from different tree species (upland oak vs. mesophytic)?*

Decomposition rates of the upland oak species (*Q. falcata* and *Q. stellata*) were higher than the mesophytic species (*U. alata* and *L. styraciflua*) in the burned Site 1. Oak trees are heliophytic, requiring open canopies and sunlight to be successful, and thus are poor competitors compared to mesophytic tree species in shady conditions. Since upland oaks are adapted to nutrient poor conditions and open canopies, their litter would be conducive to inhibiting competing tree species (e.g. through the promotion of fire) and by adding their nutrient poor leaf litter to the soil organic layer, further continuing the prevalence of nutrient poor soil (Van Nevel et al., 2014). Slowly decomposing leaf litter leads to the accumulation of deep, nutrient and moisture retaining soils more favorable to mesophytic species (Aponte et al., 2013).

Faster decomposition rates in oak litter also suggests the possibility of specialized microbial communities that can decompose litter high in tannins, which can otherwise inhibit microbial enzyme activity (Harrison, 1971; Hart et al., 2005). Given the faster decomposition rates of oak litter in burned areas, it is possible that oak litter decomposition at least partially occurs through the action of bacteria, which are generally more heat-tolerant than fungi (Neary et al., 1999; Christian, 2000; Hart et al., 2005) and are more abundant, relative to fungi, after fire

(Pietikäinen & Fritze, 1995). Thus, following fire, upland oak leaf litter might continue to decompose through surviving bacterial activity while mesophytic litter decomposition slows from a loss of fungal decomposers. Over a period of continued prescribed burning, soil and litter microbial communities may shift toward one shaped by the periodic death of fungal and bacterial decomposers and the presence of oak-specializing microorganisms (Hart et al., 2005). While bacteria may be important in fire-dominated systems, fungi are more commonly considered as key factors in litter decomposition and produce a variety of extracellular enzymes that allow them to break down otherwise recalcitrant materials (Kjoller & Struwe, 1982; de Boer et al., 2005). Increased enzymatic efficiency at the unburned Site 2 compared to Site 1 could be indicative of a lack of fungal mortality through fire, allowing fungi to continue efficiently degrading leaf material.

Within the upland oak species, *Q. falcata* decomposed faster than *Q. stellata*. This result potentially relates to litter characteristics, as *Q. stellata*, which is the more fire-tolerant, xerophytic, and slower-growing of the two species, has thick, broad and recalcitrant leaves, compared to the thinner leaves of *Q. falcata*. At Site 2 there was no difference in decomposition rates between upland oak and mesophytic litter, furthering the evidence that more rapid decomposition of oak leaves depends on fire. Between the mesophytic species, *L. styraciflua* had a faster decomposition rate than *U. alata*, again most likely because of leaf characteristics as *L. styraciflua* produces thin and easily crumbled leaf litter.

An interesting trend was found in the decomposition rates of *Q. falcata*. While decomposition rates for all other species were higher at Site 2 than at Site 1 ($k = 0.107$ vs.0.075, $p < 0.001$, $n = 30$, Fig. 1), the opposite was true for *Q. falcata* where k was higher at Site 1 than Site 2, though this difference was not significant ($k = 0.109$ vs. 0.099, $p = 0.242$, $n = 6$). While

statistical power was lacking to analyze decomposition rates of all six species at both sites in comparison to each other, this trend in *Q. falcata* mirrors that noted in a previous study that found slightly higher decomposition rates of *Q. falcata* litter in plots treated with fire during the study period (Rietl & Jackson, 2012). This observation brings up the possibility that the decomposition of this species is specifically adapted to a frequent fire environment in ways that the other species, even other fire tolerant species such as *Q. stellata*, are not.

3. How does history of restoration affect the decomposition rates of litter?

There was no apparent effect of treatment history on decomposition rate of leaf litter, although all six species were combined for this analysis. There may, however, be treatment history effects on individual litter species. For example, at Site 1 there looks to be higher decomposition rates in the old burned plots for *U. alata* and *C. tomentosa* litter. However an analysis at the fine scale of individual species at one site in one treatment would rely on a very small sample size (n =2), and was not performed because of those statistical limitations.

4. Can differences in decomposition be related to enzyme activity?

Current year prescribed fire was the most significant factor affecting leaf litter decomposition rates and enzymatic efficiency. The fire most likely led to decreased rates of decomposition and apparent enzyme efficiency at the burned site, while decomposition rates and AEE were greater at Site 2, which did not experience current year fire. Overall, enzymes were more efficient in degrading leaf litter at the unburned site than at the burned site; a result of lower k and slightly higher enzyme activity at the burned Site 1, and higher k and lower enzyme activity at unburned Site 2. Higher enzyme activity at Site 1 might be related to the presence of

charcoal produced by the burn, which can bind phenolic and aromatic compounds that otherwise inhibit enzymatic activity (Wetzel, 1992; Zachrisson et al., 1996). While an increase in enzyme activity would intuitively lead to an increase in decomposition rates, enzyme activity is only one component of a complex system, which might include differences in microbial community structure or altered environmental conditions. Litter at Site 2 had increased AEE in the old and new restored plots compared to the control plot, although this trend was not present at Site 1. This suggests that, in years between prescribed burns, enzyme efficiency increases in woodlands undergoing that type of restoration; but current year fire overrides any effect of prior restoration treatment on enzyme efficiency. When litter is allowed to breakdown solely through the process of decomposition, restoration practices may alter environmental conditions and microbial activity in favor of higher microbial AEE.

Phosphatase activities were highest at Site 2, particularly in the control plots. Phosphatase production is typically repressed when phosphorus is readily available (Sinsabaugh et al., 1993), and fire increases phosphorus availability in soils (Knoepp et al., 2005; Rau et al., 2007). Thus, burned plots (i.e. Site 1) would be expected to show lower phosphatase activity than unburned ones, as P may be more available, a trend that was suggested by our data. NAGase activity was higher at Site 1 than Site 2, possibly indicating lower nitrogen availability at Site 1. Nitrogen is easily volatilized (Neary et al., 1999; Caldwell et al., 2002), potentially leading to a loss of available N following fire and increased N demand. In response to this demand, microorganisms would produce more NAGase, as was seen here. Nitrogen can also be an important regulator of decomposition rates (Fog, 1988), suggesting that N limitation could also limit decomposition rate in this system.

Conclusions

In addition to changes in rates of nutrient mineralization, differences in leaf litter decomposition rates in relation to the success of upland oak ecosystems are likely tied to the reduction of leaf litter, as less leaf litter means more sunlight penetration and reduces physical barriers to emerging seedlings (Bergelson, 1990) for successful heliophytic graminoid and herbaceous germination in the understory (Xiong & Nilsson, 1999; Jutila & Grace, 2002; Maret & Wilson, 2005). Fire effectively removes most of the litter layer, creates a flush of phosphorus to the ecosystem, and serves to maintain an open canopy through the removal of fire intolerant mesophytic species (Nowacki & Abrams, 2008; Bowles et al., 2007). This study suggests that the restoration practices of thinning and prescribed burning increase enzymatic efficiency in the process of leaf litter decomposition in years between fires. This increased efficiency should result in increased rates of decomposition and therefore even greater reduction of the litter layer, as well as increased availability of nutrients compared to unrestored areas affected by mesophication. The combination of reduced inputs of litter from the intentionally thinned and opened canopy and increased decomposition rates due to increased enzyme efficiency should allow more solar penetration to understory and soil layers, and may allow for the regeneration of shade-intolerant species that once dominated, furthering the recuperation of this ecosystem. However, while restoration practices may alter microbial extracellular enzyme activity and decomposition rates in the long term, the effects of prescribed fire are particularly pronounced in the short term, and may alter these factors in the months immediately following fire, regardless of any prior history of restoration treatment.

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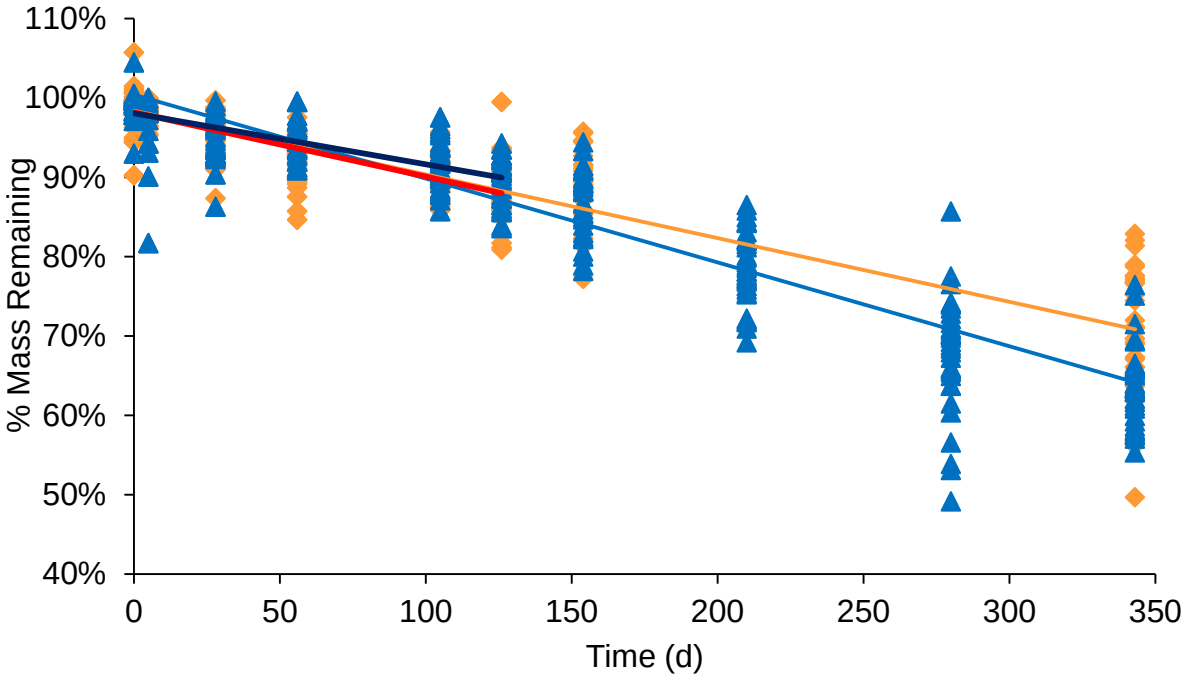
VII.APPENDIX

Appendix 1. Plot of regressions used to determine mean decomposition rates for leaf litter of six tree species (*Ulmus alata*, *Liquidambar styraciflua*, *Carya tomentosa*, *Quercus alba*, *Quercus falcata*, *Quercus stellata*) in two upland oak woodland sites (Site 1, orange diamonds; Site 2, blue triangles) undergoing ecological restoration. Pre-Burn (Site 1, red line; Site 2, navy line) indicates mass loss data from December 2013 through April 2014, when Site 1 was burned, while Site 2 was not. Whole Study (Site 1, orange line; Site 2, blue line) includes mass loss data from December 2013 through November 2014. Slope of the linear regression was then interpreted as decomposition rate, expressed as % original mass lost per day, and used to create Fig. 1.

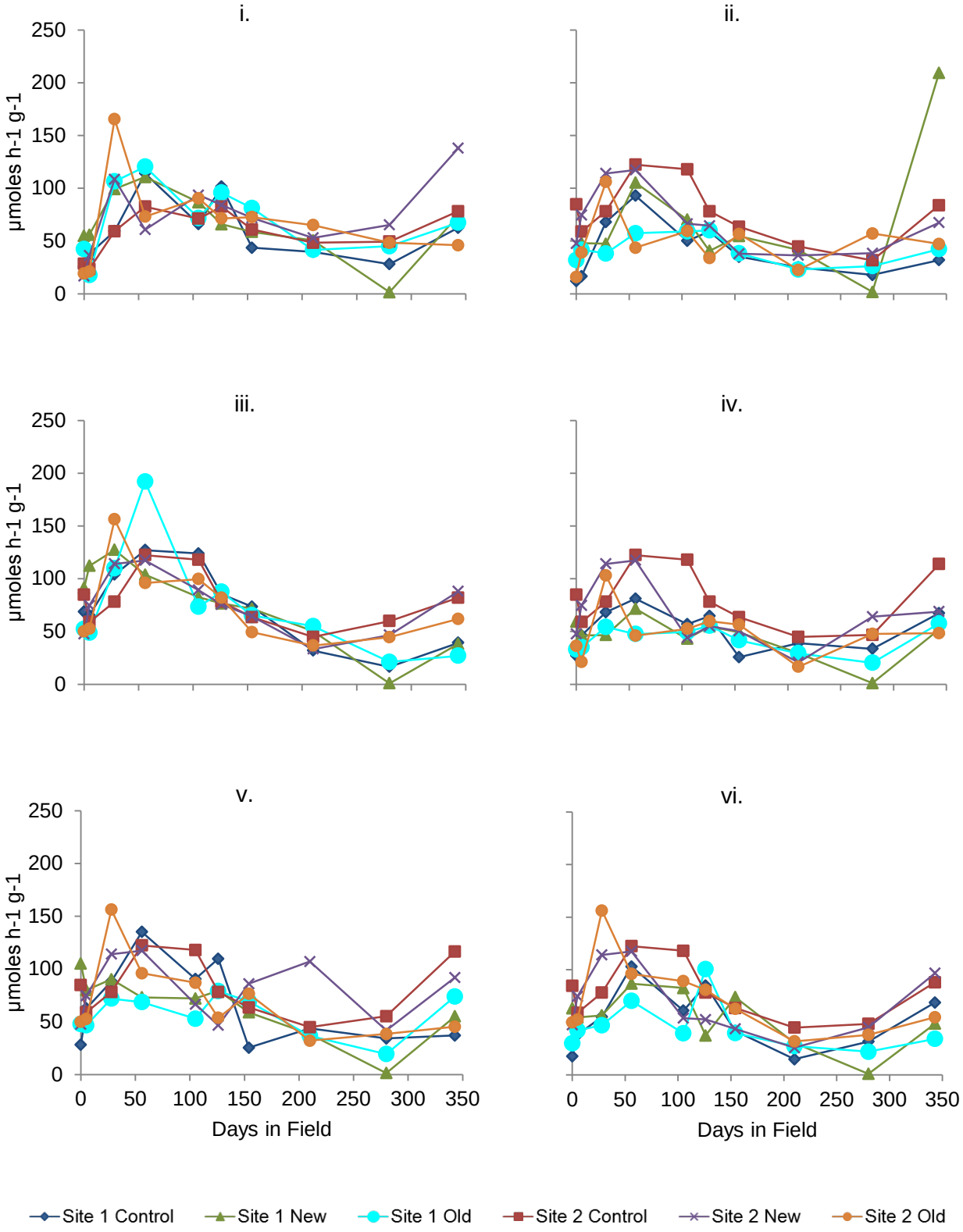


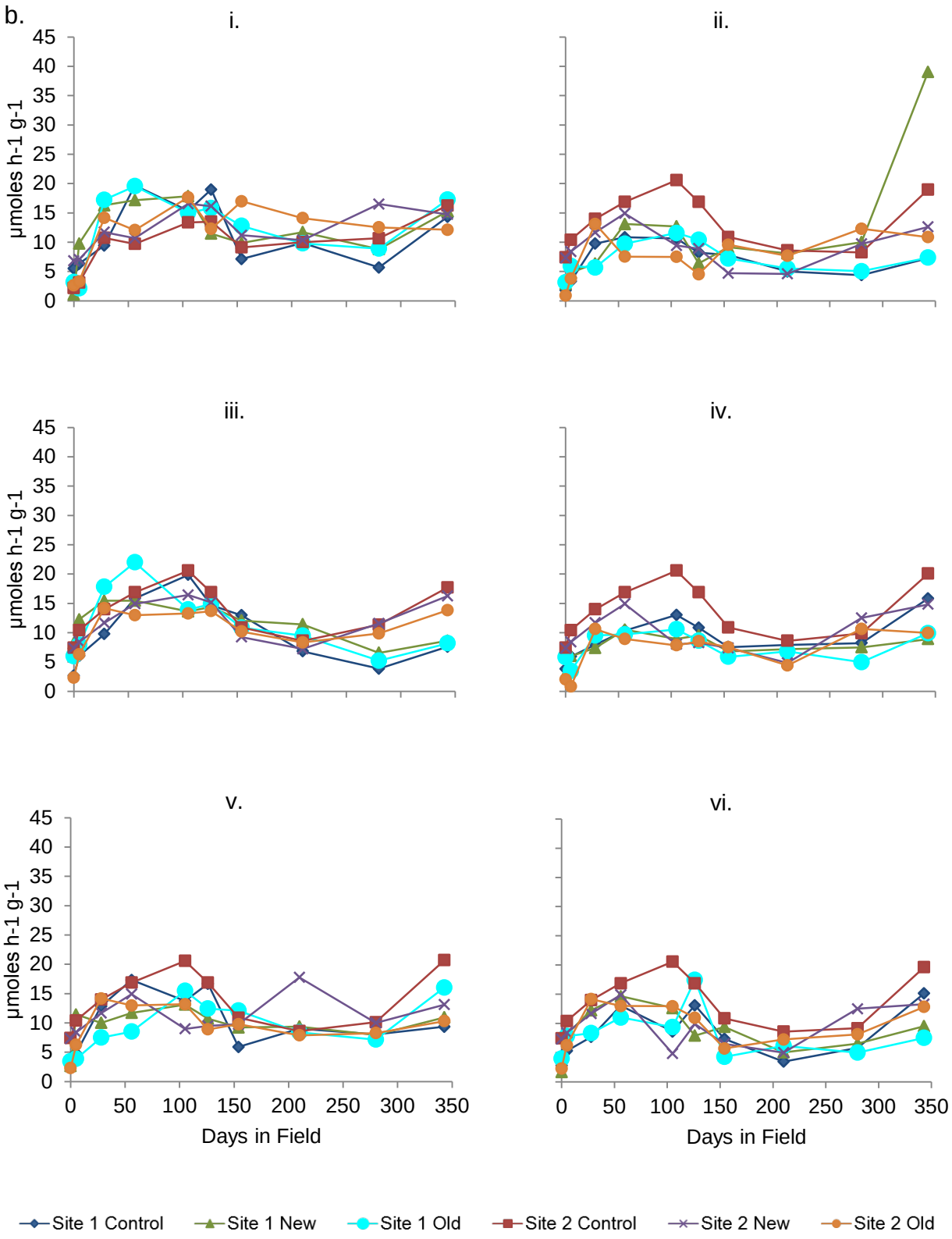
Appendix 2. Table of values for Analysis of Variance of decomposition rates expressed as % original mass lost per day in two upland oak woodland sites ("Site") undergoing ecological restoration. Site 1 was treated with a prescribed burn during the study, while Site 2 last experienced a prescribed burn four years prior. Each site consisted of "control" plots that had no restoration, "new" plots that had experienced mechanical thinning and 1-2 prescribed burns, and "old" plots that had experienced mechanical thinning and 3+ prescribed burns ("Treatment History"). Decomposition rate was calculated from litter of six different tree species ("Species:" *Ulmus alata, Liquidambar styraciflua, Carya tomentosa, Quercus alba, Quercus falcata, Quercus stellata*).

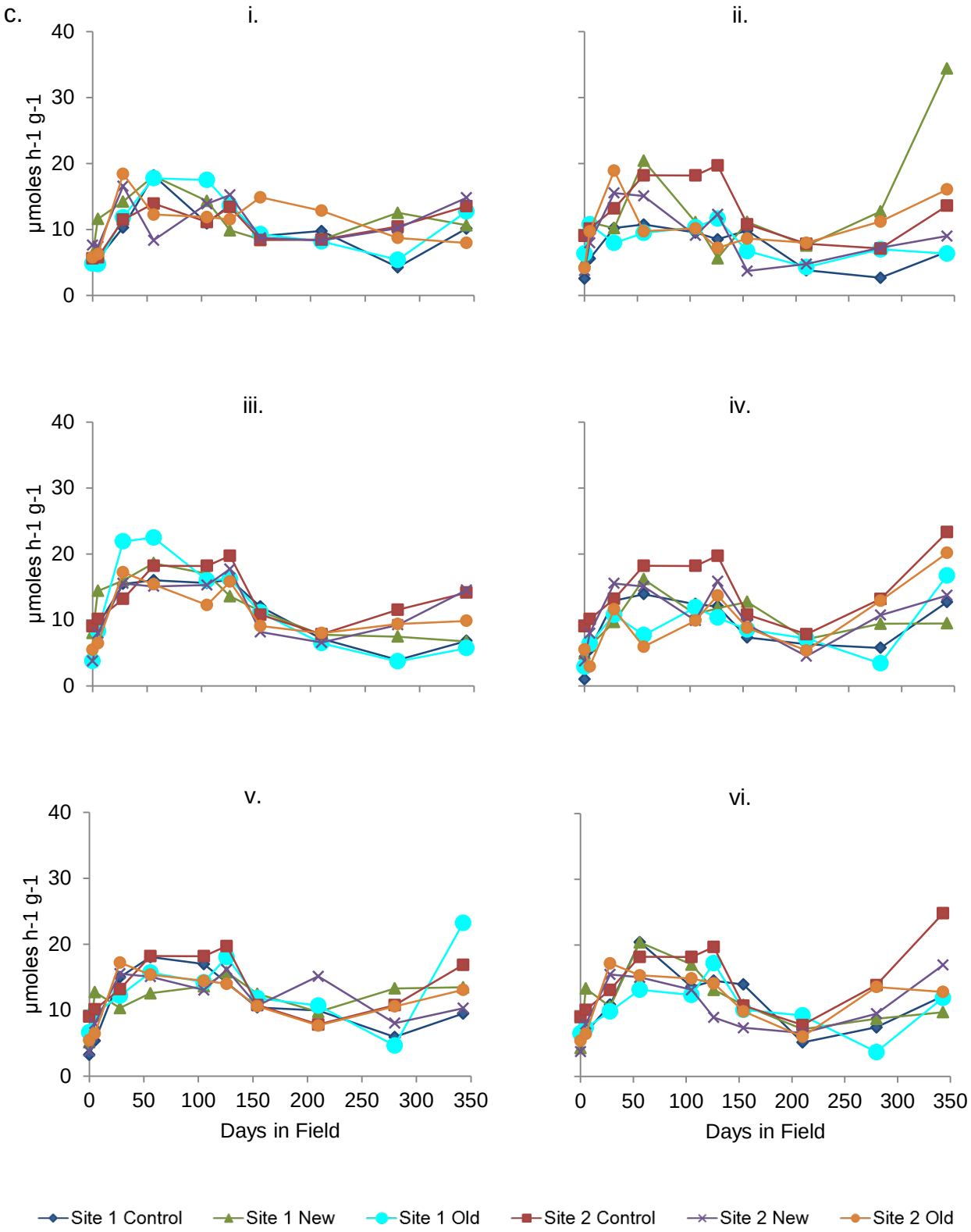
Factor	**Type II Sum of Squares**	**df**	**F value**	**Significance**
Site	1.15×10^{-6}	1	46.38	<0.001
Treatment History	2.51×10^{-7}	2	5.05	0.010
Species	5.01×10^{-7}	5	4.04	0.004
Site x Species	5.20×10^{-7}	5	4.19	0.003
Site x Treat. Hist.	1.98×10^{-7}	2	3.98	0.025
Species x Treat. Hist.	2.83×10^{-7}	10	1.14	0.355
Residuals	1.14×10^{-6}	46	-	-

Appendix 3. Temporal patterns in enzyme activity of β-glucosidase (a), cellobiohydrolase (CBH) (b), N-acetyl-β-D-glucosaminidase (NAGase) (c), phosphatase (d), phenol oxidase (e), and peroxidase (f) as well as decomposition (g) in leaf litter of six tree species (*Ulmus alata* (i), *Liquidambar styraciflua* (ii), *Carya tomentosa* (iii), *Quercus alba* (iv), *Quercus falcata* (v), *Quercus stellata* (vi)) in two upland oak woodland sites (Site 1, 2) undergoing ecological restoration. Each site consisted of "control" plots that had no restoration, "new" plots that had experienced mechanical thinning and 1-2 prescribed burns, and "old" plots that had experienced mechanical thinning and 3+ prescribed burns. Site 1 was treated with a prescribed burn during the study, while Site 2 last experienced a prescribed burn four years prior. "Days in Field" corresponds to dates after the initial day 0 sample in December 2013.

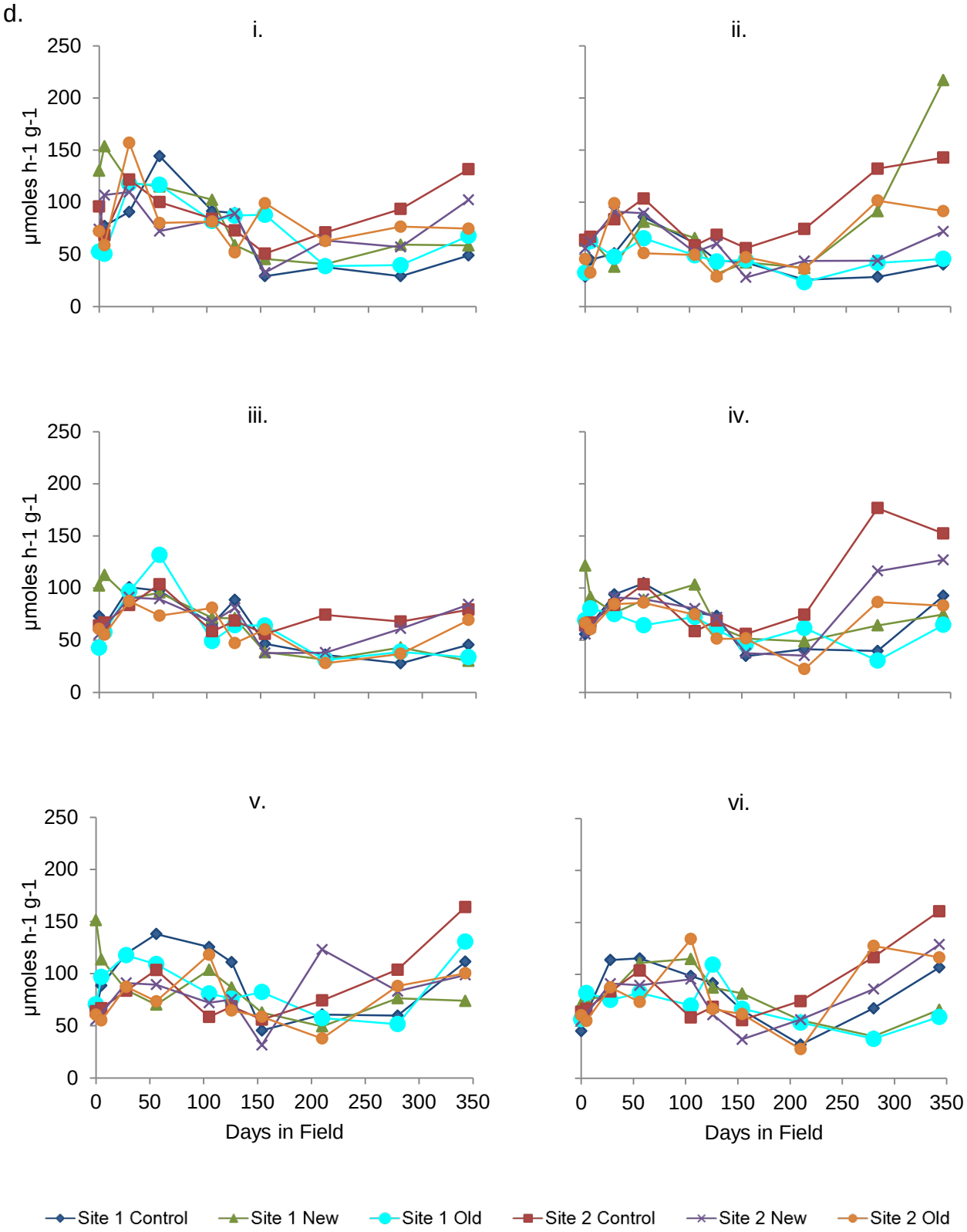
a.

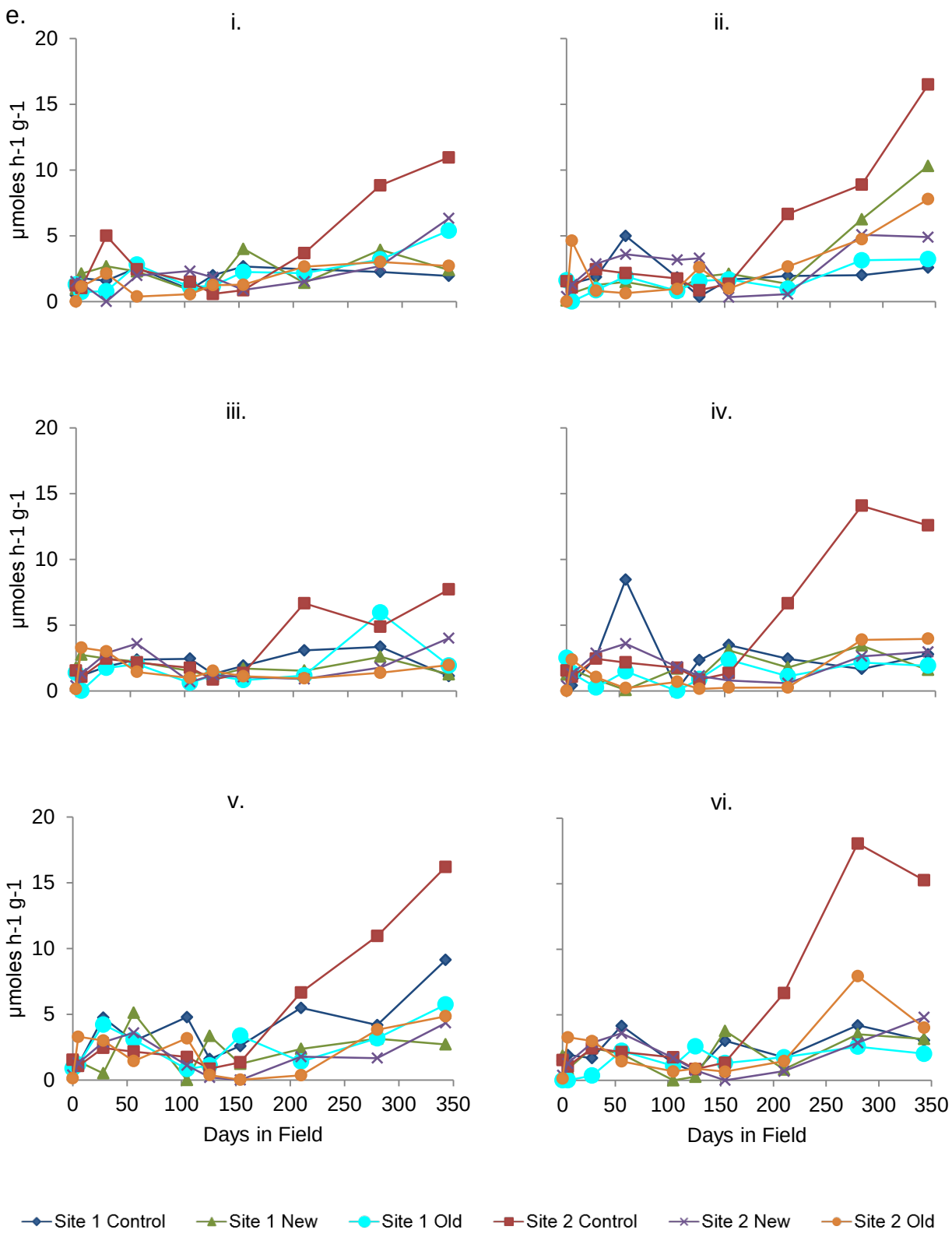

i.
ii.
iii.
iv.
v.
vi.
µmoles h-1 g-1
0
50
100
150
200
250
300
350
Days in Field
Site 1 Control
Site 1 New
Site 1 Old
Site 2 Control
Site 2 New
Site 2 Old

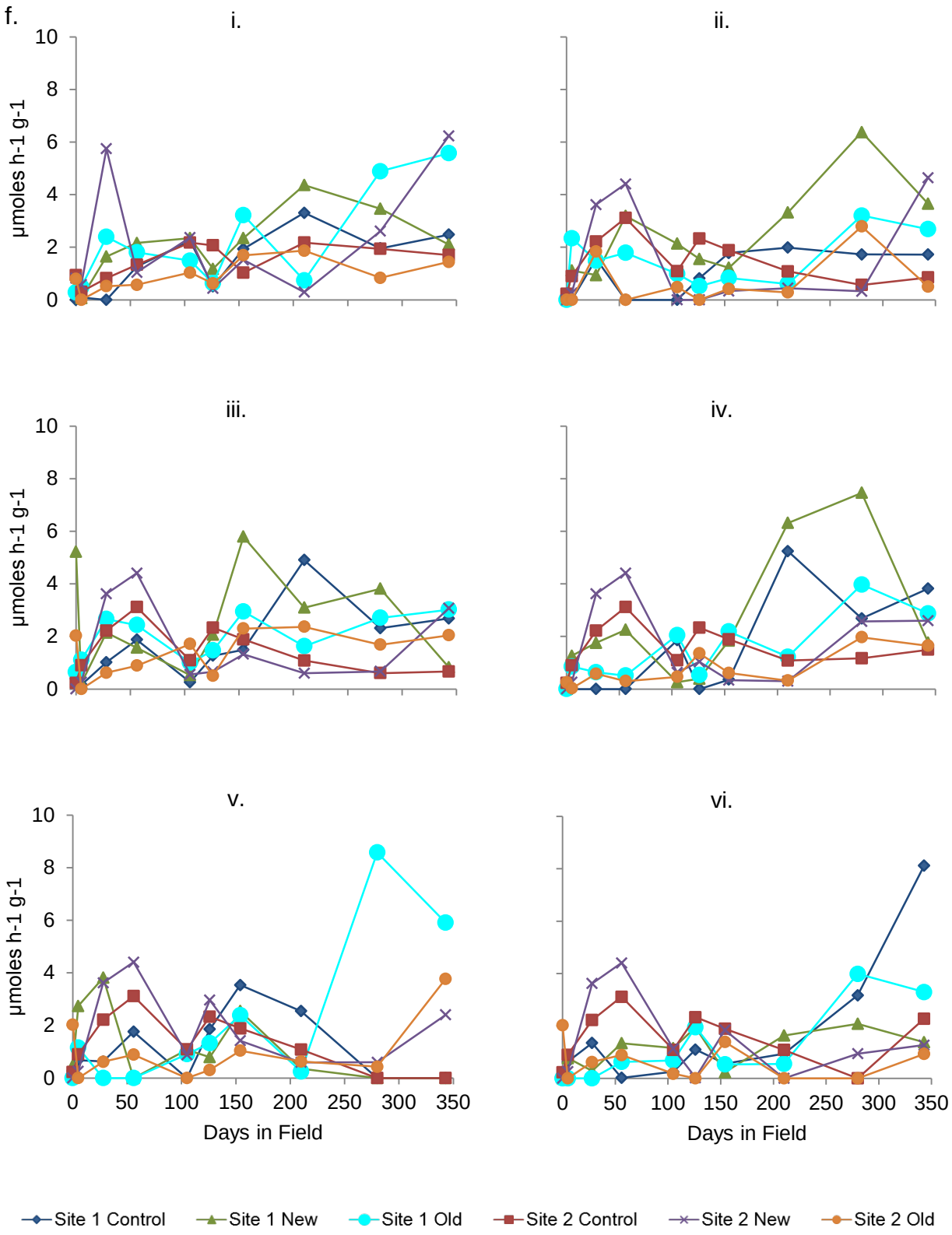

b.
i.
ii.
iii.
iv.
v.
vi.
µmoles h-1 g-1
Days in Field
0
5
10
15
20
25
30
35
40
45
0
50
100
150
200
250
300
350
Site 1 Control
Site 1 New
Site 1 Old
Site 2 Control
Site 2 New
Site 2 Old


c.
i.
ii.
iii.
iv.
v.
vi.
µmoles h-1 g-1
0
10
20
30
40
0
50
100
150
200
250
300
350
Days in Field
Site 1 Control
Site 1 New
Site 1 Old
Site 2 Control
Site 2 New
Site 2 Old

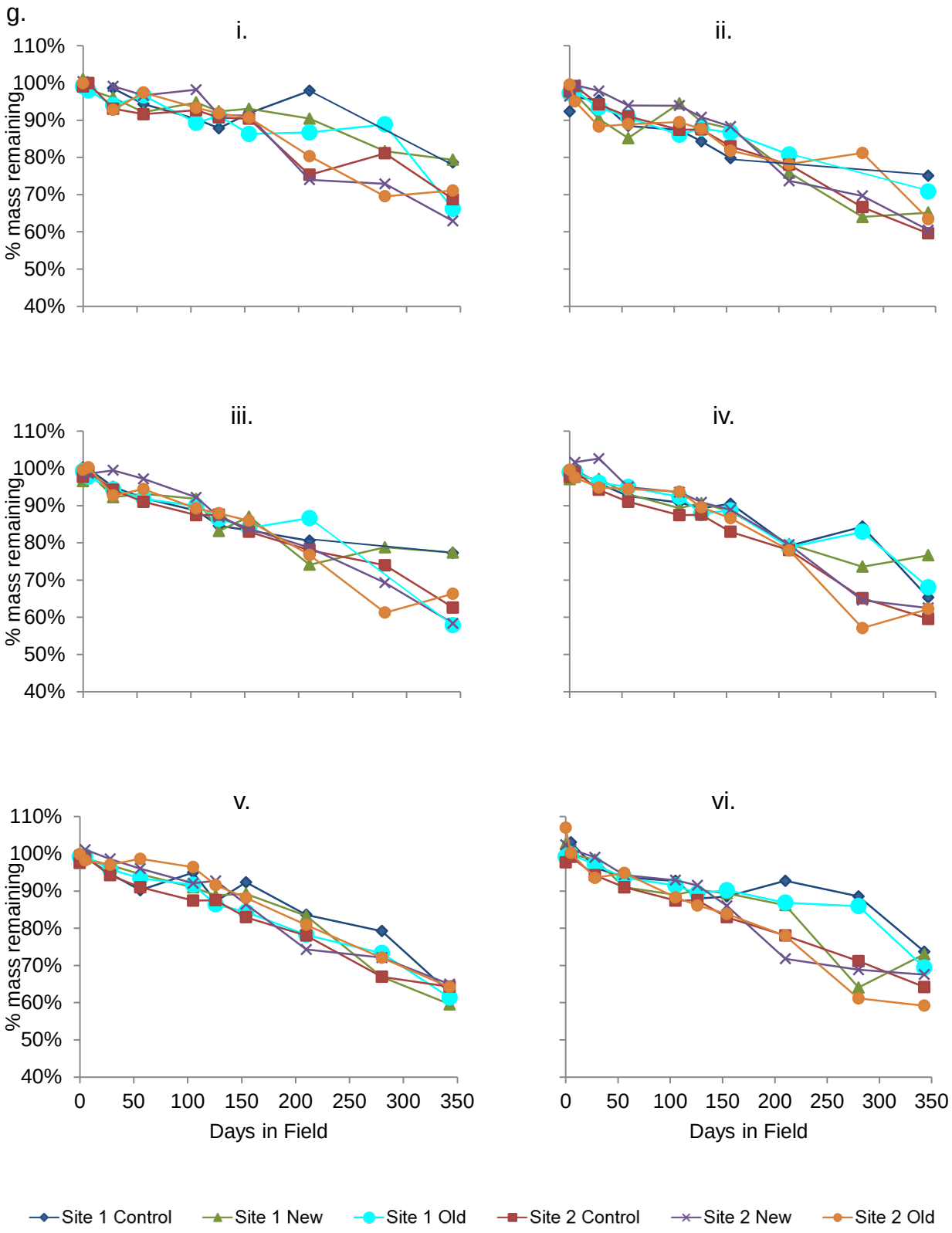
d.


i.
ii.
iii.
iv.
v.
vi.
µmoles h-1 g-1
0
50
100
150
200
250
300
350
Days in Field
Site 1 Control
Site 1 New
Site 1 Old
Site 2 Control
Site 2 New
Site 2 Old


e.
i.
ii.
iii.
iv.
v.
vi.
µmoles h-1 g-1
0
5
10
15
20
0
50
100
150
200
250
300
350
Days in Field
Site 1 Control
Site 1 New
Site 1 Old
Site 2 Control
Site 2 New
Site 2 Old


f.
i.
ii.
iii.
iv.
v.
vi.
µmoles h-1 g-1
Days in Field
0
50
100
150
200
250
300
350
2
4
6
8
10
Site 1 Control
Site 1 New
Site 1 Old
Site 2 Control
Site 2 New
Site 2 Old

g.


i.
ii.
iii.
iv.
v.
vi.
% mass remaining
110%
100%
90%
80%
70%
60%
50%
40%
0
50
100
150
200
250
300
350
Days in Field
Site 1 Control
Site 1 New
Site 1 Old
Site 2 Control
Site 2 New
Site 2 Old

Appendix 4. Linear regression statistics for decomposition rate ("Decomposition," in % mass remaining d^{-1}) as a function of days in the field (Decomposition = *k*) and cumulative enzyme activity for the extracellular enzymes phosphatase, β-glucosidase, *N*-acetyl-β-D-glucosaminidase (NAGase), cellobiohydrolase (CBH), phenol oxidase and peroxidase as a measure of apparent enzymatic efficiency (AEE, expressed as mass loss per unit enzyme activity) for six tree species *Ulmus alata*, *Liquidambar styraciflua*, *Carya tomentosa*, *Quercus alba*, *Quercus falcata*, and *Quercus stellata* in two upland oak woodland sites (Site 1, 2) undergoing ecological restoration. Each site consisted of "control" plots that had no restoration treatment, "new" plots that had experienced mechanical thinning and 1-2 prescribed burns, and "old" plots that had experienced mechanical thinning and 3+ prescribed burns. Site 1 was treated with a prescribed burn during the study, while Site 2 last experienced a prescribed burn four years prior. Numbers reported represent *k* (for decomposition, expressed as % mass loss d^{-1}) or AEE (for each enzyme, expressed as % mass loss per unit enzyme activity) ± SE (r^2).

		Site 1			Site 2		
Species		Control	New	Old	Control	New	Old
U. alata	β-glucosidase	-.001±.000 (.83)	-.001±.000 (.78)	-.001±.000 (.89)	-.001±.000 (.84)	-.001±.000 (.91)	-.001±.000 (.80)
	CBH	-.004±.001 (.81)	-.004±.000 (.79)	-.006±.000 (.91)	-.007±.001 (.87)	-.008±.001 (.93)	-.006±.001 (.85)
	NAGase	-.005±.001 (.81)	-.004±.000 (.76)	-.007±.000 (.89)	-.007±.001 (.85)	-.010±.001 (.91)	-.007±.001 (.85)
	Phosphatase	-.001±.000 (.80)	-.001±.000 (.76)	-.001±.000 (.89)	-.001±.000 (.87)	-.001±.000 (.88)	-.001±.000 (.83)
	Phenol oxidase	-.026±.009 (.80)	-.020±.005 (.79)	-.033±.003 (.93)	-.018±.001 (.89)	-.058±.006 (.90)	-.051±.009 (.85)
	Peroxidase	-.030±.010 (.79)	-.026±.007 (.78)	-.029±.002 (.93)	-.044±.014 (.81)	-.057±.006 (.84)	-.090±.037 (.90)
	Decomposition	-.056±.014 (.83)	-.052±.004 (.79)	-.093±.004 (.93)	-.073±.008 (.87)	-.105±.008 (.94)	-.088±.013 (.86)
L. styraciflua	β-glucosidase	-.001±.000 (.83)	-.001±.000 (.76)	-.002±.000 (.83)	-.002±.000 (.96)	-.002±.000 (.83)	-.002±.000 (.72)
	CBH	-.007±.002 (.78)	-.007±.002 (.77)	-.009±.000 (.82)	-.013±.001 (.97)	-.014±.002 (.84)	-.012±.000 (.75)
	NAGase	-.007±.002 (.80)	-.006±.001 (.78)	-.009±.000 (.80)	-.012±.001 (.96)	-.013±.002 (.80)	-.010±.001 (.74)
	Phosphatase	-.001±.000 (.80)	-.001±.000 (.77)	-.001±.000 (.82)	-.002±.000 (.96)	-.002±.000 (.84)	-.002±.000 (.76)
	Phenol oxidase	-.032±.014 (.77)	-.041±.007 (.82)	-.037±.002 (.82)	-.025±.001 (.79)	-.048±.012 (.75)	-.039±.001 (.74)
	Peroxidase	-.043±.009 (.58)	-.042±.015 (.68)	-.050±.006 (.87)	-.144±.020 (.94)	-.179±.071 (.76)	-.125±.023 (.71)
	Decomposition	-.061±.008 (.76)	-.071±.006 (.82)	-.075±.006 (.85)	-.111±.008 (.97)	-.111±.003 (.88)	-.105±.004 (.76)

C. tomentosa	β-glucosidase	-.001±.000 (.88)	-.001±.000 (.82)	-.001±.000 (.83)	-.001±.000 (.90)	-.002±.000 (.89)	-.001±.000 (.76)
	CBH	-.005±.000 (.84)	-.005±.000 (.82)	-.008±.001 (.90)	-.007±.001 (.91)	-.010±.001 (.93)	-.009±.002 (.81)
	NAGase	-.006±.000 (.87)	-.005±.000 (.82)	-.008±.001 (.87)	-.007±.000 (.91)	-.010±.001 (.92)	-.009±.002 (.81)
	Phosphatase	-.001±.000 (.88)	-.001±.000 (.82)	-.002±.000 (.90)	-.001±.000 (.94)	-.002±.000 (.91)	-.002±.001 (.79)
	Phenol oxidase	-.038±.002 (.84)	-.036±.007 (.81)	-.089±.027 (.96)	-.026±.005 (.92)	-.068±.005 (.91)	-.071±.017 (.82)
	Peroxidase	-.038±.012 (.68)	-.022±.006 (.71)	-.046±.005 (.97)	-.056±.003 (.85)	-.075±.009 (.85)	-.062±.015 (.86)
	Decomposition	-.066±.003 (.80)	-.059±.001 (.80)	-.116±.024 (.97)	-.093±.004 (.94)	-.123±.009 (.96)	-.104±.021 (.85)
Q. alba	β-glucosidase	-.002±.000 (.90)	-.001±.000 (.93)	-.002±.000 (.97)	-.002±.000 (.89)	-.002±.000 (.87)	-.002±.000 (.86)
	CBH	-.008±.001 (.95)	-.007±.001 (.94)	-.010±.001 (.96)	-.012±.000 (.88)	-.014±.001 (.92)	-.015±.001 (.88)
	NAGase	-.008±.001 (.92)	-.005±.000 (.93)	-.008±.001 (.99)	-.010±.000 (.89)	-.012±.000 (.89)	-.012±.002 (.88)
	Phosphatase	-.001±.000 (.90)	-.001±.000 (.93)	-.001±.000 (.95)	-.001±.000 (.89)	-.002±.000 (.89)	-.002±.000 (.85)
	Phenol oxidase	-.028±.001 (.92)	-.039±.018 (.86)	-.056±.012 (.96)	-.023±.009 (.88)	-.079±.005 (.90)	-.084±.009 (.73)
	Peroxidase	-.078±.036 (.95)	-.051±.025 (.97)	-.053±.016 (.97)	-.133±.017 (.68)	-.110±.029 (.87)	-.141±.045 (.81)
	Decomposition	-.094±.010 (.95)	-.061±.000 (.93)	-.089±.009 (.97)	-.119±.005 (.91)	-.115±.002 (.93)	-.124±.002 (.91)
Q. falcata	β-glucosidase	-.001±.000 (.66)	-.002±.000 (.87)	-.002±.000 (.99)	-.001±.000 (.77)	-.002±.000 (.93)	-.002±.000 (.79)
	CBH	-.009±.002 (.75)	-.010±.001 (.91)	-.009±.002 (.99)	-.009±.001 (.79)	-.011±.001 (.96)	-.011±.001 (.88)
	NAGase	-.008±.001 (.77)	-.008±.001 (.93)	-.007±.001 (.99)	-.007±.000 (.72)	-.010±.000 (.92)	-.009±.001 (.86)
	Phosphatase	-.001±.000 (.77)	-.001±.000 (.89)	-.001±.000 (.97)	-.001±.000 (.78)	-.001±.000 (.91)	-.001±.000 (.83)
	Phenol oxidase	-.024±.003 (.86)	-.050±.001 (.90)	-.032±.003 (.97)	-.017±.002 (.81)	-.064±.012 (.78)	-.060±.014 (.88)
	Peroxidase	-.034±.013 (.82)	-.073±.038 (.89)	-.060±.033 (.92)	-.059±.010 (.77)	-.056±.007 (.78)	-.112±.001 (.85)
	Decomposition	-.106±.026 (.85)	-.110±.009 (.93)	-.110±.001 (.98)	-.096±.007 (.81)	-.104±.005 (.97)	-.096±.008 (.89)
Q. stellata	β-glucosidase	-.001±.000 (.87)	-.001±.000 (.76)	-.002±.000 (.86)	-.002±.000 (.86)	-.002±.000 (.90)	-.002±.000 (.88)
	CBH	-.007±.002 (.89)	-.007±.000 (.82)	-.006±.002 (.84)	-.010±.001 (.88)	-.012±.001 (.92)	-.014±.001 (.91)
	NAGase	-.005±.002 (.87)	-.006±.000 (.79)	-.005±.002 (.90)	-.007±.000 (.89)	-.010±.001 (.90)	-.011±.001 (.89)
	Phosphatase	-.001±.000 (.88)	-.001±.000 (.79)	-.001±.000 (.94)	-.001±.000 (.90)	-.001±.000 (.91)	-.002±.000 (.90)
	Phenol oxidase	-.027±.008 (.92)	-.037±.013 (.89)	-.037±.020 (.86)	-.015±.001 (.85)	-.058±.014 (.76)	-.048±.012 (.83)
	Peroxidase	-.023±.003 (.78)	-.080±.023 (.75)	-.044±.023 (.93)	-.102±.032 (.49)	-.161±.095 (.68)	-.350±.017 (.89)
	Decomposition	-.072±.018 (.89)	-.077±.012 (.80)	-.084±.018 (.95)	-.099±.003 (.94)	-.107±.006 (.94)	-.132±.013 (.91)

VIII. VITA

Megan Overlander

Education:

BA Biology Augustana College, Sioux Falls, SD, 05/2010

Professional Experience:

Graduate Research and Teaching Assistant: University of Mississippi, 01/2013-05/2015

- Planed and conducted scientific research projects involving field work and lab work, including enzyme activity assays and molecular techniques such as PCR, DGGE, and next generation sequencing for microbial community analysis.
- Teach biology courses to undergraduate students.

Wildlife Biologist: Turnstone Environmental Consultants, 04/2012-08/2012

- Conducted field surveys and observations of the marbled murrelet, a threatened bird species in coastal old growth forests, following exacting ESA protocol.
- Navigated and hiked extreme forest terrain.
- Became familiar with the laws, regulations, and processes involved in logging proposals where threatened species were a concern.

Fisheries Observer: Saltwater Inc., 11/2010-11/2011

- Collected biological data while living on board a commercial fishing vessel in the Bering Sea.
- Demonstrated flexibility and resourcefulness in the organization and implementation of sampling on deck without hampering the work of the fishing crew.
- Worked long and odd hours seven days a week.

Biological Technician: US Geological Survey, 05/2011-09/2011

- Accurately collected vegetation data from sites in Oregon, Idaho, Utah, and Nevada to determine the effectiveness of seeding after wildfires on government owned rangelands.
- Camped at study sites in primitive conditions, and navigated using topographic maps and GPS units.
- Effectively used field guides and dichotomous keys to identify unknown species.

Field/Lab Technician: Cedar Creek Ecosystem Science Reserve, 09/2010-11/2010

- Conducted thorough vegetation surveys of savannahs and prairies, maintained integrity of scientific experiments, used scientific equipment to gather data, entered data into databases, assisted visiting researchers with various projects, and participated in prescribed burning.
- Conducted an individual research project, “Fungal Deposition in Low Diversity and High Diversity Plant Communities,” under the advisement of Linda Kinkel.

Plant Community Ecology Intern: Cedar Creek Ecosystem Science Reserve, 06/2008-08/2008 and 06/2010-09/2010

- Worked in a team to maintain integrity of scientific experiments, collected soil samples, entered data into computers, and assisted visiting researchers.
- Conducted an individual research project on "The relatedness of evaporation, total plant cover, and species richness in a recovered prairie ecosystem."

Teaching/Laboratory Assistant: Augustana Biology Department, 2007-2010

- Selected by Biology faculty as a student ideal for assisting in lab.
- Attended weekly meetings, prepared for weekly lab, assisted students and answered questions, graded homework, quizzes and tests.
- Has assisted for labs in Biology and Human Concerns, Biological Principles, Genetics, Principles of Ecology, and Aquatic Ecology.

Field Botanist: The Nature Conservancy, Missouri Ozarks, 05/2009-08/2009

- Collected vegetation data to determine the impact of prescribed burning in the Ozarks and its importance in the recovery of Ozark ecosystems.
- Worked in pairs to locate specific sites in rough terrain using a map and compass, accurately identified and recorded all plants growing in a defined area, and traveled to other locations in the state.

Presentations:

Strawberry (Plains) Flambé: Influence of current year fire and leaf litter species on litter decomposition rates and microbial enzyme activity in forests undergoing ecological restoration

-Master's Thesis Defense at the University of Mississippi, Oxford, MS. April 8, 2015

The influence of mesophytic and upland forest species in altering leaf litter decomposition rates in restored and unrestored upland oak woodlands

M.E. Overlander and *C.R. Jackson*

-Poster presentation at the Ecological Society of America Meeting, Sacramento, CA. August 10-15, 2014

That was then, this is now: Differences in leaf litter decomposition rates in restored upland oak forests

-Prospectus presentation at the University of Mississippi, Oxford, MS. October 30, 2013

Effects of *Juncus* "islands" on microbial community structure and activity in *Spartina* wetlands

M. E. Overlander, A. J. Rietl, J. A. Nyman, and C. R. Jackson

-Oral presentation at the Society of Wetland Scientists South Central Chapter meeting, Mississippi State University, Starkville, MS, October 19, 2013

- Poster presentation at the American Society for Microbiology joint South Central and Texas branch meeting, New Orleans, LA, November 1, 2013