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REGULAR ARTICLE

Plant controls on decomposition rates: the benefits of restoring abandoned agricultural lands with native prairie grasses

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Abstract Plant species can both directly and indirectly affect soil processes in various ways, including through functional traits related to the quantity and chemistry of biomass produced. Understanding how functional traits affect soil processes may be particularly important in restorations that specifically select a target plant community. In this study, I examined how species differing in litter traits alter decomposition, both directly via chemistry and indirectly via influences on soil microclimate. Decomposition dynamics of two old-field grasses were compared with the native prairie grass, *Andropogon gerardii*, in two Michigan old-fields. Decomposition rates were strongly, negatively related to tissue chemistry, but showed little effect of microclimate differences. Soil bacterial community composition differed between species at one site, while extracellular enzyme activities differed between species at the other site. These findings suggest plant species may be altering microbial community function. Overall, litter chemistry was the dominant factor determining decomposition rates, suggesting that restoring native prairie grasses with recalcitrant litter into grass-dominated old-fields could slow litter decomposition and ultimately lead to changes in soil carbon and nitrogen cycling. Eventually, this could lead to soils that more closely resemble the more organic-rich soils of native prairies and ultimately increase prairie plant community restoration success.

Keywords *Andropogon* · Functional traits · Litter chemistry · Microbial community · Microclimate · Restoration

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Introduction

Human activities have substantially altered plant communities in ecosystems around the world; in turn such changes in plant species composition can have a dramatic influence on soil processes (Evans et al. 2001; Mack and D'Antonio 2003a; Vitousek and Walker 1989). Recent research has focused on using plant functional traits to predict how changes in plant species composition alter soil processes (Eviner 2004; Eviner et al. 2006). Species can alter soil processes directly via traits relating to litter production and chemistry, and indirectly via traits that influence microclimate (e.g., water usage, aboveground biomass production). Both direct and indirect effects can alter soil microbial communities (e.g.,

activity, abundance, composition), potentially leading to feedbacks between plant and soil processes which can further alter nutrient cycling. Traits related to litter chemistry and biomass are often measured to examine how plants alter soil processes (Dijkstra et al. 2006; Hobbie 1992; Lovett et al. 2004; Wardle et al. 1998); however these traits are mainly considered in the context of direct effects on soil processes.

Until recently, restoration has focused more on restoring target plant communities than on the importance of restoring soil processes (Callaham et al. 2008; Eviner and Hawkes 2008; Heneghan et al. 2008; Pavao-Zuckerman 2008). However, the link between species traits and soil processes provides a strong argument for considering how species selected for restoration may impact soil processes, especially the traits of the dominant species (Eviner and Hawkes 2008). Plant and soil feedbacks have been identified as an important consideration in restoration projects (Heneghan et al. 2008). The selection of species with traits that are likely to impact soil processes could be used as an important tool in early stages of restoration projects to select species which may help to direct or accelerate the restoration of particular soil functions prior to broader scale attempts at restoring entire plant communities (Eviner and Hawkes 2008).

Decomposition is a fundamental process determining the rate of nutrient recycling in the soil, and is thus an essential factor to restoration efforts. Decomposition is largely controlled by three factors: environmental conditions, litter quality and quantity, and soil microbial communities (Swift et al. 1979). Thus, plants can directly influence decomposition through litter characteristics and indirectly through effects on environmental conditions, both of which may affect microbial communities.

Species with recalcitrant litter (i.e., higher C:N or lignin:N) typically have slower decomposition rates (Drenovsky and Batten 2007; Ehrenfeld et al. 2001; Hobbie et al. 2006), and litter quality can affect microbial community activity and abundance (Blackwood et al. 2007; Strickland et al. 2009; Wardle et al. 2004). Plants may select for a microbial community that is better able to decompose its own litter than litter from another species, although support for this hypothesis is mixed (Ayres et al. 2006; Gholz et al. 2000; Strickland et al. 2009; Vivanco and Austin 2008). Environmental factors, such as soil temperature and moisture, exert strong controls on soil microbial function (Aerts 2006; Leiros et al. 1999; Van Meeteren et al. 2007; Yuste et al. 2007), and plants influence these factors in a variety of ways (reviewed in Eviner and Chapin 2003), including water usage, litter layer thickness, and biomass. Several recent studies (Eviner 2004; Eviner et al. 2006; Mack and D'Antonio 2003b) have suggested that microclimate can be as or more important than litter chemistry as a determinant of soil process rates.

This study represents a unique, trait-based approach to examining species effects on ecosystem processes by focusing on how the restoration of a dominant prairie grass species may directly and indirectly affect decomposition rates. In southwestern Michigan, agricultural development has restricted native prairie grasses (Gotshall 1972) to remnants, and these species are mostly absent from abandoned agricultural fields (old-fields). Old-fields throughout the Midwest are typically colonized by a successional trajectory of C_3 species, many of which are non-native (Averett et al. 2004; Foster and Gross 1997; Gross and Emery 2007; Inouye and Tilman 1988, 1995). However, little is known about how trait differences between these species may have directly and indirectly altered decomposition dynamics in old-field systems.

My objective was to determine how the reintroduction of the native C_4 prairie grass, *Andropogon gerardii* Vitman., directly and indirectly affects decomposition rates compared to old-field grasses. I expected *A. gerardii*'s more recalcitrant litter to decompose slower than the more labile old-field grass litter. To determine the importance of the indirect effect of microclimate, I examined decomposition of each litter type, as well as a cellulose substrate, in plots dominated by each species (i.e., a reciprocal transplant design). If microclimate was an important driver of decomposition, I expected the thicker litter layer of *A. gerardii* to create a moist environment thereby increasing decomposition rates relative to the environment created by the old-field grasses. Because plants can both directly and indirectly impact soil microbial communities, it is difficult to determine causality with microbial differences. However, if species exert a selective pressure on microbial communities to better decompose their own litter, I expected differences in microbial communities, and each species litter would decompose faster in their home soil than in soil under other species.

Methods

Study sites

This experiment was established in two old-fields located at Michigan State University's W.K. Kellogg Biological Station (KBS) in southwestern Michigan, USA (Kalamazoo County; 42°24′N, 85°24′W, elev. ~280 m). This region had extensive prairies and savannas prior to agricultural development, and *A. gerardii* was a common component of those grasslands (Burbank et al. 1992; Gotshall 1972). Both old-fields were abandoned over 35 years ago following decades of row crop agriculture (Burbank et al. 1992; Foster and Gross 1997), and have been dominated by non-native C_3 grasses since least the early 1990's. *Bromus inermis* (Leyss; smooth brome) dominates Turkey Meadow while *Elymus repens* (L; quack grass) dominates McKay Field. Nomenclature follows the USDA Plants Database (plants.usda.gov). Monocultures of *A. gerardii* were established in 1995 by transplanting seedlings into clipped plots with minimal soil disturbance, weeded for 1 year, and then abandoned in 1996 (Foster 1999). After 11 years, experimental plots remain dominated by *A. gerardii*. Throughout the study, samples collected in the *A. gerardii* plots refers to areas dominated (>95% biomass) by *A. gerardii*, and samples collected from the old-field grass plots refers to areas 3–5 m from the *A. gerardii* plots that are dominated (>75% biomass) by old-field grasses and contain no *A. gerardii*. Both fields have glacial, sandy loam soils (Foster and Gross 1997) in the Kalamazoo Series (Typic Hapludalfs), although McKay Field has a higher sand fraction. Mean annual precipitation is 890 mm and mean annual temperature is 9.7°C.

Study species

Andropogon gerardii and the two common non-native old-field grasses (*Bromus inermis* and *Elymus repens*) differ in a variety of traits expected to influence soil processes. *Andropogon gerardii* and the old-field species differ widely in the amount and chemistry of tissue they produce (Baer et al. 2002; Camill et al. 2004; Craine et al. 2002b; Mahaney et al. 2008; Tjoelker et al. 2005; Wedin and Tilman 1990). In a related study comparing the effects of native prairie grasses and these old-field grasses on soil carbon (C) and nitrogen (N) cycling, Mahaney et al. (2008) found no significant differences between *B. inermis* and *E. repens* surface litter, shoot biomass, or green tissue chemistry (C:N or acid detergent fiber (ADF): N), suggesting that these species would have similar effects on soil processes. Indeed, Mahaney et al. (2008) found that soils under *A. gerardii*, with 5 to 6-fold greater shoot biomass and more recalcitrant tissue (higher C:N, ADF:N), tended to have slightly slower N cycling rates and significantly greater surface litter accumulation (3–4 times higher) than soils under the old-field grasses.

Reciprocal transplant litterbag decomposition experiment

I compared the in situ decomposition rates of *A. gerardii* and *E. repens* at McKay Field, and *A. gerardii* and *B. inermis* at Turkey Meadow. To do this, I performed a reciprocal transplant litterbag experiment using a three factor factorial design: Site (Turkey Meadow or McKay Field), Litter Type (*A. gerardii* or old-field grass), and Placement (under *A. gerardii* or old-field grass). In total, there were four treatments combinations in each site, with six replicates for each of five collection dates. In October 2005, senesced, standing aboveground tissue from a minimum of 15 randomly selected plants of each species was collected, air-dried, cut into 6–8 cm pieces, and gently mixed to homogenize. Standing litter was used because it represents the new litter inputs to the surface litter layer each winter (via wind or under the weigh of snow) but it had not been in direct contact with the soil microbial community. Approximately 4 g of air-dried litter was placed into 10 cm×10 cm polyester litterbags (0.17 cm mesh), which were placed under the surface litter in November 2005.

Litterbags (n=6 per treatment combination) were collected after 142, 213, 284, 374, and 709 days. Immediately after collection, soil and plant debris was removed and the litter was weighed to determine a field-moist weight. The litter was dried for 48 h at 65°C and reweighed. For each bag, I calculated percent moisture using the litter mass before and after oven-drying, and calculated the percent mass remaining relative to the initial litter mass. The mass remaining data across dates were then used to calculate decay constants (k) for each replicate using both a linear and a single exponential model following Trofymow et al. (2002). To determine initial litter chemistry for each

species, I analyzed a finely ground (<1.0 mm) litter subsample for C and N concentrations with an Elemental Analyzer (Costech Analytical, Ventura, CA) and Acid Detergent Fiber content (lignin and the more recalcitrant hemicellulose compounds) with an Ankom Fiber Analyzer (Macedon, NY).

Cellulose decomposition experiment

I used a factorial design with 3 factors: Site (Turkey Meadow or McKay Field), Placement (under *A. gerardii* or old-field grass), and Litter layer (present or removed) to examine how the environment under each species affected the decomposition of a standard cellulose substrate. To examine the effect of surface litter on decomposition, the surface litter was removed by hand from six plots (0.5 m× 0.5 m; −Litter treatment) and left intact in six plots for both *A. gerardii* and old-field grasses (+Litter treatment). One 100 cm^2 polyester litterbag filled with 4 g of cellulose filter paper (Whatman No.1) was placed in each plot in late May 2006. Bags were placed on the soil surface (under the litter layer in the +Litter treatment). After 354 days, the cellulose filters were collected, soil and plant debris was removed, and the filters were weighed before and after oven-drying for 24 h at 65°C. I calculated moisture content as an index of the moisture environment experienced by the decomposer community. I calculated the percent mass remaining relative to the initial mass of the cellulose. To obtain a general index of how the species affected maximum daily soil temperatures, I measured temperatures (at the soil surface in the −Litter plots and underneath the litter layer in the +Litter plots) in June, July, October and November 2006, on sunny afternoons (three measurements per plot).

Soil and microbial community characteristics

I collected and composited soil samples (3.8 cm diameter, 0–5 cm depth) from under *A. gerardii* and the old-field grasses at each site (3 replicates for each species, 10 composited cores per replicate from across the site) in November 2007 and immediately sieved (4 mm) each sample. One fresh soil subsample was subsequently frozen at −80°C for potential enzyme activity and soil microbial community analyses. Soil storage temperatures have not been found to have a significant influence on enzyme activities (DeForest 2009). CN analysis was performed on a finely ground (<2 mm), air-dried subsample with an Elemental Analyzer.

To examine differences in the functioning and energetic status of the microbial community under different plant species, I measured the potential activity of extracellular enzymes involved in litter degradation. Enzymes associated with the breakdown of phosphate esters (acid phosphatase), chitin (β-1, 4-N-Acetylglucosaminidase), cellulose (β-D-1,4-Cellobiosidase, α-1,4-Glucosidase, and β-1,4-Glucosidase), and hemicellulose (β-1,4-Xylosidase) were analyzed using methylumbelliferone-linked model substrates (DeForest 2009; DeForest et al. 2004a, b; Saiya-Cork et al. 2002). The enzymes responsible for lignin breakdown (phenol oxidase and peroxidase) were estimated colorimetrically using L-3,4-dihydroxyphenylalanine as a substrate. Assays were conducted in 96 well-plate format (Saiya-Cork et al. 2002) and fluorescence or absorbance was measured with a Synergy HT (BioTek, Winooski, VT).

I used terminal restriction fragment length polymorphism (TRFLP) to describe the structure of the bacterial and fungal communities, targeting 16 S rDNA for bacteria and the ITS gene for fungi. DNA was extracted from 0.5 g soil samples with MoBio Powersoil DNA extraction kits. PCR was performed on the purified DNA using two labeled primers for bacteria [338f (HEX), 926r (FAM)] and one labeled [58A2f (FAM)] and one unlabeled (ITS4) primer for fungi using a protocol previously successful at isolating fungal (Burke et al. 2005) and bacterial (Burke et al. 2006) DNA. Restriction digestions of the PCR product were performed using restriction enzyme *Msp*I for bacteria and *Alu*I for fungi. TRFLP analysis was performed at the Cornell University Life Sciences Core Laboratories Center on an Applied BioSystems 3730xl DNA Analyzer using a liz 600 size standard. Individual operational taxonomic units (OTUs; ±0.5 base pairs) were created using peaks comprising at least 1% of the total peak area.

Statistical analyses

Soil and plant chemistry data and soil potential exoenzyme activities were compared for Species and Site using Two-way ANOVA (SigmaStat 3.5). The old-field species traits were also compared using t-tests (SigmaStat 3.5). Linear and exponential litter decay

rates (k) were evaluated using Three-way ANOVA (Site, Litter type, and Placement; SigmaStat 3.5), but only the exponential model is reported as this model had a better fit and there was no difference in the statistical conclusions of the ANOVA. For any significant interaction, post-hoc Tukey contrasts were performed. Litter mass remaining and moisture was compared over the two-year period using Repeated Measures ANOVA (Site, Litter type, and Placement; Systat 11) and Greenhouse-Geisser (G-G) values are reported for within subject comparisons. For any significant interaction, post-hoc univariate F tests were performed. Linear regressions were performed between the tissue nutrients and both k values and mass remaining after 2 years (SigmaStat 3.5). Cellulose paper mass remaining and moisture levels were evaluated using Three-way ANOVA with Site, Placement, and Litter layer (+Litter or −Litter) as factors (SigmaStat 3.5). Repeated Measures ANOVA (Site, Placement, and Litter layer) was used to compare soil temperature differences (Systat 11) and Greenhouse-Geisser (G-G) values are reported for within subject comparisons. For any significant interaction, post-hoc univariate F tests were performed. Ordinations of the bacterial and fungal communities were performed using non-metric multidimensional scaling (NMS, PCOrd 5) with Sørensen as the distance measure. Multi-response permutation procedures (MRPP) were used to examine community differences between sites and species using Euclidean distance (PCOrd 5).

Results

Reciprocal transplant experiment

Andropogon gerardii litter was more recalcitrant, having significantly higher C:N ($F_{1,8}$=51.5, p<0.001) and ADF:N ($F_{1,7}$=49.22, p<0.001) than the old-field species (Table 1). Additionally, there were no significant differences in tissue quality between sites (CN: $F_{1,8}$=4.0, p=0.081; ADFN: $F_{1,7}$=1.8, p=0.222), indicating that *E. repens* and *B. inermis* had similar litter chemistry (Site*Species: CN: $F_{1,8}$=1.1, p=0.326; ADFN: $F_{1,7}$=0.9, p=0.372; Table 1). Indeed, comparisons of *E. repens* and *B. inermis* tissue chemistry showed that they did not differ in C, N, C:N, ADF, or ADF:N (t-tests: p>0.05). In both sites, mass remaining over the two-year period for *A. gerardii* litter was significantly larger than for the old-field species (Litter Type: $F_{1,37}$=124.40, p<0.001), although there were significant differences in *A. gerardii* decomposition between sites (Site*Litter Type) in the early stages of decomposition (Day 142 and 213; $F_{1,37}$>5.0, p<0.03), which disappeared by Day 284 (Fig. 1). There were no significant differences between litter placement location (Placement: $F_{1,37}$=1.3, p=0.26). There were differences in mass remaining between sites (Time*Species: $F_{4,148}$=6.1, G-G=0.002) at collections on Days 142, 213, and 709. Using an exponential model, litter decay (k) rates were significantly slower for *A. gerardii* litter in both sites ($F_{1,40}$=23.93, p<0.001), faster in Turkey Meadow than McKay Field ($F_{1,40}$=6.81, p=0.013), and did not differ between placement locations ($F_{1,40}$=0.41, p=0.526). When collected, litter located under *A. gerardii* had significantly higher moisture content than litter placed under old-field grasses at all collection dates except Day 709 (Time*Placement: $F_{4,148}$=5.7, G-G=0.002), and moisture contents differed between sites at collections on Day 213 and 709 (Time*Site $F_{4,148}$=7.5, G-G<0.001). Moisture content did not differ between litter types (Litter Type: $F_{1,37}$=2.91, p=0.096). There was a strong negative correlation between mass remaining and litter moisture over the 2 years (p<0.001 r=0.636). Linear regressions showed a strong negative relationship between tissue chemistry (C:N and ADF:N) and decomposition estimates (k and mass remaining after 2 years; Table 2).

Table 1 Chemistry of the senesced shoot tissue for the species used in the Reciprocal transplant experiment. Acid detergent fiber (ADF) is primarily lignin and recalcitrant hemicellulose compounds. Data shown are mean (SE). Both variables were significantly higher for *Andropogon gerardii* compared to the old-field grasses (*Bromus inermis, Elymus repens*; Species main effect, p<0.001)

Site	Species	C:N	ADF:N
Turkey Meadow	*A. gerardii*	83.17(6.77)	151.57(13.56)
	B. inermis	47.02(4.40)	80.37(13.67)
McKay Field	*A. gerardii*	101.14(11.64)	178.50(19.74)
	E. repens	52.65(2.86)	84.89(4.87)

Cellulose decomposition experiment

The removal of surface litter (−Litter) significantly decreased decomposition at both sites ($F_{1,39}$=4.74, p=0.036, Fig. 2). The moisture content of the cellulose

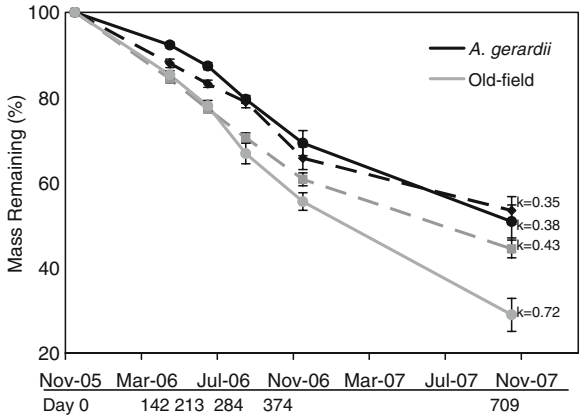


Fig. 1 Litter mass remaining (% of initial) across time and the exponential decay rate (k) for the Reciprocal transplant experiment, averaged across the placement (under *Andropogon gerardii* or old-field species) treatment. *Solid lines* represent the mass remaining in Turkey Meadow, while *dotted lines* represent McKay Field. *Black lines* (both *solid* and *dotted*) represent *A. gerardii* litter, while *Gray lines* represent the old-field grass litter (*Bromus inermis* in Turkey Meadow, *Elymus repens* in McKay Field)

filters at the time of collection differed between sites when litter was left intact or removed ($F_{1,39}$= 4.17, p=0.048), but did not differ between placement under *A. gerardii* compared to under old-field grasses ($F_{1,39}$=0.96, p=0.334). There were no significant differences in the cellulose moisture content between treatments at McKay Field, but the cellulose substrate was significantly moister in +Litter versus −Litter plots at Turkey Meadow (p= 0.008). This was likely driven by the higher moisture content of cellulose collected from the +Litter plots in Turkey Meadow compared to those from +Litter plots in McKay Field (p=0.041). Surface soil temperatures were significantly (~2.0–2.7°C) higher under old-field species than *A. gerardii* in June, July and November (Time*Species $F_{3,120}$=2.8, G-G= 0.042), and were significantly different between sites in July, October and November (Time*Site: $F_{3,120}$= 17.9, G-G<0.001; Fig. 3). Litter removal from the plot did not significantly affect mid-day soil temperatures (Litter Layer: $F_{1,40}$=3.7, p=0.061).

Soil and microbial community characteristics

The bacterial community ordination using the forward primer showed separation of the microbial communities along 3 axes (Stress = 3.309, Fig. 4). MRPP showed significant community differences between the sites (A=0.131, p=0.009), but not the plant species (A= 0.019, p=0.254). MRPP comparisons of the significant site*species interaction found significant bacterial community differences between species at McKay Field (A=0.264, p=0.027) but not Turkey Meadow (A=0.187, p=0.076). The ordination of the fungal communities showed no separation of sites or species, suggesting that the communities were similar (Stress <1, data not shown). Neither community differed in richness or diversity (p>0.05).

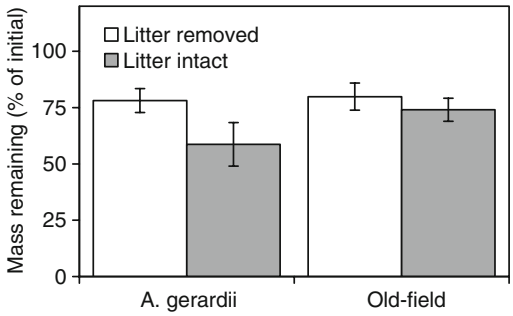
Potential activities of phenol oxidase and α-1,4-Glucosidase did not differ between sites or species (Table 3). Many enzyme activities were higher in Turkey Meadow than in McKay Field (for both species: β-1,4-N-Acetylglucosaminidase, acid phosphatase, β-1,4-Glucosidase; for *A. gerardii* only: β-D-1,4-Cellobiosidase, β-1,4-Xylosidase), but only a few enzymes differed between species, with *A. gerardii* soils having higher activity than the other grasses (in both sites: β-1,4-N-Acetylglucosaminidase; in Turkey Meadow: β-D-1,4-Cellobiosidase, β-1,4-Xylosidase). There was only one instance where soils from under the old-field grasses had higher activities, and that was for peroxidase in Turkey Meadow. Additionally, I found no significant differences in soil total C or N between species or sites (p> 0.09). Soil C:N was higher in soils under *A. gerardii* in McKay Field (p=0.002) but did not differ in Turkey Meadow (p=0.649).

Discussion

As expected, the old-field grasses had significantly more labile litter than *A. gerardii*, and these lower values were strongly correlated with faster decompo-

Table 2 Simple linear regressions between decomposition metrics (mass remaining after 2 years and exponential k values) and litter chemistry variables (C:N and ADF:N). N=8 for all regressions, using mean values for each treatment combination (2 Sites * 2 Placements * 2 Species)

Decomposition metric	Predictor	t-statistic	p-value	R^2
Mass remaining	C:N	3.60	0.011	0.68
Mass remaining	ADF:N	3.35	0.015	0.65
Exponential k	C:N	−2.78	0.032	0.56
Exponential k	ADF:N	−2.57	0.042	0.52



	$F_{1,39}$	p
Site	2.2	0.143
Placement	1.3	0.268
+/-Litter	**4.7**	**0.036**
Site*Pl	0.1	0.779
Site*+/-L	0.3	0.615
Pl*+/-L	0.2	0.661
Site*Pl*+/-L	0.2	0.633

Fig. 2 Mass remaining (% of initial) for cellulose filters placed under either *Andropogon gerardii* or the old-field species *Elymus repens* or *Bromus inermis* (Placement treatment), with litter intact (+L) or with litter removed (−L), and averaged across sites

sition rates. My results follow a pattern that has been found in many studies (Ehrenfeld et al. 2001; Hobbie et al. 2006; Taylor et al. 1989); labile tissue decomposes faster. These results confirm that litter chemistry is an important driver of decomposition rates in these old-field communities. A small difference in decomposition between the two old-field species appears at the end of the second year, despite the nearly identical tissue chemistry, but this difference was not significant. The overall slower decomposition rates for *A. gerardii* suggest that restoring prairie grasses with recalcitrant litter will increase surface litter build-up and decrease soil C and N cycling rates.

Despite the strong correlation between litter chemistry and decomposition rate, the mechanism(s) behind these differences in decomposition rates remain unclear. Evidence of a shift in microbial community composition at one site (Fig. 4) and a shift in microbial activity in the other site (Table 3) suggests a microbial-based explanation, but one which may have multiple drivers. Given the link between enzyme production and litter decomposition, I expected that enzymes would differ between plant species based on tissue chemistry. At Turkey Meadow, soils under *A. gerardii* typically had greater pools of active enzymes than soils under *B. inermis*, suggesting greater decomposer activity in soils under *A. gerardii*. Higher chitin degrading enzymes under *A. gerardii* could indicate greater fungal biomass or the relative importance of fungi to decomposition, although the TRFLP results did not show bacterial or fungal community composition differences in soils under those two species. *Andropogon gerardii* and *B. inermis* are both arbuscular mycorrhizal species, but it is unknown whether they differ in their colonization rates or amount of fungal biomass they can support. Greater potential cellulose and hemi-cellulose degrading enzyme activities under *A. gerardii*, with its more recalcitrant tissue, suggests a connection between enzyme production and tissue chemistry. In contrast, I found few differences in the potential enzyme activities between *A. gerardii* and *E. repens* at McKay Field, suggesting that microbial activity did not respond to tissue chemistry differences at this site.

Instead, microbial communities in McKay Field appeared to respond to differences between *A. gerardii* plots and the *E.repens* plots by shifting bacterial community composition. Bacterial communities under *A. gerardii* and *B. inermis* were similar, while communities under *A. gerardii* and *E. repens* were

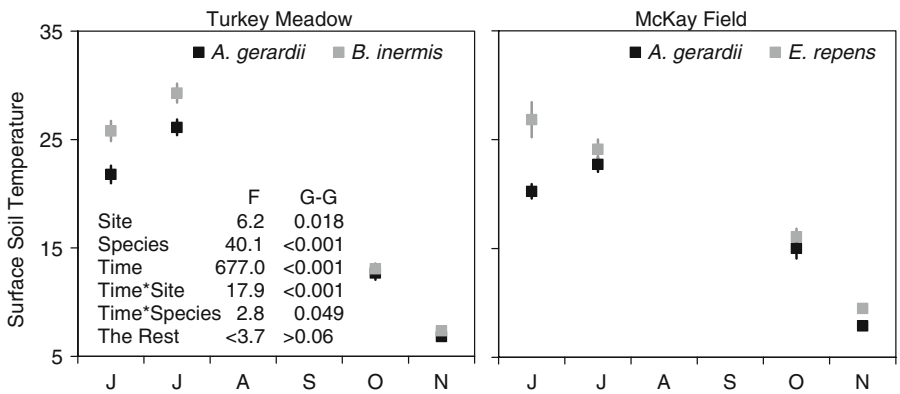


Fig. 3 Surface soil temperature (°C) in *Andropogon gerardii, Bromus inermis* and *Elymus repens* plots in 2006, averaged across the +/− Litter treatment. Greenhouse-Geisser adjusted p-values for log-transformed data are reported for time variables, and untransformed data are shown

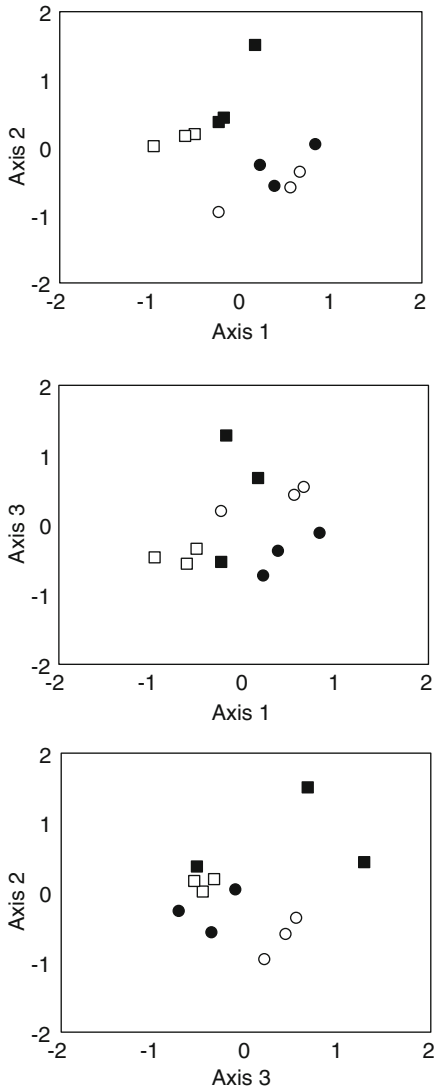


Fig. 4 Non-metric multidimensional scaling ordination of the bacterial communities under *Andropogon gerardii* and the old-field species, *Elymus repens* or *Bromus inermis*. *Square* symbols represent communities in Turkey Meadow (■□), while *circles* represent communities in McKay Field (●○). Communities under *A. gerardii* (■●) are shown as *solid* symbols, while communities under the old-field grasses are shown as *open* symbols (□○)

significantly different. This indicates that the soil physical or chemical environment under *A. gerardii* and *E. repens* varied enough to influence bacterial community composition, despite that fact that no microbial activity differences were apparent. Functional trait differences between *A. gerardii* and *E. repens* in McKay Field might have altered bacterial community composition, while those same functional trait differences in Turkey Meadow could have led to differences in microbial activity (e.g., enzyme production). Such mixed results are not uncommon in studies linking microbial and plant community dynamics (reviewed in Wardle 2006). Decomposer community activities can correspond to both litter chemistry and site conditions, as shown in other studies (Sinsabaugh et al. 2002; Waldrop and Zak 2006). Thus, it is unknown whether the differences in microbial communities were caused directly by differences in litter quality, indirectly by differences in microclimate conditions, or some other trait(s) differences between *E. repens* and *B. inermis* that were not measured. Ultimately, the different mechanisms by which the soil microbial community responded to plant species differences did not affect the outcome: decomposition rate differences between species were consistent across sites.

Despite differences in moisture and microbial community characteristics between soils under each species at both sites, litter decomposition rates did not differ based on its placement under a particular species. This suggests that while the microbial communities differed, the microbes decomposing surface litter under *A. gerardii* and the old-field grasses are functionally similar, or redundant (i.e., the microbial communities under the different species decompose identical litter at similar rates). Several studies have found evidence to support the "home-field advantage" hypothesis (Gholz et al. 2000), which suggests that plants select for microbial communities that are better able to decompose their own litter than introduced litter from another location (Castanho and de Oliveira 2008; Vivanco and Austin 2008). I found no evidence of a home-field advantage, potentially because the litter chemistry between the old-field grasses and *A. gerardii* was not sufficiently different from a microbial perspective (Strickland et al. 2009).

Overall, while I found evidence for microclimate differences between *A. gerardii* and the old-field plots, I found little evidence to suggest that these differences affected decomposition rates. The lack of evidence suggests that litter quality was the primary factor controlling decomposition rates. I had anticipated that these microclimate differences would translate into a divergence in decomposition rates, and the strong positive correlation between mass loss and litter moisture further supported my expectation. Dickson and Wilsey (2009) also found that both litter

Table 3 Soil chemistry and potential extracellular enzyme activity of soil collected from under *Andropogon gerardii* and the old-field species (*Bromus inermis*, *Elymus repens*) in November 2007. Extracellular enzymes were measured in nmol $h^{-1}g^{-1}$ soil. For significant interactions, superscript letters denote significant differences from post-hoc Tukey comparisons ($p<0.05$)

	Model output[1]			Turkey Meadow		McKay Field	
	Site	Plot	Site * Plot	*A. gerardii* mean(SE)	*B. inermis* mean(SE)	*A. gerardii* mean(SE)	*E. repens* mean(SE)
Carbon (%)	0.63	0.67	2.2	2.17(0.49)	2.83(0.23)	2.37(0.14)	2.18(0.16)
Nitrogen (%)	3.8	2.9	0.71	0.16(0.03)	0.20(0.02)	0.14(0.01)	0.15(0.01)
Acid phosphatase	14.2*	0.64	0.92	853(112)	840(88)	484(32)	621(54)
α-1,4-Glucosidase	4.3	4.2	2.0	9.56(0.91)	10.31(2.08)	5.29(0.80)	9.53(0.41)
β-1,4-N-Acetyl-glucosaminidase	17.1*	7.0*	1.9	203(36)	119(16)	88(13)	61(6)
β-D-1,4-Cellobiosidase	39.8**	15.7*	26.7**	119(8)^{a}	65(5)^{b}	51(7)^{c}	58(2)^{bc}
β-1,4-Glucosidase	9.7*	0.7	0.07	364(22)	387(54)	237(20)	279(43)
β-1,4-Xylosidase	26.2**	5.0	8.4*	63.9(6.3)^{a}	42.8(4.5)^{b}	30.9(2.2)^{c}	33.7(1.8)^{bc}
Phenol oxidase	1.0	1.0	1.0	0.0(0.0)	0.0(0.0)	13.2(13.2)	0.0(0.0)
Peroxidase	0.01	12.2*	6.0*	434(235)^{a}	1,385(24)^{b}	837(46)^{ab}	1,006(212)^{ab}

[1] F statistic followed by *p*-value (<0.001**, <0.05*)

quality and microclimate affected decomposition rates of prairie species. The surface soil temperature differences were expected based on the relatively small amount of surface litter and shoot biomass associated with the old-field species relative to *A. gerardii* (Mahaney et al. 2008). Eviner (2004) found that species had a large influence on soil temperatures, with both lower daily fluctuations in plots with higher graminoid shoot biomass and litter, and a negative correlation between summer afternoon temperatures and litter quantity. Regardless of these differences, I found no evidence to suggest that temperature or moisture limited decomposition rates during the summer and autumn months. The only factor that affected cellulose decomposition was the presence or absence of surface litter (+/− Litter Layer), but given the overall lack of microclimate difference found for this treatment, it is likely that either some unmeasured aspect of microclimate was sufficiently altered by the removal of surface litter to influence decomposition, or that the physical removal of litter altered the microbial community in a manner that reduced decomposition rates.

Results presented here demonstrate that litter quality, even within the graminoid guild, exerts a dominant control on a species' decomposition rate in a particular site. While this study focused on only a few species, my findings should hold for a variety of grass species common to old-fields and native prairies that are similar in their tissue characteristics (Craine et al. 2002a; Craine et al. 2002b; Tjoelker et al. 2005). While it is possible that differences in traits not considered in this study between *B. inermis* and *E. repens* affected microbial communities differently, these species did not differ in their decomposition rate. This, combined with the findings from Mahaney et al. (2008) of no significant differences between *B. inermis* and *E. repens* surface litter, shoot biomass, and tissue chemistry, suggests that other similar old-field species would be analogous in their effects on decomposition. In addition, Mahaney et al. (2008) found no significant differences in tissue C:N and ADF:N between *A. gerardii* and two other prairie grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*), which suggests that those prairie species would have comparable decomposition rates. These findings imply that communities restored to dominance by these native prairie grasses will impact C and N cycling via slower decomposition rates relative to many grasses typical of successional old-field communities. These prairie species also have greater shoot biomass than many old-field grasses and these combined factors will likely lead to an increase in surface litter accumulation, which may increase soil moisture, reduce summer temperature extremes, and alter microbial community structure and function. All of these factors are important to consider in restoration planning.

This type of trait-based approach readily applies to situations where the dominant species is replaced (i.e., via invasion, restoration, extinction or altered environmental conditions) by another species differing in functional traits that are likely to influence soil processes. Indirect (microclimate) and direct (litter substrate chemistry) mechanisms for plant effects on microbial processing of C and nutrients need to be evaluated. Understanding the relative importance of the direct and indirect species effects on soil processes will improve our ability to predict how shifts in species composition may alter ecosystem processes such as decomposition rates on a broad scale. However, evidence pointing to multiple drivers of microbial community response to plant species composition, which is the functional link between plant species traits and the soil process rates being measured, reveals another important consideration. Understanding and predicting such fine resolution mechanisms driving soil processes may be where a broader consideration of suites of species' traits, such as between *E. repens* and *B. inermis*, becomes important. More detailed studies examining the microbial community are imperative to fully understanding the mechanistic driver or drivers responsible for changes in soil processes.

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