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Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland

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Key words: *Aegilops triuncialis*, annual grasslands, carbon, decomposition, litter quality, nitrogen, plant invasions, serpentine soil.

Abstract

Invasive plant species alter plant community composition and ecosystem function. In the United States, California native grasslands have been displaced almost completely by invasive annual grasses, with serpentine grasslands being one of the few remaining refugia for California grasslands. This study examined how the invasive annual grass, *Aegilops triuncialis*, has altered decomposition processes in a serpentine annual grassland. Our objectives were to (1) assess how*A. triuncialis* alters primary productivity and litter tissue chemistry, (2) determine whether *A. triuncialis* litter is more recalcitrant to decomposition than native litter, and (3) evaluate whether differences in the soil microbial community in *A. triuncialis*-invaded and native-dominated areas result in different decomposition rates of invasive and/or native plant litter. In invaded plant patches, *A. triuncialis* was approximately 50% of the total plant cover, in contrast to native plant patches in which *A. triuncialis* was not detected and native plants comprised over 90% of the total plant cover. End-of-season aboveground biomass was 2-fold higher in *A. triuncialis* dominated plots compared to native plots; however, there was no significant difference in belowground biomass. Both above- and below-ground plant litter from *A. triuncialis* plots had significantly higher lignin:N and C:N ratios and lower total N, P, and K than litter from native plant plots. Aboveground litter from native plots decomposed more rapidly than litter from *A. triuncialis* plots, although there was no difference in decomposition of belowground tissues. Soil microbial community composition associated with different soil patch types had no effect on decomposition rates. These data suggest that plant invasion impacts decomposition and nutrient cycling through changes in plant community tissue chemistry and biomass production.

Abbreviations: DANR – Department of Analytical and Natural Resources; ICP-AES – inductively coupled plasma-atomic emission spectrometry

Introduction

Plant invasions can have dramatic effects on aboveground plant community composition, often creating near monocultures in what were previously more diverse plant communities (Pal 2004; Zedler and Kercher 2004; Erskine Ogden et al. 2005). Most research, therefore, has focused on questions related to plant demography, plant community composition, and invasive plant management strategies (e.g., DiTomaso et al. 1999; Kedzie-Webb et al. 2001; Meekins and McCarthy 2002). However, there is an increasing appreciation for the impacts of invasive plant species on ecosystem functions (Ehrenfeld 2003). Although soil microorganisms mediate or control many ecosystem processes, relatively little is known about the interactions between soil microbial communities and plant invasions (but see Klironomos 2002; Kourtev et al. 2002a, b; Kourtev et al. 2003; Batten et al. 2006). Given the dramatic effects of invasive plants on aboveground communities, it is reasonable to consider the role plant invasions play belowground. Thus, if invasive plant species change soil microbial community composition, there may be associated effects on microbially mediated ecosystem processes.

Microbial enzymes catalyze many of the chemical reactions that comprise biogeochemical cycling of plant residues (Sylvia et al. 2005). During decomposition, organic compounds are metabolized by soil microorganisms, releasing plant-available nutrients. Labile compounds such as hemicellulose, cellulose, and chitin (from plant residues and dead microbial biomass) are readily degraded, while more recalcitrant compounds such as lignin become part of the more slowly cycling nutrient pool. Since different microorganisms are able to degrade substrates of varying complexity (Sylvia et al. 2005), changes in microbial community composition may lead to altered decomposition rates or pathways.

Plant tissue chemistry also can influence decomposition rates and microbial community composition. Fungi and bacteria typically have C:N ratios about 10 and 4, respectively (Sylvia et al. 2005). Thus, microbial decomposition of substrates with high C:N ratios is limited by N availability, and plant residues with higher C:N and lignin:N ratios are more resistant to decomposition (Hobbie 1992; Hättenschwiler and Vitousek 2000). Additionally, because of the difference in C:N ratios between functional groups, fungi are better able to degrade lower quality (higher C:N) substrates than bacteria. A study by Bossuyt et al. (2001) revealed that substrate quality altered fungal:bacterial ratios, with lower quality substrates (C:N = 108) favoring fungi and higher quality substrates (C:N = 20) favoring bacteria. Given the differences in plant litter chemistry among species and functional groups, changes in plant species composition (e.g., invasion) may influence not only decomposition rates and subsequent release of nutrients into the soil environment (Melillo et al. 1982; Hobbie 1996) but also microbial community composition.

We investigated how the invasion of *Aegilops triuncialis* (barb goatgrass) alters decomposition in a California serpentine grassland. We focused the study on serpentine grasslands, as they are one of the remaining refugia for native California plants, which for the most part have been displaced by invasive species. Previous research showed that *A. triuncialis* changes the soil microbial community composition as it invades these grasslands; despite variation over the two-year study, the invaded and native microbial communities significantly differ in their phospholipid fatty acid composition (Batten et al. 2006). For example, this previous study showed that *A. triuncialis*-invaded soil tended to contain greater amounts of two fatty acid biomarkers for bacterial genera involved in the sulfur cycle (i17:1 and i17:1 ω5c) and of a biomarker for arbuscular mycorrhizal fungi (16:1 ω5c). Additionally, invaded soils contained higher microbial fatty acid diversity than soils dominated by native plant species. In addition, an initial survey of the serpentine grassland revealed that soils invaded by *A. triuncialis* are depleted in a variety of plant nutrients (NO_3^-, P, K, SO_4^{2-}, Ca, Fe, Cu, Zn, and Mn) (K.M. Batten, unpublished data), and that there is more standing end-of-season dead biomass in *A. triuncialis* patches than in native plant patches (K.M. Batten and R.E. Drenovsky, personal observation). We hypothesize that *A. triuncialis* is contributing to these changes in soil chemistry rather than establishing in areas of depleted soil nutrients. At our sites, *A. triuncialis* continued to expand its range by 20–40% into areas previously dominated by native plants from 2000–2003 (Batten et al. 2006). Additionally, its range in California is not limited to low nutrient soils, as were used in this study. *A. triuncialis* can be found in over 20 California counties (Peters et al. 1996), and other authors have studied competitive populations on more nutrient-rich California soils (DiTomaso et al. 2001, Eviner and Chapin 2005), such as those developed from sandstones and shales. Together, these data suggest *A. triuncialis* is a successful competitor and is not confined solely to areas of depleted soil nutrients.

Based on these observations, we addressed the following questions in areas dominated by *A. triuncialis* and in areas dominated by native vegetation. (1) Does *A. triuncialis* significantly alter biomass production patterns? (2) Is *A. triuncialis* litter more recalcitrant to decomposition, leading to the higher standing dead biomass in *A. triuncialis*-dominated plots? (3) If *A. triuncialis* litter is more recalcitrant, are more nutrients ''held'' in this litter, potentially leading to decreased levels of plant-available soil nutrients in invaded areas? (4) Do differences in the soil microbial community in *A. triuncialis*-invaded and native-dominated soils result in different decomposition rates of invasive and/or native plant litter?

Methods

Study species and site characteristics

Our study was conducted in a serpentine grassland located within the University of California Donald and Sylvia McLaughlin Natural Reserve in Yolo, Lake, and Napa Counties, 120 km north of San Francisco, California (USA). The climate is Mediterranean, with cool, wet winters and hot, dry summers. Mean annual precipitation is 725 mm, and mean annual temperature is 18.1 °C. The serpentine soils at this site are derived from mafic and ultramafic substrates. Due to the rocky nature of the soil, plant-rooting depth, in general, is shallow with a few exceptions of deep tap-rooted species (K.M. Batten, personal observation).

The plant communities at the study site are a mosaic of areas dominated by annual native forbs and areas dominated by *A. triuncialis*. Nearly all species at the study site are annual plants that germinate in the winter wet season, flower in early to mid spring, and senesce in early summer. As annuals, all biomass produced by these plants (other than seeds) is litter and therefore a source of nutrients and carbon. In primarily native plant areas, forbs are dominant; whereas, in areas invaded by *A. triuncialis*, grasses are dominant. *A. triuncialis* is a C_3, winter annual grass of Eurasian origin. It was first introduced to California in the early 1900s, spreading quickly throughout the state and decreasing rangeland quality (Peters et al. 1996). Currently, it is listed as a California Department of Food and Agriculture noxious weed (DiTomaso et al. 2001).

Selection and characterization of study plots

In late April 2003, six representative 1 m^2 plots were identified within patches dominated by either native forbs or *A. triuncialis* (for a total of 12 plots). These plots were directly adjacent to plots that had been sampled for microbial community analysis in Batten et al. (2006). Disturbance from previous soil sampling prevented us from locating our plots in the exact location of the previous study. All plants within each plot were identified, and their percent cover was determined. Following plant senescence in August 2003, all aboveground biomass was harvested, dried (40 °C), and weighed to determine differences in aboveground primary productivity. Root biomass was quantified by excavating 25% of the plot area to a depth of 12 cm: each plot was divided into quadrats, and a subsample of soil from each quadrat was excavated (soil volume = 7500 cm^3 $quadrat^{-1}$). The roots and soil were transported on ice, and the roots were washed from the soil, dried (40 °C), and weighed to determine root biomass differences. Shoot and root tissue (hereafter, ''litter'') was then ground with a ball mill, and subsamples were analyzed for nutrient analyses (hereafter, ''litter chemistry''). Total C and N were analyzed by micro-Dumas combustion (Fisons Instruments, Milan Italy). The amount of acid-soluble lignin and total P, K, Ca, and Mg was determined by the University of California Department of Analytical and Natural Resources (DANR) Analytical Laboratory. Soil from the upper 10 cm also was collected from inside the 1 m^2 plots, dried (40 °C), sieved (2 mm), and analyzed for soil nutrients (hereafter, ''soil chemistry''). Total C and N were analyzed by micro-Dumas combustion (Fisons Instruments, Milan Italy), and bicarbonate-extractable P and ammonium acetate-extractable K were measured by inductively coupled plasma-atomic emission spectrometry (ICP-AES) (Thermo Jarrell Ash, Franklin MA).

Determination of litter decomposition rates in the field

In the field, litter decomposition rates were measured by determining mass loss of litterbags. Above- and below-ground litter from native and invaded plots was composited within litter type, yielding four categories of litter: native aboveground, native belowground, invaded aboveground, and invaded belowground. All litter was cut into 2.5 cm-long pieces and homogenized before being weighed into mesh bags (1 mm^2 mesh size). 15.0 g of oven-dried (40 °C; 24 h) litter was placed in each mesh bag. In October 2003, litterbags were reciprocally transplanted into the field in areas adjacent to the plots, yielding six replicates of the eight treatment combinations (two litter types [native or invaded], two tissue types [shoot or root], and two soil types [native or invaded]). Since we were interested in the possible role that differential soil microbial community composition could have on litter decomposition, each area was mowed to approximately 5 cm, prior to litterbag placement, to ensure equal contact between the soil and litterbags at each site. Aboveground litterbags were positioned on top of the soil and nailed into place, and belowground litterbags were buried to a depth of 5 cm. Each month, from November 2003 to April 2004 (wet, winter season), six replicates per treatment were harvested. Litterbags were rinsed to remove soil, and any new growth (i.e., living roots and shoots) was removed from the bags prior to oven-drying and weighing. Decomposition constants were calculated for each litter type using a single negative exponential model, as described in Aerts and deCaluwe (1997) and Ehrenfeld et al. (2001).

Statistical analyses

Univariate ANOVA was used to characterize differences between native and invaded areas with respect to community composition of dominant plant functional groups and above- and belowground biomass production. Post-hoc Tukey's tests ($\alpha = 0.05$) were used to make comparisons between treatment means. Multivariate ANOVA (MANOVA) followed by univariate ANOVA of the individual variables was used to determine differences among native and invaded areas with respect to soil and plant litter chemistry. Since only differences within litter tissue type were of interest, above- and below-ground litter mass loss were analyzed separately. Decomposition rate constants were compared using analysis of covariance (ANCOVA) as described in Zar for comparison of multiple slopes (Zar 1999). All statistical analyses were carried out using Statistical Analysis Software (SAS) for Windows v8.1 (SAS Institute 2001).

Results

Plot characterization in native and invaded areas

Native plots had significantly higher percent cover of native forbs (2.2-fold greater, $P < 0.0001$) and native grasses (82-fold greater, $P < 0.0001$) than invaded plots (Figure 1). Invaded plots had significantly higher percent cover of *A. triuncialis* ($P < 0.0001$) than native plots; by definition, native plots contained no *A. triuncialis*. However, there was no significant difference in the percent cover of other non-native plants in native and

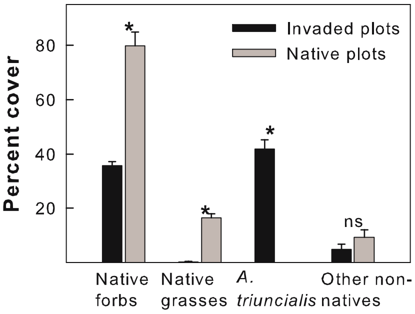

Figure 1. Plant community characterization of native and invaded plots. Different functional groups (native forbs, native grasses, *A. triuncialis*, and other non-natives) are represented as percent cover. Data are means ±SE ($n = 6$). Asterisks indicate significant differences between percent cover of a functional group in native and invaded plots ($P < 0.05$). No significant difference between percent cover of a functional group in native and invaded plots are indicated by "ns" ($P > 0.05$).

Table 1. Summary of chemical properties of soils from native and invaded plots.

Soil Type	Total N g kg^{-1}	Olsen P mg kg^{-1}	Exch-K Mg kg^{-1}
Native	1.6 (0.1)^{a}	7.5 (0.4)^{a}	150.8 (5.8)^{a}
Invaded	1.3 (0.05)^{b}	4.8 (0.2)^{b}	80.3 (6.9)^{b}

Data are means (S.E.) ($n=6$). Letters indicate significant differences between means following a post-hoc Tukey's test ($\alpha = 0.05$).

invaded plots ($P=0.2$). Overall, native forbs accounted for approximately 80% of total cover in native plots and *A. triuncialis* accounted for over 40% of total cover in invaded plots.

Soil chemistry

Soil chemical properties from native and invaded plots were significantly different (Table 1, overall MANOVA $P<0.0001$). Soil total N, and extractable P and K were 1.3, 1.6, and 1.9-fold higher in soil from native plots than invaded plots ($P=0.0005$, $P<0.0001$, and $P<0.0001$, respectively).

Litter biomass and tissue chemistry

As hypothesized, end-of-season aboveground biomass was significantly greater in invaded plots compared to native plots (1.9-fold greater, $P=0.0007$) (Figure 2a). Although belowground biomass was slightly higher in invaded plots, this difference was not significant ($P>0.05$) (Figure 2b). Litter from native and invaded plots differed significantly in their above- and belowground tissue chemistry (overall MANOVA $P=0.01$ and $P=0.01$, respectively) (Figure 3a–g). Overall, similar trends were observed for above- and belowground tissues. Concentrations of N, P, K, and Ca were 1.4, 1.4, 1.3, and 1.6-fold higher in aboveground litter from native plots than invaded plots ($P=0.0007$, 0.002, 0.003, and 0.003 respectively). In contrast, C:N and lignin:N were 1.3 and 1.2-fold higher in aboveground litter from invaded plots than litter from native plots ($P=0.002$ and $P<0.0001$, respectively). Aboveground litter Mg concentrations did not differ between native and invaded plots ($P>0.05$). Similarly, belowground litter from native plots was 1.5, 1.4, and 2.5-fold higher in N, P, and K concentrations than belowground litter from invaded plots ($P=0.008$, 0.009, 0.006 respectively). Belowground litter from invaded plots was significantly higher in Mg concentrations than belowground litter from native plots (2.3-fold higher, $P=0.002$). Invaded belowground litter also had a significantly higher C:N than native litter (1.5-fold greater, $P=0.0006$), and although there was a trend for higher belowground lignin:N ratios in invaded litter compared to native belowground litter, this trend was not significant ($P>0.05$).

Field decomposition experiment

Above- and belowground litter from native plots tended to decompose more quickly than litter from invaded plots; however, the decomposition constants were only significantly different between litter types for aboveground litter ($P=0.02$; Table 2, Figure 4). Averaging litter decomposition constants across soil types, mass loss from above- and belowground litter from native plots

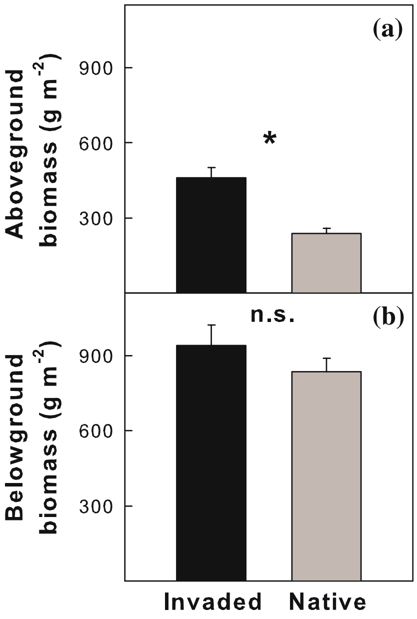

Figure 2. Aboveground (a) and belowground (b) biomass from native and invaded plots. Data are means ±SE ($n=6$). Asterisks indicate significant differences between means following a post-hoc Tukey's test ($\alpha = 0.05$). Ns indicates no significant difference between means following a post-hoc Tukey's test ($\alpha = 0.05$).

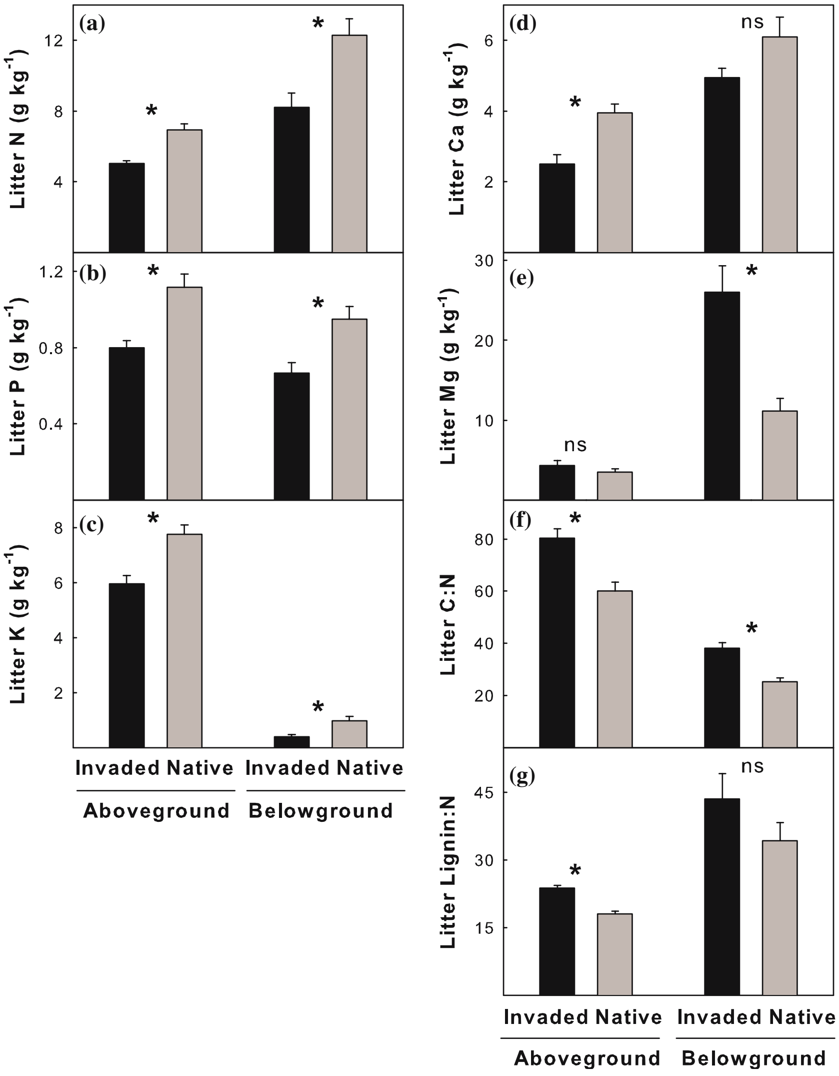

Figure 3. Elemental composition of above- and belowground litter from invaded and native plots. Data are means ±SE ($n=6$). Above- and belowground comparisons were compared separately. Asterisks indicate significant differences between means following univariate comparison by ANOVA. Ns indicate no significant difference between means. Overall MANOVAs for both above-and belowground tissues were significant ($P<0.05$).

occurred at rates 1.2-fold and 1.5-fold faster than above- and belowground litter from invaded plots. Soil type (i.e., exposure to different microbial communities), however, had no significant effect on decomposition rates ($P>0.05$). The significance of the belowground regressions was strongly influenced by the apparent increase in mass in April (Figure 4b, Table 2). When the April values were omitted, significance of all regressions increased ($P<0.0004$).

Discussion

Based on field observations, we hypothesized that *A. triuncialis* produces significantly more biomass than native plants. In our study plots, *A. triuncialis* accounted for >40% of the total cover and increased aboveground biomass production by more than 2-fold. Increased biomass production and primary productivity commonly is observed following invasion by exotic species

Table 2. Decomposition rate constants (k, year^{-1}) for litter from invaded and native plots decomposing in native and invaded soil.

Litter type	Soil type	k (yr^{-1})	$r^{2\dagger}$	P
Aboveground litter				
Native	Native	0.75^a	0.80	< 0.0001
	Invaded	0.74^a	0.80	< 0.0001
Invaded	Native	0.59^b	0.72	< 0.0001
	Invaded	0.62^b	0.83	< 0.0001
Belowground litter				
Native	Native	0.88^a	0.11	0.05
	Invaded	0.76^a	0.28	0.0009
Invaded	Native	0.69^a	0.23	0.003
	Invaded	0.37^a	0.30	0.0006

P values refer to the significance of the regressions used to calculate the rate constant (k). Significance of regressions for belowground litter was strongly influenced by the final measurement in April. When April data were omitted, significance of all regressions increased ($P < 0.004$ for all comparisons). The effects of litter type, soil type, and the interaction of litter type×soil type on decomposition rates were included in our ANOVA model. Only litter type was significant. Lowercase letters indicate significant effects of litter type on rate constants.

†The r^2 values are derived from regression analyses of ln $(\text{mass}_t/\text{mass}_0) = -kt$, where mass_0 is the initial litter mass and mass_t is the litter mass at time t.

(Ehrenfeld 2003). By growing faster and/or larger than co-occurring species, invasive species can gain a competitive advantage by out-competing for resources such as light and nutrients (Lambers et al. 1998). Additionally, in the field we have observed that *A. triuncialis* maintains vegetative growth later in the growing season than most of the other spring-blooming native plants (with the exception of the native bunch grasses and the tar plants, *Hemizonia congesta* and *Holocarpha virgata*, which account for < 10% of total plant cover in invaded plant patches) (data not shown). This longer growing season likely leads not only to greater biomass but also to potentially greater nutrient uptake into *A. triuncialis* tissue; however, further research into the timing and acquisition of plant nutrient uptake in this community is required.

At the ecosystem level, abundant production of low quality biomass can slow decomposition (Mack and D'Antonio 2003a), as was observed in our study. Comparing decomposition rate constants, aboveground litter from invaded plots decomposed more slowly than aboveground native litter, leading to more standing dead biomass at the beginning of a new growing season in invaded plant patches compared to native plant patches. Similar trends were observed for belowground litter but were not significant; the lack of significance between these treatments may be due to germination of seedlings within the belowground litterbags, especially in the later months of the study (e.g., the apparent mass increase in April).

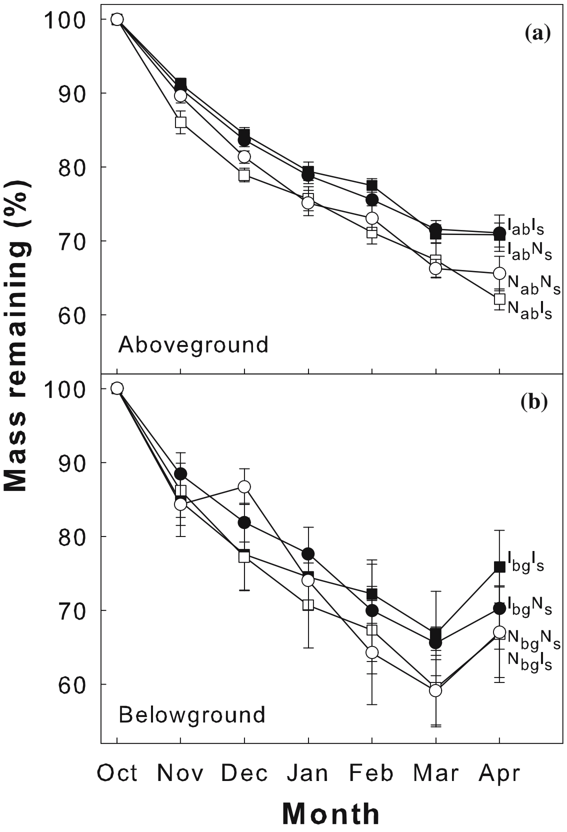

Figure 4. Aboveground (a) and belowground (b) native and invasive litter mass loss in native and invaded soil. Data are means ± SE ($n = 6$). Decomposition rate constants are reported in Table 2. Treatments are indicated as litter type (I = invasive [*A. triuncialis*] litter, N = native litter), tissue type ($_{ab}$ = aboveground, $_{bg}$ = belowground), and soil type (I_s = invaded (*A. triuncialis*) soil, N_s = native soil).

Decomposition rates may be influenced by differences in litter chemistry and/or soil microbial community composition. Litter from invaded plots had significantly higher C:N and lignin:N ratios and was significantly reduced in total N, P, and K. Higher concentrations of carbon and lignin relative to N and lower concentrations of macronutrients (e.g., N and P) often are correlated with slower decomposition rates (Vitousek 1982; Aerts and de Caluwe 1997; Evans et al. 2001). Calculating nutrient pools (biomass×nutrient concentration) is another way to compare the amount of nutrients retained litter, incorporating not only nutrient concentrations but also the difference in biomass between litter types. In aboveground litter, N, P, K, Ca, and Mg pools were ≥1.9-fold higher in litter from invaded plant patches. Together, our biomass, decomposition rate, and nutrient pool data suggest that *A. triuncialis* produces large amounts of low quality, decomposition-resistant litter. Microbial breakdown of *A. triuncialis* litter was likely nutrient-limited and may have contributed to slower release of nutrients back into the soil pool. Although invaded plant patches have higher aboveground biomass, and thus presumably more labile carbon to support microbial biomass production, no differences in microbial biomass previously were observed between patch types (Batten et al. 2006). Additionally, ^{15}N pool dilution data do not support faster rates of N mineralization in invaded plant patches, as would be expected if the resident microbial communities were responding positively to greater labile C pools in invaded plant patches (K.M. Batten, unpublished data). In this low nutrient system, incorporation of large amounts of low quality residues should increase the soil C:N ratio and C storage, diluting soil N and likely limiting microbial biomass production and activity.

Overall, we hypothesized that slower decomposition of residues from invaded plant patches correlates with lower soil nutrient concentrations in these areas. Indeed, soil in invaded patches was significantly lower in total N, bicarbonate-extractable P, and ammonium acetate extractable K. Lower soil nutrient concentrations in invaded plant patches may be due to *A. triuncialis*' demonstrated higher biomass production, extended growing season, and slower decomposition rate.

Contrary to one of our initial hypotheses, differences in soil microbial community composition associated with the different soil patch types did not influence litter decomposition rates. It is possible that our field measurements were too coarse or too short in duration to observe variation in decomposition rates due to compositional differences in microbial communities. Under more controlled laboratory conditions, it is possible that we would have had a greater ability to detect subtle differences in decomposition rates. In a microcosm study measuring microbial community composition and decomposition of substrates of varying complexity, oak and grassland soils contained distinctly different microbial communities but had similar capabilities to metabolize simple substrates (Waldrop and Firestone 2004). These data suggest if there is high functional redundancy for a process, changes in microbial community composition may not necessarily lead to changes in ecosystem function.

The observed pattern of slower nutrient cycling following plant invasion contrasts with other reports on the effects of invasive species on belowground processes. Faster N-cycling rates following woodland to grassland type-conversion (Mack and D'Antonio 2003b) and higher nitrification rates and N mineralization rates in areas invaded by an exotic woody shrub and C_4 grass (Ehrenfeld et al. 2001) have been observed following invasion. Additionally, in a review of the belowground effects of invasive species, increased N mineralization and nitrification rates were observed in 11 of 16 studies (Ehrenfeld 2003).

Ehrenfeld (2003) also reviewed studies of decomposition in invaded areas and noted that faster decomposition rates were observed in 10 of 14 cases. However, in those examples where invasive species were more resistant to decomposition, it was suggested that high concentrations of secondary compounds (e.g., lignin, monoterpenes) contributed to slower nutrient cycling rates. Our data support this conclusion; litter from invaded plots had higher lignin:N ratios than litter from native plots. Similarly, in the Great Basin, a higher lignin:N in the invasive annual grass, *Bromus tectorum*, was correlated with lower potential rates of net N mineralization, when compared to soils from areas with the native perennial bunchgrasses *Hilaria jamesii* and *Stipa hymenoides*, which had lower lignin:N ratios (Evans et al. 2001). In general, species from low nutrient habitats, including presumably exotic, non-N fixing species in these systems, tend to produce lower quality litter that is more resistant to decomposition (Hobbie 1992, Aerts and Chapin 2000). These data suggest, then, that these more stress-tolerant invaders have quite different ecosystem-level effects on decomposition and nutrient cycling than species invading more nutrient-rich habitats (i.e., invasive species do not have similar effects across all ecosystem types).

Overall, variation in decomposition rates between litter from native and invaded plots was more strongly influenced by differences in litter chemistry than by differences in soil microbial community composition. Higher biomass production of low quality litter by *A. triuncialis* over time will lead to higher soil C levels and decreased soil C:N. In these already low nutrient soils, slower nutrient cycling may negatively affect native plant establishment, possibly limiting the ability of native species to successfully compete with *A. triuncialis* in the areas in which it has invaded. Additionally, the ability of *A. triuncialis* to retain nutrients in its biomass may also limit the success of other exotic species in areas dominated by *A. triuncialis*. This phenomenon contrasts with work from areas invaded by N-fixing species, which can increase the invasibility of the system (Yelenik et al. 2004). The ability of *A. triuncialis* to not only tolerate but to possibly exacerbate low nutrient conditions could pose a threat to serpentine ecosystems, habitats regarded as refugia for native California grassland species (Harrison 1999).

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