Plant functional group identity differentially affects leaf and root decomposition

JENNIE R. McLAREN and ROY TURKINGTON

Department of Botany, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

Abstract

Losses of species and changes in the composition of plant communities are likely to influence numerous ecosystem functions. Changes in the plant-soil interactions that control decomposition, in particular, could alter carbon and nutrient cycling in soils and further alter other ecosystem functions. The effects of plant communities on decomposition may depend both on the type of tissue being decomposed and also on the different stages of the decomposition process. We used an experimental design where single plant functional groups were removed from a northern grassland to examine the role of plant identity in determining both short-term and long-term above- and belowground decomposition rates. Plant removals were conducted across fertilization and fungicide treatments to examine environmental context-dependency of functional group identity effects on decomposition. There were significant effects of plant functional group identity on aboveground decomposition, with the loss of grasses and forbs slowing decomposition, whereas the effects on belowground decomposition were rare and transient. Effects of plant identity on decomposition were consistent in both short- and long-term decomposition studies indicating that the influences of identity on the decomposition environment remained consistent throughout the different stages of the decomposition process. Both fertilizer and fungicide treatments affected overall decomposition rate, but there were few interactions between these treatments and plant removals. Although current species loss is likely to be happening in concert with environmental changes, the role a species plays in determining ecosystem functions such as decomposition may not be context-dependent in these northern environments, and this may provide greater predictive power in determining the effects of species loss with changing environments. Further, as plant identity shows significant effects on litter decomposition rates, the effects of current and predicted future biodiversity losses may depend specifically on which species are lost.

Keywords: biodiversity, decomposition, ecosystem function, fertilization, long-term decomposition, mycorrhizae, removal experiment, root decomposition

Received 7 October 2009 and accepted 12 November 2009

Introduction

Biodiversity loss is one of the largest impacts humans have had on ecosystems during this past century and there is a growing concern on the potential effects of this loss. This concern has led to numerous studies examining whether current losses in biodiversity will negatively affect the functioning of ecosystems (Hooper *et al.*, 2005; Balvanera *et al.*, 2006; Cardinale *et al.*, 2006, 2007; Duffy, 2009). Loss of species or functional groups necessarily affects the composition of communities and it has often been reported that the effects of community composition can be just as important as those of changing species diversity (see Hooper & Vitousek, 1998; Scherer-Lorenzen *et al.*, 2003). Studies are rare that directly examine the role of the type, rather than the number, of species on ecosystem functioning through influences on both the abiotic and biotic environment.

The majority of studies examining the effects of biodiversity on ecosystem functioning have focused on the impacts of changing plant diversity on primary productivity, whereas other ecosystem functions such as soil nutrient availability and decomposer activity have been less frequently studied (Hooper *et al.*, 2005; Balvanera *et al.*, 2006). Although there is consistent evidence for a positive relationship between plant diversity and primary productivity (Balvanera *et al.*, 2006; Cardinale *et al.*, 2006), reported effects of plant diversity on litter decomposition processes are less clear (Hector *et al.*, 2000; Knops *et al.*, 2001; Wardle *et al.*, 2006). Soils hold more than twice as much carbon as vegetation or the atmosphere (Jobbagy & Jackson, 2000), and influence over decomposition processes not only affects the incorporation of vegetation carbon into the soils, but also the early stages of its release back into the atmosphere. Between 50% and 90% of all primary

Correspondence: Jennie McLaren, tel. + 1 604 822 2141, fax + 1 604 822 6089, e-mail: jmclaren@interchange.ubc.ca

productivity will enter detrital food webs (McNaughton et al., 1989) and decomposition of this material provides a major source of carbon and nutrients to the soils, and is thus an important determinant of other ecosystem functions such as productivity and nutrient cycling. Most previous studies have used artificially constructed communities, such as diversity gradients (Hector et al., 2000; Milcu et al., 2008; Scherer-Lorenzen, 2008) or plant monocultures (Hobbie et al., 2006), to examine plant-driven environmental effects on decomposition. However, Diaz et al. (2003) argue that it is preferable to remove species or functional groups from established natural communities because they take place in communities that have undergone natural assembly processes and have natural species abundances.

Large scale variation in climate is the most important determinant of the rate of litter decomposition (Aerts, 1997) but the rate is also controlled by local conditions such as variation in soil moisture (Bryant et al., 1998), soil nutrients (Knorr et al., 2005) and the decomposer community (Dang et al., 2005). The identity and composition of the plant community itself can influence these same local conditions, such as soil moisture and nutrients (Hooper & Vitousek, 1997; McLaren & Turkington, in press), thus potentially influencing decomposition through changes in the local decomposition environment. Although numerous studies have examined environmental influences on decomposition (e.g. Hobbie, 1996; Prescott et al., 1999), only a few have examined plant-driven environmental influences and these often report weak (Hector et al., 2000) or no significant effects (Knops et al., 2001) (although see Ashton et al., 2005; Hobbie et al., 2006). Further, the effects of plant composition on decomposition may be context-dependent on environmental conditions. The processes that are currently causing a shift in the environmental properties of ecosystems, such as nitrogen deposition, can also result in the loss or changes in the types of species present in a community (Hooper et al., 2005). Few experiments, however, examine the effects of diversity on ecosystem properties in more than one environmental context.

Most litter decomposition studies are relatively short-term, often only occurring for a single growing season. In tropical regions most dead plant material will completely decompose in a single season, but in more temperate regions up to 70% of leaf tissue can still remain after the first year (Aerts, 1997) and longer-term experiments are necessary. Although climatic influences on longer-term litter decomposition are often assumed to be similar to those on first year litter decomposition (Aerts, 1997), the phase of the decomposition process has been shown to determine both the chemical control of decomposition (Berg et al., 1996) and element loss from litter (Rustad, 1994). Both litter quality and quantity change through time with the easily decomposable material disappearing first resulting in the accumulation of more recalcitrant material (Harmon et al., 2009). Thus, it may be inappropriate to extrapolate plant-driven control over short-term litter decomposition patterns to patterns of longer-term decomposition, especially in northern ecosystems where litter decomposes very slowly.

A large proportion of the plant biomass available for decomposition is root tissue, especially in grasslands (Seastedt, 1988). Soil organic matter in grasslands originates primarily from root death and decomposition (Gill & Burke, 2002) and root decomposition is a major source of carbon and nutrient turn-over in most systems (Dornbush et al., 2002). Despite the important influence on ecosystem carbon dynamics, few general principles have been defined for the factors that affect root decomposition rates (Silver & Miya, 2001). Decomposing roots are buried and thus experience different moisture conditions, microbial communities and nutrient availability than leaves (Ostertag & Hobbie, 1999) and the extremes in these environmental variables may be buffered in the soil (Silver & Miya, 2001).

In this study, we examined the influence of plant functional group identity on decomposition rates of leaf and root material over both short-term (single growing season) and long-term (up to 5 years) decomposition processes. We removed single functional groups (graminoids, legumes and nonleguminous forbs) from a series of plots in a northern grassland. We examined whether the influence of a functional group on decomposition rates was dependent on environmental context, by conducting these removals under different fertilization and mycorrhizal environments. These environments were chosen to represent different 'environmental contexts', and both are relevant to future environmental change.

Materials and methods

This removal experiment was part of a larger experiment examining the role of plant functional group identity in determining various ecosystem functions. McLaren & Turkington (in press), describe the methods in detail, and they are in described briefly below.

Site description

The study area is a dry grassland near Kluane Lake in the south-western Yukon in northern Canada (61°04.218N 138°23.018W). The area receives a mean annual precipitation of ca. 230 mm, about half of which falls as rain during the summer, but also includes an average annual snowfall of about 100 cm. The grassland is surrounded by a closed to relatively open spruce forest community dominated by *Picea glauca* (Moench) Voss. Grassland species were divided into three

functional groups, namely, graminoids (grasses and sedges; dominated by *Poa glauca* Vahl and *Carex stenophylla* Wahlenb. ssp. *eleocharis* (Bailey) Hultén), forbs (dominated by *Erigeron caespitosus* Nutt., *Artemisia frigida* Willd.), and legumes (dominated by *Oxytropis campestris* (L.) DC.); all nomenclature follows Cody (2000).

Experimental plant communities

Experimental plots were established in May 2003 and maintained annually for 5 years through the 2007 growing season. The experiment was a $4 \times 2 \times 2$ fully crossed factorial design (4 removal treatments, $+$/0 fertilizer, $+$/0 fungicide). Each of the 16 treatments was replicated five times, for a total of 80 plots.

There were four removal treatments: independent removal of each of the three functional groups (graminoids, forbs and legumes) and a no-removal control. In 2003, plants were removed from the plots using Round-up™ glyphosate, a nonselective herbicide. Herbicide was painted precisely to the leaves and once plants had visibly yellowed, stems of selected plants were clipped at soil level and removed from the plots. Removal treatments were maintained in 2004 using herbicide application and clipping, and in the subsequent 3 years the very minimal regrowth was clipped at ground level early in the growing season.

Fertilizer and fungicide treatments were applied upon completion of the removals (July 20) in 2003 and in early June of each subsequent year. Fertilizer was applied each year to half the plots in granular form at a rate of $17.5 \, \text{g N m}^{-2}$, $5.8 \, \text{g P m}^{-2}$ and $5.8 \, \text{g K m}^{-2}$. This application rate was used to be consistent with many other studies being done in the area (e.g. John & Turkington, 1997; Turkington *et al.*, 2002). Half of the plots received the fungicide Benlate™ (active ingredient benomyl) as a soil drench ($2 \, \text{L m}^{-2}$ plot) every 2 weeks from early-June to mid-August at a rate of $2.5 \, \text{g benomyl m}^{-2}$ per application, and the other half of the plots received an equivalent amount of water. Benomyl applications reduced mycorrhizal colonization rates from 50% to <10% of root intersections (J. McLaren, unpublished data).

Decomposition experiment

Fresh leaf and root material from *Elymus trachycaulus* (Link) Gould ex Shinners collected near Kluane Lake, YT, was dried at 40 °C for 48 h and placed separately in $10 \times 5 \, \text{cm}$ litter bags made from 1 mm mesh nylon screening. *E. trachycaulus* was chosen because sufficient leaf and root material was available, and it was present, but not dominant, in the experimental area.

Aboveground litter bags contained 0.5 g of dried leaf material; leaves were collected and cut into 8 cm lengths so as to fit into the litter bags. Belowground litter bags contained 0.25 g of dried root material; roots were washed free of soil and the 0.5–2 mm diameter size class was separated out. Aboveground bags were placed into gaps in the vegetation, in contact with the litter layer, and secured to the surface. Belowground bags were sprayed with water before being inserted into the soil to a depth of 7 cm (the majority of the roots in this system are within this depth) at an angle of 45°, and secured to the surface with a nylon tether.

We examined both single-season (short-term) and multiple-year (long-term) decomposition for leaf and root litter. For long-term decomposition, five aboveground and belowground bags were placed into each plot in mid-July 2003, once the experimental communities had been established. One of each type of litter bag was collected in mid-August of each year, after the plants in the surrounding community had senesced, from 2003 to 2007. In the fourth year of the study (2006) onward, only aboveground bags were processed due to our inability to distinguish between root litter and root growth penetration of the belowground bags. To measure short-term decomposition, an additional replicate for both above- and belowground bags was placed into the plots in early-June of each year between 2004 and 2006 and collected at the end of that growing season (i.e., mid-August of the same year); thus single growing season decomposition rates were collected for each year. We also determined winter decomposition rates for a single season: bags of each type were placed into plots in mid-August 2005, and removed in early-June 2006. After removal from plots, decomposed leaf and root litter was removed from the bags, dried at 60 °C for 48 h and weighed. 'Loss bags' were created for each year and litter bag type; bags were carried into the field, and returned to the laboratory to determine handling loss, and initial litter bag weights were corrected depending on handling loss.

Fresh plant material was used for both the above- and belowground decomposition experiments. Although senesced material is often preferable for decomposition studies, fresh plant material was used as a standard substrate to assess the effects of our treatments on decomposition through effects on the decomposition microenvironment and decomposer activity because it was easy to collect, and sufficient green material was available for the number of replicates required. We chose to use dried green plant material as a standard substrate, rather than cotton strips or filter paper, as the plant material more closely resembles natural sources of decomposition. However, to determine whether effects of functional group removals would differ for fresh and senesced plant material, in the 2006 growing season, an additional set of aboveground litter bags was created using freshly senesced litter collected in August 2005. No belowground bags were created for these replicates; freshly senesced root material is difficult to distinguish from older root material, and many root decomposition studies use live roots (Ostertag & Hobbie, 1999).

Analysis

Decomposition is expressed as a percent loss of mass based on oven-dry mass of litter pre- and postcollection. Single-season decomposition rates were analyzed using a four-way ANOVA on percent decomposition with the main effects being functional group removal, fertilizer, fungicide, and year (considered a nominal variable). Multiyear decomposition rates were analyzed using a four-way ANOVA on percent decomposition with the main effects being functional group removal, fertilizer, fungicide and number of years since establishment

(considered a continuous variable). When there was a significant interaction with year, or between environments, analyses were run independently for each year or environment level. Winter decomposition bags and bags containing senesced litter (both single year analyses) were analyzed using a three-way ANOVA with the main effects being functional group removal, fertilizer, and fungicide. For all analyses, when removal treatments were significantly different, they were compared using a Tukey's post-hoc comparison of means. All data fit the assumptions of the ANOVA and no transformations were required. All analyses were conducted using JMP statistical software (2003 SAS Institute, Cary, NC, USA).

Results

Aboveground decomposition

Aboveground decomposition was affected by plant functional group identity (Table 1); specifically, removal of grass and forb functional groups significantly decreased single-season leaf decomposition rates (Fig. 1a). The effect of plant functional group removal did not interact with any other environmental variable (fertilizer or fungicide) (Table 1). Fertilization also had no direct effect on the single-season decomposition rate (Table 1). Fungicide, however, affected decomposition directly, resulting in a decrease in the single-season leaf decomposition rate (Table 1, Mean proportion litter remaining 0.638 ± 0.005 no fungicide vs. 0.656 ± 0.005 fungicide). The relative pattern of aboveground decomposition remained the same in the winter (Removal: $F_{3,80} = 5.36$, $P = 0.002$; Fig. 2a) although only grass, not forb, removal resulted in a significant response. Likewise, in winter, aboveground decomposition but was not affected by fertilizer (Fertilizer: $F_{1,80} = 1.79$,

$P = 0.19$) but decreased with fungicide application (Fungicide: $F_{1,80} = 8.00$, $P = 0.006$; Mean proportion litter remaining 0.655 ± 0.008 no fungicide vs. 0.690 ± 0.010 fungicide).

Long-term aboveground decomposition was also affected by functional group identity (Table 2); specifically, removal of the grass functional group significantly decreased the multipleyear leaf decomposition rates (Fig. 1c). The effect of removals did not vary across years decomposed, fertilizer or fungicide treatments (no interactions with Removal, Table 2). There was a significant Fungicide × Fertilizer interaction (Table 2), although when analyzed independently across fungicide levels, fertilizer did not affect decomposition either with ($F_{1,200} = 0.32$, $P = 0.57$) or without ($F_{1,200} = 2.84$, $P = 0.09$) fungicide.

Belowground decomposition

Functional group removals did not affect single-season decomposition rates (Fig. 1b). The effect of removals on single-season belowground decomposition depended on year (Table 1) being significant only in 2003 (2003 Removal: $F_{3,80} = 4.56$, $P = 0.006$), when removal of legumes decreased decomposition rates below the no-removal plots. Neither environmental variable, fungicide nor fertilizer, had any effect on single-season belowground root decomposition (Table 1). The effect of functional group removals on winter belowground decomposition rates depended on fertilizer (Removal × Fertilizer: $F_{3,80} = 6.28$, $P = 0.001$). In non-fertilized plots, functional group removal had a significant effect on decomposition rate (Removal: $F_{3,80} = 5.09$, $P = 0.005$) with loss of forbs resulting in slower decomposition

Table 1 Summary of four-way ANOVA for single-season leaf decomposition (2003–2006) and root decomposition (2003–2006)

Source	df	F_{leaf}	Prob$_{leaf}$	F_{root}	Prob$_{root}$
Removal	3	**17.565**	**<0.001**	0.607	0.611
Fungicide	1	**7.934**	**0.005**	0.011	0.916
Fertilizer	1	1.270	0.261	2.108	0.148
Year	3	**29.927**	**<0.001**	**46.104**	**<0.001**
Removal × Fungicide	3	1.645	0.179	1.511	0.212
Removal × Fertilizer	3	0.249	0.862	0.200	0.896
Removal × Year	3	1.169	0.315	**1.942**	**0.047**
Fungicide × Fertilizer	1	0.001	0.981	0.067	0.795
Fungicide × Year	1	0.700	0.553	1.295	0.277
Fertilizer × Year	1	0.927	0.428	0.897	0.443
Removal × Fungicide × Fertilizer	3	0.973	0.406	0.991	0.397
Removal × Fungicide × Year	3	0.663	0.742	1.120	0.349
Removal × Fertilizer × Year	3	1.010	0.432	0.357	0.954
Fungicide × Fertilizer × Year	1	1.222	0.302	1.493	0.217
Removal × Fungicide × Fertilizer × Year	3	0.888	0.536	0.840	0.580

Bold values are significant at $P < 0.05$.
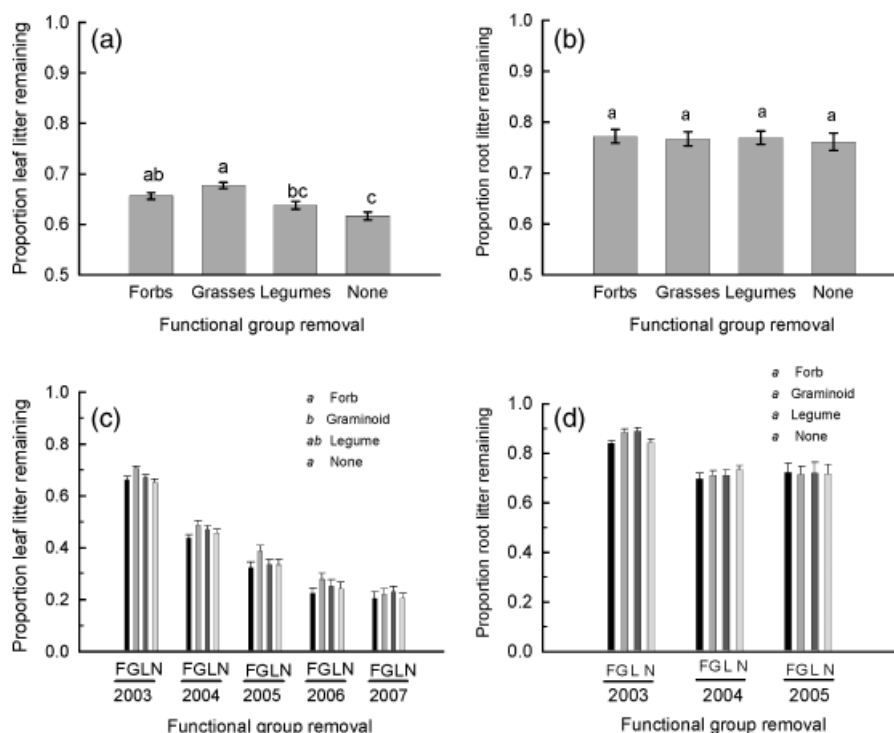
Fig. 1 Mean (+1 SE) proportion material remaining in different plant functional group removal treatments for (a) single season leaf decomposition 2003–2006 (b) single season root decomposition 2004–2006 (c) multiple season leaf decomposition 2003–2007 and (d) multiple season root decomposition 2003–2005. Different letters indicate significant differences between removal treatments (Tukey's comparison of all means). Removal treatments did not interact with year for multiple season decomposition (c and d), and thus Tukey's comparison of all means is pooled across years.

than loss of grasses (Fig. 2b). In fertilized plots, removal had no effect on decomposition rate (Removal: $F_{3,80} = 2.60$, $P = 0.07$, Fig. 2c). There was no effect of removal on long-term belowground decomposition rate (Table 2, Fig. 1d). There was a significant interaction between fertilizer and years since establishment (Table 2), but in independent yearly analyses there was no significant effect of fertilizer in any year.

Fresh vs. senesced leaves

The effect of functional group removals on decomposition for senesced leaves was similar to that of fresh leaves, although only grass, not forb, removal resulted in a significant response (Removal: $F_{3,80} = 5.95$, $P < 0.001$; Fig. 3). The direct effects of environmental treatments on decomposition differed between green and senesced leaves. Fertilizer increased decomposition of the senesced leaves (Fertilizer: $F_{1,80} = 4.70$, $P = 0.03$; Mean proportion litter remaining 0.906 ± 0.007 no fertilizer vs. 0.888 ± 0.006 fertilizer) whereas fungicide application had no effect (Fungicide: $F_{1,80} = 3.31$, $P = 0.07$).

Discussion

In this study, we show that plant functional group identity has a direct influence on aboveground decomposition rates by changing the decomposition microenvironment and that the importance of functional group identity differed between above- and belowground decomposition. For aboveground decomposition, both grasses and forbs create a microenvironment that increases the rate of decomposition, but the effects of identity on belowground decomposition are less frequent and transient. Further, we show that functional group identity affects both short-term and long-term decomposition rates in the same way, despite the nature of the decomposing material changing through time.

Above-ground decomposition

This is one of only a few studies to report significant effects of the living plant community composition on decomposition rates; plant functional groups affect short-term aboveground decomposition differentially, with the removal of grasses and legumes both slowing
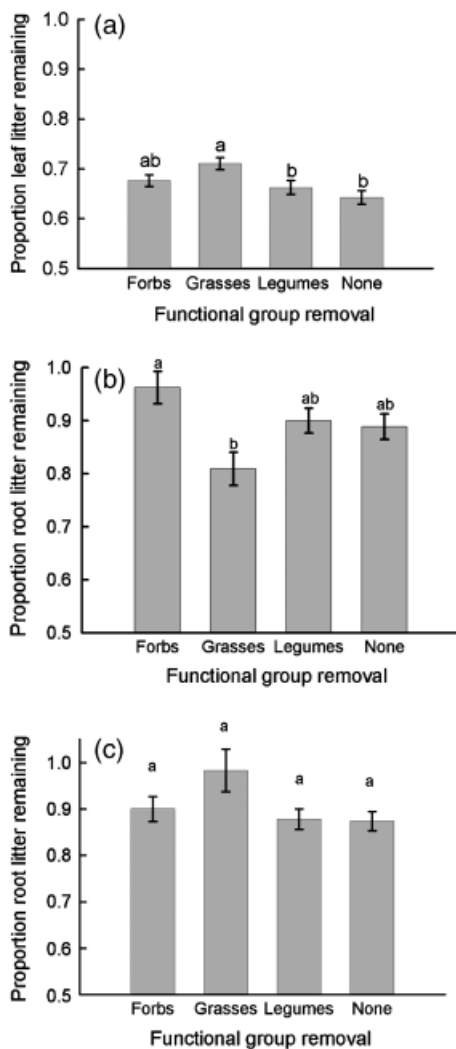
Fig. 2 Mean (±SE) proportion material remaining in different plant functional group removal treatments for winter decomposition in (a) leaves, (b) roots in unfertilized plots and (c) roots in fertilized plots. Different letters indicate significant differences between removal treatments (Tukey's comparison of all means).

decomposition. Earlier work on environmental effects on decomposition focused on large-scale environment-driven decomposition (Hobbie, 1996; Prescott et al., 1999), but predicted losses of plant diversity and changes in community composition have resulted in recent interest in the potential for plant-driven effects on decomposition. Effects of the surrounding plant community diversity on decomposition are rare (Knops et al., 2001; Milcu et al., 2008; but see Scherer-Lorenzen, 2008), but effects through changing plant composition are more common (Hobbie et al., 2006; Vivanco & Austin, 2008). Wardle et al. (1999) had to remove all of the vegetation before he detected an effect on the decomposer food chain, and in later studies he showed that removal of different shrub species slowed the rate

of decomposition (Wardle & Zackrisson, 2005; Jonsson & Wardle, 2008).

Removals had similar effects on decomposition in winter as in summer, with removal of grasses slowing decomposition. During winter, microclimatic differences between vegetation types may be minimized by snow cover (Moore, 1984). The maintenance of functional group differences in these conditions provides evidence that the grasses may increase the rate of decomposition through effects on the biotic, rather than abiotic, decomposition environment. In addition to differences between functional groups, similar amounts of leaf material were lost over winter as during the growing season. Although perhaps unexpected, in northern ecosystems much of the litter decomposition occurs over the winter months, when the soil is mainly frozen (Moore, 1984; Hobbie & Chapin, 1996). Our over-winter leaf decomposition was measured during the nongrowing season and includes the fall freeze-up and spring melt and substantial decomposition occurs during these seasons. Litter mass loss may be due to physical processes associated with freezing and-thawing (Hobbie & Chapin, 1996) or possibly due to microbial decomposition of the litter, as soil respiration has been measured at temperatures below 0 °C (Brooks et al., 1996).

Decomposition studies rarely examine longer-term processes, with many studies being a single year and 3 years the maximum for most (Aerts et al., 2006; Harmon et al., 2009). The mechanisms behind short-term decomposition likely differ from longer-term decomposition, where the more recalcitrant material remains, and long-term decomposition may be less influenced by differences in environmental conditions (Harmon et al., 2009). In our study, the removal of grasses consistently decreased decomposition rates through the first 5 years of decomposition, and functional group removals had the same effects on both short-term and long-term decomposition rates. Although the material decomposing changes over time, and thus the decomposition processes also change, the influences of the different plant functional group remained consistent.

The ability of grasses and forbs to increase the rate of decomposition may be through changes in the abiotic or biotic (decomposer community) environment. Few of the previous studies reporting plant-driven effects on decomposition identified a mechanism for these effects but they have suggested both changes in the abiotic environment through temperature effects (Hobbie et al., 2006) and in the biotic environment with changes in the decomposer community occurring with plant invasion (Ashton et al., 2005). In a concurrent study we characterized the influence of these functional groups on

Table 2 Summary of four-way ANOVA for multi-year growing season leaf decomposition (2003–2006) and root decomposition (2003–2005)

Source	df	F_{leaf}	$Prob_{leaf}$	F_{root}	$Prob_{root}$
Removal	3	**4.580**	**0.004**	0.348	0.791
Fungicide	1	0.115	0.734	2.408	0.122
Fertilizer	1	2.194	0.139	1.620	0.205
Year	1	**1144.439**	**<0.001**	**59.465**	**<0.001**
Removal × Fungicide	3	1.642	0.179	1.637	0.182
Removal × Fertilizer	3	0.115	0.951	0.721	0.540
Removal × Year	3	0.877	0.842	0.561	0.642
Fungicide × Fertilizer	1	**9.618**	**0.002**	1.091	0.298
Fungicide × Year	1	3.427	0.065	0.007	0.934
Fertilizer × Year	1	0.014	0.906	**3.911**	**0.049**
Removal × Fungicide × Fertilizer	3	0.957	0.413	1.307	0.273
Removal × Fungicide × Year	3	2.093	0.101	0.661	0.577
Removal × Fertilizer × Year	3	1.561	0.199	0.666	0.574
Fungicide × Fertilizer × Year	1	1.191	0.276	0.002	0.960
Removal × Fungicide × Fertilizer × Year	3	0.908	0.437	1.853	0.139

Bold values are significant at $P < 0.05$.
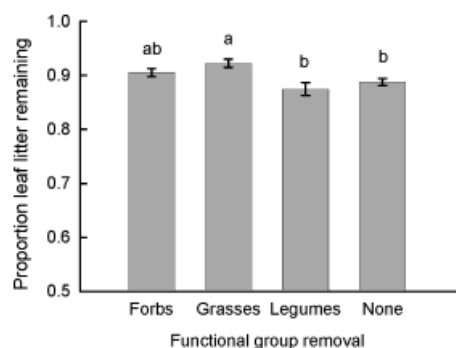
Fig. 3 Mean (±SE) proportion of leaf material remaining in different plant functional group removal treatments for senesced leaves. Different letters indicate significant differences between removal treatments (Tukey's comparison of all means).

numerous soil properties (McLaren & Turkington, in press). Abiotic photo-degradation may be an important component of decomposition in dry grasslands (Parton *et al.*, 2007), but functional groups showed no difference in their effects on light interception (McLaren & Turkington, in press). Further, plants may compete with saprobes for nutrients (Moorhead *et al.*, 1998) and this may be affected by the different competitive abilities of the functional groups. Although we earlier reported an effect of functional group identity on soil nutrients (McLaren & Turkington, in press), there was no effect of fertilization on decomposition in this study, suggesting that limitation of nutrients by plant competition would not produce the observed effects. Finally, the presence of forbs and grasses decreased soil moisture (McLaren & Turkington, in press) which we predict

would have a negative effect on decomposition in this dry ecosystem, not the positive influence of these groups as observed. Finally, in this same community, Marshall (2008) was unable to detect any effect of plant functional group identity on the soil microbial community as measured by changes in substrate induced respiration or PLFA profiles. The methods used to examine the microbial community, however, may not be adequately sensitive. Because grass leaves were used as the decomposition substrate, there is a possibility that by removing grasses as a treatment we may have lost their associated microbiota that may be required for grass decomposition – however, this would not explain the negative effect we similarly detected when we removed forbs. Thus, none of the biotic or abiotic variables we measured (light interception, soil nutrients and soil moisture) can account for our observed effects of functional groups on decomposition rates. Clearly there are other effects of functional groups on the decomposition environment, either abiotic or biotic, that we did not measure which are responsible for functional group identity effects on decomposition. For example, Hobbie *et al.* (2006) reported that the effects of trees on soil temperature may affect litter decomposition.

A concern with using removal experiments to examine effects of plant composition on decomposition rates is that the removal effects may confounded by the differing amounts of aboveground biomass removed with each treatment, or to differing amounts of below-ground biomass remaining (and decomposing) after removals. The functional groups removed in this experiment all have significantly different aboveground

biomass, with the removal of the most biomass in the forb removal treatment and the least with legume removals (McLaren & Turkington, in press). Although we did not directly account for differing amounts of biomass removed we conclude that the effects of removals on decomposition are not due simply to differences in biomass between removal treatments because grasses were not the dominant functional group in this community yet they had the most consistent positive effect on decomposition. Differing amounts and qualities of roots decomposing in the soils are more difficult to account for, and potential effects of these are often ignored in removal experiments. One would predict that the effects of these roots would decrease through time, as the biomass becomes incorporated into the soil. The effects of removals on short-term decomposition, however, are consistent across all 5 years for aboveground decomposition, and after the first year for belowground effects, and we are confident that the effects of decomposing roots resulting from removals play, at most, a minor role in the effects of functional group composition on litter decomposition.

The effect of plant functional group identity on aboveground decomposition was not context-dependent for either fertilization or fungicide treatments. These treatments were chosen to represent different 'environmental contexts' and both are relevant to future environmental change. Global warming is expected to cause an increase in soil nutrient levels, especially in northern latitudes, because higher temperatures increase mineralization rates of both nitrogen and phosphorus (Chapin et al., 1995; Shaver et al., 2000). Additionally, the presence of mycorrhizal fungi may change a plant's response to changes in nutrient status. Soil nitrogen levels influence both the functioning of mycorrhizae and also their degree of mutualism with plants (Johnson, 1993). In addition to not having an interaction with the removal treatments, fertilization had no effect on aboveground decomposition directly during either the growing season or during the winter. The effect of fertilization is variable in different systems and has been reported to accelerate the rate of decomposition (Madritch & Hunter, 2003), have no effect (Hobbie, 2000) or slow the rate of decomposition (Prescott et al., 1999) and may be highly dependent on the quality of the litter (Prescott et al., 1999; Hobbie, 2000; Knorr et al., 2005). The direct effect of fungicide, in contrast, was a slowing of leaf decomposition during both seasons. We expected that fungicide treatment would decrease mycorrhizal colonization rates and thereby increase decomposition because mycorrhizal infected plants may better be able to compete with soil saprobes for nutrients (Christensen & Jakobsen, 1993). The decrease in decomposition rate may be the result of

a few different mechanisms. The saprophytic fungi may have been negatively affected by benomyl application resulting in a decreased decomposition rate. A related study in the fifth season of this project, however, found that fungicide did not affect PLFA profiles or total fungal biomass of the soil flora (Marshall, 2008). As such, any effect of fungicide on soil saprophytic fungi would likely be positive (compensating for the loss of mycorrhizae), resulting in a positive effect on decomposition. Alternatively, arbuscular mycorrhizae have been reported to have direct saprotrophic capabilities (Hodge et al., 2001), and may have had a direct role in decomposing the leaves.

We used fresh leaf material, rather than senesced litter, as the standard decomposition source. Although decomposition rates of fresh litter were faster than senesced litter, the effect of functional group removals was similar for the two litter types, with removal of grasses decreasing decomposition rate in both fresh and senesced litter. Additionally, the effect of identity on litter decomposition was not context dependent for either decomposition material. Thus the fresh litter used in this experiment provides an appropriate approximation for the effect of functional group removals on litter decomposition. The direct effects of the environmental context (fungicide and fertilizer) did differ between the two materials. Although fungicide slowed decomposition of fresh material, there was no effect on the senesced litter. In contrast, fertilizer had no effect on fresh material, yet accelerated the decomposition of senesced litter. We would have predicted the opposite result, as we considered the fresh litter to be a higher quality litter (both because of its lower C:N and faster decomposition) which is expected to be more limited by fertility levels whereas low quality litter is more limited by carbon (Prescott et al., 1999; Hobbie, 2000; Knorr et al., 2005).

Belowground decomposition

Neither short-term nor long-term root decomposition were influenced by functional group removals. In contrast with leaves, root decay rates are often much more closely linked with root quality as opposed to environmental parameters (Silver & Miya, 2001). This is likely because roots occur in the soil and both they, and the community of decomposers, are well buffered from environmental extremes (Silver & Miya, 2001). Therefore, the plant community may have little effect on root decomposition rates unless they affect the quality of the root tissue itself, through compositional changes or changes in soil fertility levels – an effect that was not be measured in this study.

The only effects of functional group removals on belowground decomposition were transient effects on short-term decomposition, and did not parallel those for leaf decomposition. During the first growing season after removal treatments were established, removal of legumes caused a decrease in decomposition rate. Fertilization had no effect on root decomposition so it is not likely that the effects of legume removal are due to the loss of their nitrogen fixation abilities from the community. Although the effects were transient, it is also unlikely to be a direct effect of the removals as the legumes had the least biomass removed of all three removal treatments (McLaren & Turkington, in press). The identity of the surrounding plant community could positively affect root decomposition through a variety of mechanisms. Living roots, depending on species, exude a variety of different rhizodeposits (Clarholm, 1985), easily metabolizable carbon compounds that may enhance microbial degradation. Different functional groups may dry out the soil at different rates (McLaren *et al.*, 2004) and drying and rewetting of soils can both increase and decrease the rate of root decomposition (van der Krift *et al.*, 2002).

In contrast to winter leaf decomposition, effects of removals on winter root decomposition differed from those during the growing season, and were also dependent on fertilizer application. Without fertilizer, removal of forbs slowed decomposition rate while removal of grasses increased the rate. Although the type of roots used in the litter bags were the same in the different removal treatments, the general decomposition environment may be altered by the quality of the other associated roots of the living species. Decomposition rates have been reported to be negatively correlated with root C : N (Silver & Miya, 2001) and grasses are often characterized by their high C : N and low decomposability (Wardle *et al.*, 1997). Thus, removing grasses from a community may decrease the overall C : N of the root material, improving resource conditions for decomposers. Conversely, removal of forbs should increase the proportion of high C : N grass roots in the community, creating poorer conditions for decomposition. The effect of removal disappeared with fertilization – the additional nutrients would likely swamp any differences in resource availability due to changes in C : N in the roots.

In conclusion, we show that the composition of the living plant community influences aboveground decomposition rates through effects on the decomposition microenvironment. Grasses and forbs both promote decomposition, thus changes in plant community composition may result in shifts in the carbon dynamics of this northern ecosystem. These effects of the surrounding plant community may be tempered, in part, by the lack of influence on root decomposition, which is buffered by the soil environment. Although both fertilizer and fungicide influenced overall decomposition rates, there were few interactions between removal treatments and these environmental variables. Species change is currently happening in concert with environmental change, and therefore to predict the microenvironment effects of species loss, we must understand the role that different plant species will play in this new environment. We have shown that the roles of different plant functional groups remain constant within an ecosystem, even if the environmental variables differ, and this provides us with much greater predictive power in determining the effects of species loss on ecosystem functioning.

Acknowledgements

References

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.

Aerts R, van Logtestijn R, Karlsson PS (2006) Nitrogen supply differentially affects litter decomposition rates and nitrogen dynamics of sub-arctic bog species. *Oecologia*, **146**, 652–658.

Ashton IW, Hyatt LA, Howe KM, Gurevitch J, Lerdau MT (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecological Applications*, **15**, 1263–1272.

Balvanera P, Pfisterer AB, Buchmann N, He JS, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.

Berg B, Ekbohm G, Johansson MB, McClaugherty C, Rutigliano F, DeSanto AV (1996) Maximum decomposition limits of forest litter types: a synthesis. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **74**, 659–672.

Brooks PD, Williams MW, Schmidt SK (1996) Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry*, **32**, 93–113.

Bryant DM, Holland EA, Seastedt TR, Walker MD (1998) Analysis of litter decomposition in an alpine tundra. *Canadian Journal of Botany*, **76**, 1295–1304.

Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–992.

Cardinale BJ, Wright JP, Cadotte MW *et al.* (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18123–18128.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.

Christensen H, Jakobsen I (1993) Reduction of bacterial-growth by a vesicular-arbuscular mycorrhizal fungus in the rhizosphere of cucumber (*Cucumis sativus* L). *Biology and Fertility of Soils*, **15**, 253–258.

Clarholm M (1985) Interactions of bacteria, protozoa and plants leading to mineralization of soil-nitrogen. *Soil Biology & Biochemistry*, **17**, 181–187.

Cody WJ (2000) *Flora of the Yukon Territory*. NRC Research Press, Ottawa.

Dang CK, Chauvet E, Gessner MO (2005) Magnitude and variability of process rates in fungal diversity-litter decomposition relationships. *Ecology Letters*, **8**, 1129–1137.

Diaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution*, **18**, 140–146.

Dornbush ME, Isenhart TM, Raich JW (2002) Quantifying fine-root decomposition: an alternative to buried litterbags. *Ecology*, **83**, 2985–2990.

Duffy JE (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, **7**, 437–444.

Gill RA, Burke IC (2002) Influence of soil depth on the decomposition of *Bouteloua gracilis* roots in the shortgrass steppe. *Plant and Soil*, **241**, 233–242.

Harmon ME, Silver WL, Fasth B *et al.* (2009) Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. *Global Change Biology*, **15**, 1320–1338.

Hector A, Beale AJ, Minns A, Otway SJ, Lawton JH (2000) Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos*, **90**, 357–371.

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503–522.

Hobbie SE (2000) Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian Montane forest. *Ecosystems*, **3**, 484–494.

Hobbie SE, Chapin FS (1996) Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry*, **35**, 327–338.

Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karolewski P (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology*, **87**, 2288–2297.

Hodge A, Campbell CD, Fitter AH (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature*, **413**, 297–299.

Hooper DU, Chapin FS, Ewel JJ *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.

Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs*, **68**, 121–149.

Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, **10**, 423–436.

John E, Turkington R (1997) A 5-year study of the effects of nutrient availability and herbivory on two boreal forest herbs. *Journal of Ecology*, **85**, 419–430.

Johnson NC (1993) Can fertilization of soil select less mutualistic mycorrhizae. *Ecological Applications*, **3**, 749–757.

Jonsson M, Wardle DA (2008) Context dependency of litter-mixing effects on decomposition and nutrient release across a long-term chronosequence. *Oikos*, **117**, 1674–1682.

Knops JMH, Wedin D, Tilman D (2001) Biodiversity and decomposition in experimental grassland ecosystems. *Oecologia*, **126**, 429–433.

Knorr M, Frey SD, Curtis PS (2005) Nitrogen additions and litter decomposition: a meta-analysis. *Ecology*, **86**, 3252–3257.

Madritch MD, Hunter MD (2003) Intraspecific litter diversity and nitrogen deposition affect nutrient dynamics and soil respiration. *Oecologia*, **136**, 124–128.

Marshall CB (2008) *Effects of plant functional group removal on soil microbial diversity and composition*. MSc Thesis, University of British Columbia, Vancouver, 93 pp.

McLaren JR, Turkington R (in press) Ecosystem properties determined by plant functional group identity. *Journal of Ecology*.

McLaren JR, Wilson SD, Peltzer DA (2004) Plant feedbacks increase the temporal heterogeneity of soil moisture. *Oikos*, **107**, 199–205.

McNaughton SJ, Oesterheld M, Frank DA, Williams KJ (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, **341**, 142–144.

Milcu A, Partsch S, Scherber C, Weisser WW, Scheu S (2008) Earthworms and legumes control litter decomposition in a plant diversity gradient. *Ecology*, **89**, 1872–1882.

Moore TR (1984) Litter decomposition in a subarctic Spruce-Lichen Woodland, Eastern Canada. *Ecology*, **65**, 299–308.

Moorhead DL, Westerfield MM, Zak JC (1998) Plants retard litter decay in a nutrient-limited soil: a case of exploitative competition? *Oecologia*, **113**, 530–536.

Ostertag R, Hobbie SE (1999) Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. *Oecologia*, **121**, 564–573.

Parton W, Silver WL, Burke IC *et al.* (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, **315**, 361–364.

Prescott CE, Kabzems R, Zabek LM (1999) Effects of fertilization on decomposition rate of *Populus tremuloides* foliar litter in a boreal forest. *Canadian Journal of Forest Research*, **29**, 393–397.

Rustad LE (1994) Element dynamics along a decay continuum in a red spruce ecosystem in Maine, USA. *Ecology*, **75**, 867–879.

Scherer-Lorenzen M (2008) Functional plant diversity affects decomposition processes in experimental grasslands. *Functional Ecology*, **22**, 547–555.

Scherer-Lorenzen M, Palmborg C, Prinz A, Schulze ED (2003) The role of plant diversity and composition for nitrate leaching in grasslands. *Ecology*, **84**, 1539–1552.

Seastedt TR (1988) Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology*, **69**, 59–65.

Shaver GR, Canadell J, Chapin FS *et al.* (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience*, **50**, 871–882.

Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia*, **129**, 407–419.

Turkington R, John E, Watson S, Seccombe-Hett P (2002) The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study. *Journal of Ecology*, **90**, 325–337.

van der Krift TAJ, Kuikman PJ, Berendse F (2002) The effect of living plants on root decomposition of four grass species. *Oikos*, **96**, 36–45.

Vivanco L, Austin AT (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *Journal of Ecology*, **96**, 727–736.

Wardle DA, Bonner KI, Barker GM *et al.* (1999) Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs*, **69**, 535–568.

Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, **79**, 247–258.

Wardle DA, Yeates GW, Barker GM, Bonner KI (2006) The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biology & Biochemistry*, **38**, 1052–1062.

Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. *Nature*, **435**, 806–810.