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Wood Decomposition Following a Perennial Lupine Die-Off: A 3-Year Litterbag Study

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Abstract

Woody debris is a conspicuous feature of many ecosystems and can be a large pool of stored carbon and nutrients. In the California coastal prairie, yellow bush lupines (*Lupinus arboreus*) experience mass die-offs, producing large quantities of woody detritus. Live lupines are fed upon by the stem-boring caterpillars of the ghost moth, *Hepialus californicus*, and outbreaks of ghost moths are one factor contributing to lupine die-offs. A common detritivore, the terrestrial isopod *Porcellio scaber*, frequently inhabits ghost moth tunnels in lupine wood. We used a litterbag experiment to test the hypothesis that *H. californicus* increases decomposition of woody lupine detritus by facilitating its use by *P. scaber*. Isopod access to wood was crossed with simulated ghost moth boring to measure the independent and interactive effects of these two arthropods on total mass loss, as well as on carbon, nitrogen, and lignin dynamics. Isopods initially colonized litterbags but were not more abundant on *L. arboreus* logs that had simulated ghost moth boring than on logs without boring. They were rare in litterbags collected at 12 months or later and had no effect on wood decomposition. Simulated ghost moth boring increased wood decomposition ($P = 0.0021$), from 50.5 to 55.1% mass loss after 3 years. This effect was likely due to increased surface area for microbial utilization of the wood. Lupine wood had an initial lignin content of 14.70 ± 0.67%, but lignin did not appear to decompose during the 3 years of this study, and by the end of the experiment accounted for 32.6 ± 1.12% of the remaining wood. Neither ghost moth boring nor isopod access affected lignin loss. Lupine wood from a die-off in 2002 was estimated to have contained three times more nitrogen per unit area than the yearly input of annual grass litter. The slow decomposition of lupine wood, however, restricts the rate at which nitrogen is released into the soil and results in the storage of carbon and nutrients in lupine wood for several years following such die-offs.

Key words: woody debris; herbivore; coastal prairie; detritivore; isopod; *Lupinus arboreus*; *Hepialus californicus*; *Porcellio scaber*; nitrogen; lignin.

Introduction

Production and decomposition, the two fundamental ecosystem processes, determine the flow of nutrients and energy within communities. Studies of detritivores have largely focused on their effects on decomposition, although they can affect production by altering the availability of nutrients. Similarly, studies of herbivores have generally focused on their effects on production, although herbivores can influence decomposition through a wide variety of mechanisms (Hunter 2001; Bardgett and Wardle 2003). Over successional time scales,

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herbivores may alter litter inputs by changing plant species composition (Pastor and others 1993; Jefferies and others 1994; Olofsson and Oksanen 2002). On shorter time scales, within a plant generation, herbivores can affect decomposition by trampling soil, litter, or vegetation (Zacheis and others 2002); altering soil and litter temperature or moisture by reducing vegetation cover (Chapman and others 2003); or by changing the quantity or quality of litter inputs. Changes to litter quality can occur through the conversion of foliage to feces (McNaughton and others 1988; Bazely and Jefferies 1985; Cochran and others 2000; Christenson and others 2002; Zimmer and Topp 2002; Fonte and Schowalter 2005), the induction of leaf abscission before nutrient resorption (Chapman and others 2003, 2006; Fonte and Schowalter 2005), the alteration of plant growth patterns or resource allocation (Kielland and others 1997; Bryant 2003; Semmartin and Ghersa 2006), or the induction of phenolics or other plant defenses (Findlay and others 1996; Harrison and Bardgett 2003; Schweitzer and others 2005; Chapman and others 2006). In addition to modifying litter quality, herbivores such as boring insects can modify the physical structure of litter through their feeding on leaves and wood (Edmonds and Eglitis 1989). We investigated whether this latter form of herbivory alters the decomposition of woody debris produced by the borer's host.

Root- and stem-boring caterpillars of the ghost moth (*Hepialus californicus*) are abundant in California coastal prairie and appear to have important ecological effects on this community (Strong and others 1995; Maron and Jefferies 1999; Preisser 2003). The host of *H. californicus* is the yellow bush lupine, *Lupinus arboreus*, a native, perennial, nitrogen-fixing shrub. *L. arboreus* forms dense stands in the coastal prairie, which experience periodic die-offs. Cover by live *L. arboreus* can decrease from over 50 to close to 0% in a season, and then recover within 2–3 years (Strong and others 1995). Such die-offs occur irregularly, at intervals of 2–10 years (Strong and others 1995). Because of nitrogen fixation by live lupines and the input of nitrogen-rich lupine litter, the soils in lupine stands become enriched with nitrogen (Maron and Jefferies 1999). Following lupine die-offs, these soils support high levels of production by annual grasses and forbs (Maron and Connors 1996; Maron and Jefferies 1999). *H. californicus* appears to be a particularly destructive herbivore; ghost moth caterpillars can suppress seed set of mature lupines (Preisser 2003) and kill lupine seedlings (Strong and others 1999). Periods of heavy ghost moth herbivory are one cause of lupine die-offs (Strong and others 1995; Maron 1998; Maron and Jefferies 1999; Maron and Kauffman 2006). We were interested in the effect of prior feeding by ghost moth caterpillars on the decomposition of lupine wood following a 2002 lupine die-off.

The impacts of herbivores on decomposition have primarily been studied for leaf litter, whose decomposition occurs over months or years in most ecosystems and releases nutrients to support new primary production (Swift and others 1979). In contrast to leaf litter, woody debris decays on decadal time scales (Harmon and Hua 1991; Laiho and Prescott 2004) and acts as a long-term store of carbon and nutrients (Krankina and others 1999; Laiho and Prescott 2004; Kim and others 2006). During its slow decomposition, woody debris provides habitat for a wide diversity of organisms (Harmon and others 1986; Grove 2002; Lohr and others 2002; Gomez and others 2003; Ucitel and others 2003; Lee 2004; Åström and others 2005; Díaz and others 2005; Hutto 2006), reduces soil erosion and increases soil moisture retention (Harmon and others 1986; Haranto and others 2003). High concentrations of recalcitrant compounds, especially lignin, slow the decomposition of such litter (Melillo and others 1982; Laiho and Prescott 2004). Wood decomposition depends critically on lignolytic fungi, which are capable of digesting lignin. Arthropods are ubiquitous inhabitants of decomposing wood (Grove 2002) and also contribute to its decomposition (Buxton 1981; Collins 1981; Ebert and Zedler 1984; Edmonds and Eglitis 1989; Torres 1994; Songwe and others 1995; Müller and others 2002; Takamura 2001; Schuurman 2005). The terrestrial isopod *Porcellio scaber* is an abundant detritivore in the California coastal prairie. *P. scaber* is commonly found living and feeding on dead lupine wood, especially in ghost moth bores. We were interested in two separate questions regarding the decomposition of lupine wood following a lupine die-off. First, what is the role of *P. scaber* in the decomposition of lupine wood following a lupine die-off, and does boring by ghost moth caterpillars facilitate *P. scaber*'s utilization of lupine wood? Second, does dead lupine wood, which has a high nitrogen content, a low lignin content, and a small diameter compared to tree wood, store nutrients, as coarse woody debris does in forest ecosystems, or rapidly release nutrients, as leaf litter does in most ecosystems?

We conducted a 3-year litterbag study to measure the independent and interactive effects of *H. californicus* and *P. scaber* on the decomposition of lupine wood following a lupine die-off. The results

of the litterbag study were combined with field surveys of the dead wood produced by a lupine die-off at our study site, the Bodega Marine Reserve (BMR), to estimate the fate of wood mass and nitrogen. We tested the hypotheses that ghost moth herbivory increases the decomposition rate of lupine wood by facilitating the utilization of the wood by *P. scaber*, and that the decay of lupine wood provides an additional pulse of nitrogen to coastal prairie soil following a die-off.

Materials and Methods

Site Description

The University of California BMR is a 146 ha reserve in Sonoma Co., California (38°19′N, 123°4′W). BMR is located on the Bodega Head, a narrow peninsula surrounded by the Pacific Ocean. The reserve has a Mediterranean climate: rainfall is concentrated between November and March, but frequent fog moderates the summer drought. The western portion of BMR, on the Pacific plate, is coastal prairie with sandy loam soil. The eastern portion of the reserve, in the San Andreas fault zone, is sand dunes. BMR's coastal prairie hosts a mix of native Californian and introduced European grasses and forbs. The dunes are dominated by the introduced European beachgrass *Ammophila arenaria*. BMR is naturally treeless and contains only three species of shrubs, of which *L. arboreus* is the most abundant. *L. arboreus* is found in both coastal prairie and dune habitats. In the coastal prairie, *L. arboreus* grows in dense stands, which experience episodic recruitment events and mass die-offs (Maron and Jefferies 1999). In the dunes, *L. arboreus* occurs at lower density and has a more stable population size (Maron and Kauffman 2006). The ghost moth has an annual life cycle. *H. californicus* caterpillars feed first on fine roots, then move to larger roots, and eventually bore upwards through the stem in preparation for pupation (Strong and others 1996). Moths emerge from lupines, mate, and oviposit during the winter and spring.

The dominant macrodetritivore at BMR is *P. scaber*, a terrestrial isopod that reaches densities of 340 m^{-2} (J.L. Bastow unpublished data). Although native to western Europe, *P. scaber* is now found throughout the world (Harding and Sutton 1985). Terrestrial isopods are generalist scavengers that feed primarily on dead plant matter (Sutton 1972), although they also consume seedlings (Paris and Sikora 1965), insect eggs (Ehler 2002), feces (Hassall and Rushton 1982; Zimmer and Topp 2002), and dead arthropods. *P. scaber* increases the decomposition rate of both annual grass litter (Bastow and others 2008) and lupine leaf litter (J.L. Bastow unpublished data).

Litterbag Construction and Processing

We collected *L. arboreus* wood without borer damage from the dune habitat at BMR, where lupines typically have lower densities of the ghost moth caterpillars. Lupine stems without caterpillar damage are rare in the coastal prairie (D.R. Strong, personal observation). We girdled 24 *L. arboreus* bushes in August 2003 and collected the girdled lupines a month later. Live, apparently healthy bushes were used instead of dead ones to ensure that the wood was of comparable freshness (comparable time since death). This method assumes, however, that girdled lupines are comparable to naturally deceased lupines in terms of their wood quality. After collection, lupines were stripped of small branches (<2 cm diameter), and the stems were cut into 23.9 cm (SD 0.8 cm) unbranched lengths of wood. We did not use sections with ghost moth tunnels in the experiment. The logs were, on average, 3.8 cm in diameter (SD 0.6 cm) and 4.0 years old (SD 1.0 year), based on growth rings.

We acquired 120 *L. arboreus* logs. We used 24 of these to determine the relationship between wet weight and dry weight based on linear regression. The remaining 96 logs were randomly assigned to one of the four treatments in a factorial design and one of four time periods. The two factors, each with two levels, were simulated ghost moth boring versus no simulated boring crossed with isopod access versus isopod exclusion. Naturally occurring dead *L. arboreus* logs in the coastal prairie were found to have an average of 5.2 ghost moth bores (SD 4.7, $N = 304$), which were 6.6 mm in diameter (SD 0.9, $N = 16$) and 9.3 cm in length (SD 2.9, $N = 17$). In order to simulate ghost moth boring, we therefore drilled five 10-cm-long holes in the log with a 6.5-mm-diameter drill. We did not use naturally occurring ghost moth boring because selective oviposition by the moths or branch selection by the caterpillars might have led to differences in wood quality between bored and non-bored logs. Preliminary experiments showed that isopods readily colonized simulated ghost moth tunnels in the lab.

Litterbags were constructed from 0.5-mm mesh nylon screen and were 40 cm × 25 cm. In order to allow isopods access to half of the lupine logs, we melted 200 holes (about 0.75 cm diameter) in half of the litterbags with a soldering gun. Each log was weighed, and its dry weight estimated using the

regression between wet weight and dry weight (dry weight (g) = 2.32 + 0.45 wet weight (g), $R^2 = 0.97$). Litterbags were laid out in a randomized 8 by 12 grid in the coastal prairie (Mussel Point) on October 3, 2003. We left the *L. arboreus* logs in the field for 0.5, 1, 2, or 3 years, collecting six replicates of each of the four treatments at each of the four sampling points.

We repeated the first two sampling periods (6 and 12 months) the following year because the first spring (2004) was unusually dry and isopod abundances appeared to be lower than normal. In August of 2004, we girdled an additional 16 *L. arboreus* bushes, from which we obtained 72 lengths of *L. arboreus* wood. This second batch of logs averaged 24.0 cm (SD 1.2 cm) in length, 3.9 cm (SD 0.6 cm) in diameter, and 3.8 (SD 0.7) years old. We used 24 of these *L. arboreus* logs to make a second regression of wet weight to dry weight (dry weight (g) = −0.24 + 0.42 wet weight (g), $R^2 = 0.98$), and randomly assigned the remaining 48 logs to one of the four treatments described above. These 48 logs were placed in the field on October 1, 2004, when the 1-year samples from the first batch were collected. We left the *L. arboreus* logs from the second batch in the field for 0.5 or 1 year, collecting six replicates of each treatment combination at each sampling point.

Collected litterbags were stored at 4°C until processing. To process litterbags, we counted the number of isopods and other arthropods in each litterbag and calculated the moisture content and dry weight of the wood remaining. In addition, we measured the nitrogen, carbon, and lignin content of half of the first batch of *L. arboreus* logs (that is, half of the logs placed in the field in 2003, three replicates of each treatment at each of the four sampling points, 48 logs). We used six of the *L. arboreus* logs from the first wet weight–dry weight regression to estimate initial carbon, nitrogen, and lignin. We subsampled these 54 *L. arboreus* logs by sawing through the wood and collecting the sawdust. Logs were sawed through at least 12 times, along the entire length of the log, to produce at least 6 g of sawdust. Sawdust was then ground and analyzed by the UC Agriculture and Natural Resources Analytical Laboratory. Carbon and nitrogen contents were determined by gas chromatography in a Thermo Finnigan Flash 1112 elemental analyzer. Lignin content was determined using acid detergent fiber analysis (AOAC 1997), followed by combustion to account for ash content. The exponential decay constant, k, of lupine wood was calculated using Olson's (1963) equation for the proportion of litter remaining after time t:

$$L_t/L_0 = e^{-kt}. \quad (1)$$

Data Analysis

We used factorial ANOVAs to analyze the data. All ANOVAs included simulated ghost moth boring (present or absent), isopod access (present or absent), and time (6, 12, 24, or 36 months) as fixed factors, along with all two- and three-way interactions between these factors. The effects of these factors on the remaining mass of *L. arboreus*, abundance of isopods, and the relative carbon, nitrogen, and lignin contents were analyzed in separate ANOVAs. Response variables that were expressed as percentages were arcsine square root transformed (Sokal and Rohlf 1995). The abundance of *P. scaber* (isopods/litterbag) was log transformed. Tukey tests were used for mean separation of the time factor and interaction terms when these terms were significant in the overall ANOVA. A value of $\alpha = 0.05$ was used to determine significance in all analyses. We performed all analyses using JMP IN 4.0.3 (SAS Institute).

The effect of isopod access on *L. arboreus* mass loss was used to estimate the effect of isopods on the rate of decomposition of lupine wood, and the interaction between isopod access and simulated boring indicated whether facilitation of isopods by *H. californicus* affects the rate of wood decomposition. The effect of melting holes in the litterbags on isopod number was used to determine the effectiveness of the isopod exclusion, and the effect of simulated boring on isopod number was used to determine whether *H. californicus* boring facilitates isopod use of the wood.

Lupine Wood Survey

To estimate the biomass of dead lupine wood produced by an *L. arboreus* die-off in fall of 2002, we surveyed five lupine populations within BMR on March 4, 2003. The populations included one dense lupine stand that had experienced high mortality (Lower Draw), two sparser populations that had also experienced high mortality (Bay Shore and Mussel Point), and two populations that had experienced relatively little mortality (Dune and Upper Draw). Within each population, we used a random walk to select ten plots (each 2×2 m^2) in which to survey lupines. We measured the trunk diameter of all live and dead lupines at ground level within each plot. A regression of lupine trunk diameter to wood dry weight, based on 16 har-

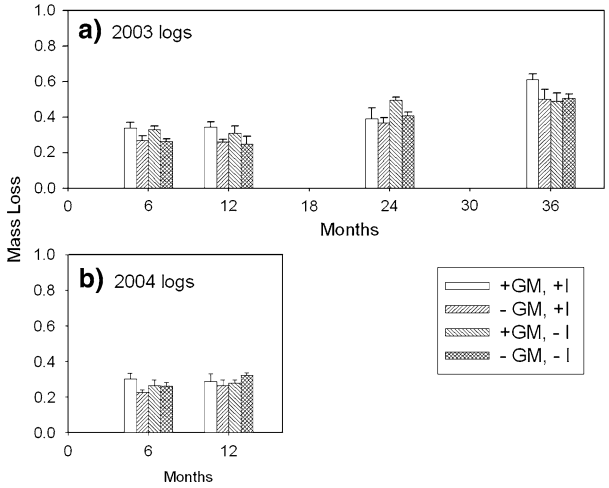

Figure 1. Mass loss of lupine wood in litterbags after 6, 12, 24, and 36 months in the field, expressed as a proportion of the original mass. +GM treatments received simulated ghost moth boring, whereas −GM treatments were not drilled. +I treatments were in litterbags with holes to allow isopod access, whereas litterbags in the −I treatments excluded isopods and other macrodetritivores. Lupine wood placed in the field in fall 2003 is shown in the top panel (**A**) and wood placed in the field in fall 2004 is shown in the bottom (**B**).

vested and oven-dried dead lupine bushes (dry weight (g) = −648 + 341 stem diameter (cm), $R^2 = 0.88$), was used to estimate the biomass of dead lupine wood within each plot. The biomass of lupine foliage was not included in the biomass estimates. We compared the biomass, nitrogen content, and decomposition of lupine wood to that of annual grasses in the surrounding prairie following the end-of-growing season senescence using data from a previous study (Bastow and others 2008; J.L. Bastow, unpublished data).

Results

Lupine Decomposition

Lupine wood lost 28.2 ± 1.0% (mean ± SE) of its dry weight in the first 6 months of this experiment and lost 52.8 ± 2.2% after 3 years (Figure 1). Mass loss increased during every time interval except the second, which spanned from months 6 to 12. There was no difference in decomposition during the first year between the logs placed in the field in 2003 and those placed in 2004. These two sets were combined in subsequent analyses. Simulated ghost moth boring increased wood decomposition (Table 1) from 32.5 ± 1.4 to 37.1 ± 1.5%, averaged over all sampling dates. Isopod access, however, had no effect on wood decomposition, and there was no interaction between isopod access and simulated ghost moth boring on wood decomposition. There was no interaction between time and either treatment.

The exponential decay constant, k, of lupine wood, averaged over all treatments, was 0.29 y^{-1} (0.24–0.35, 95% confidence interval). Excluding lupine wood collected at 6 months did not significantly affect the decay constant (0.25–0.29, 95% CI), indicating that the estimate of k was not influenced by the seasonality of decomposition during the first year. Simulated ghost moth boring increased k from 0.26 to 0.32 y^{-1}.

Isopod Abundance

Porcellio scaber was abundant in isopod access litterbags collected after 6 months but was otherwise rare in litterbags (Figure 2). There were 42.5 ± 8.5 isopods/litterbag (0.24 ± 0.05 g dry mass) in the isopod access litterbags after 6 months, compared to only 1.0 ± 0.6 isopods/litterbag 6 months later. The isopod access treatment was successful (Table 1); only 0.25 ± 0.14 isopods/litterbag were found after 6 months in the isopod exclusion treatment, and this declined to only 0.042 ± 0.042 isopods/litterbag 6 months later. There was an interaction between isopod access and time, because *P. scaber* was found primarily in the isopod access treatment during the first 6 months. There was no effect of simulated ghost moth boring on the abundance of isopods in litterbags, nor was there any interaction between ghost moth boring and isopod access or ghost moth boring and time on the abundance of *P. scaber* in litterbags.

Small numbers of ants and spiders were also found in litterbags assigned to the isopod access treatment. Although ants were found in fewer than 5% of the isopod access litterbags, spiders were present in a majority of such litterbags, but averaged only 1.08 ± 0.34 spiders/litterbag (range 0–3).

Lupine Wood Quality

Lupinus arboreus wood contained 48.47 ± 0.28% carbon, 1.04 ± 0.08% nitrogen, and 14.70 ± 0.67% lignin by mass when initially collected for this experiment. Carbon content, expressed as a percentage of the remaining mass, changed little over the course of the experiment (Table 1, Figure 3A) because the loss of carbon from the logs closely tracked the total mass loss (Figure 5). Logs collected after 36 months were 49.10 ± 0.31% carbon by mass. Carbon content was unusually low (47.67 ± 0.38%) in the isopod access, non-ghost moth bored treatment at the final

Table 1. Results of ANOVAs on Lupine Mass Loss, Isopod Abundance and Percent Carbon, Nitrogen, and Lignin in the Remaining Lupine Wood

Factor	Ghost moth boring (1)		Isopod access (1)		Time (3)		GM X I (1)		GM X T (3)		I X T (3)		GM X I X T (3)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Lupine mass loss (128)	9.86	0.0021	0.051	0.82	60.26	<0.001	1.48	0.23	0.12	0.95	2.47	0.065	1.34	0.26
Isopod abundance (128)	0.15	0.70	97.64	<0.001	93.89	<0.001	0.46	0.50	0.69	0.56	81.04	<0.001	1.10	0.35
Carbon (32) (%)	0.18	0.67	0.14	0.71	1.29	0.29	14.71	<0.001	1.94	0.14	4.96	0.0061	4.36	0.011
Nitrogen (32) (%)	0.036	0.85	0.32	0.58	7.97	<0.001	0.67	0.42	0.62	0.61	2.32	0.094	0.73	0.54
Lignin (32) (%)	2.85	0.10	0.75	0.39	42.41	<0.001	0.43	0.52	1.78	0.17	1.30	0.29	0.67	0.58

F statistics and P-values from ANOVAs on lupine mass loss, isopod abundance, and percent carbon, nitrogen, and lignin in the remaining lupine wood. All ANOVAs included simulated ghost moth boring (GM), isopod access (I), and time since placement (T) as factors, as well as all of their two- and three-way interactions. Numbers in parentheses after factors are the degrees of freedom for that term in the ANOVAs, whereas numbers in parentheses after response variables are the degrees of freedom for the error term for that response.

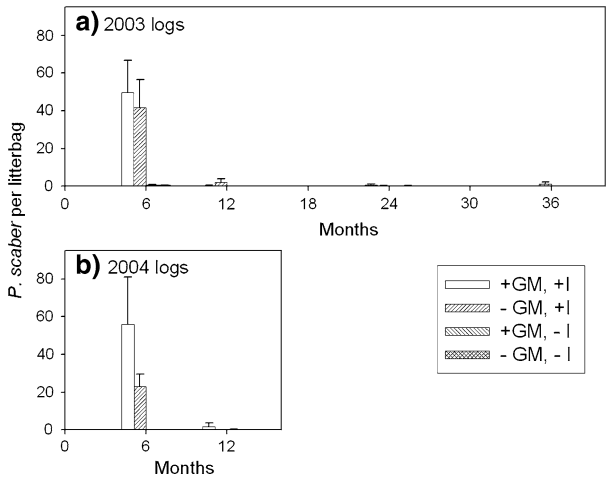

Figure 2. Number of isopods (*P. scaber*) found in litterbags. Treatments and panels are the same as in Figure 1.

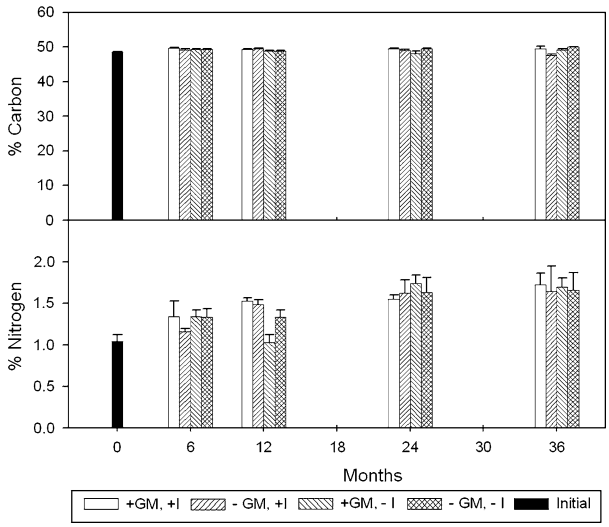

Figure 3. Carbon (top panel) and nitrogen (bottom panel) content of lupine wood at the beginning of the experiment (*black bars*) and after 6, 12, 24, and 36 months of decomposition in the field. Treatments are the same as in Figure 1. Wood analyzed for initial values was not assigned to any treatment. Only wood placed in the field in fall 2003 was analyzed for carbon and nitrogen contents. Carbon and nitrogen contents are expressed as a percentage of the mass of remaining wood.

sampling point. This lead to significant interactions between ghost moth boring and isopod access, isopod access and time, and a significant three-way interaction in the overall ANOVA. It is unclear, however, why this particular treatment combination would have caused unusually low carbon content in decomposing wood, and this finding may have resulted from a small number of replicates of unusual initial quality. There were no other treatment effects on carbon content.

The nitrogen content of the lupine logs, expressed as a percent of the remaining mass, increased during decomposition (Table 1, Figure 3B). After a year, nitrogen content increased to 1.34 ± 0.07% by mass, and after two more years it increased to 1.68 ± 0.09%. There were no effects of simulated ghost moth boring or isopod access on nitrogen content. *L. arboreus* logs lost nitrogen throughout the experiment (Figure 5), but the nitrogen content of the remaining wood increased because the loss of nitrogen lagged behind total mass loss.

The lignin content of the *L. arboreus* wood, expressed as a percent of the wood remaining, also increased during decomposition, but did so more rapidly than nitrogen content (Table 1, Figure 4). After 1 year of decomposition, lignin accounted for

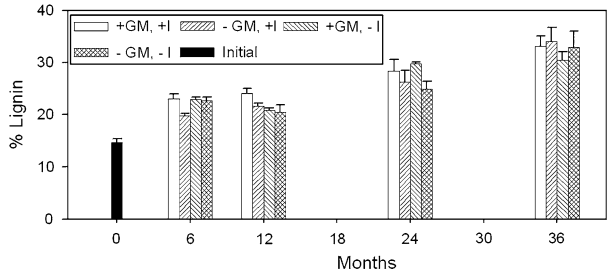

Figure 4. Lignin content of lupine wood at the beginning of the experiment and after 6, 12, 24, and 36 months of decomposition in the field. Treatments are the same as in Figure 1. Wood analyzed for initial values was not assigned to any treatment. Only wood placed in the field in fall 2003 was analyzed for lignin content. Lignin content is expressed as a percentage of the mass of remaining wood.

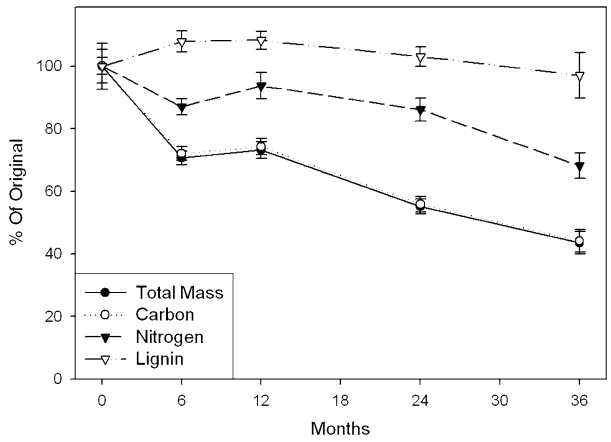

Figure 5. Lupine mass (*solid circles*), carbon (*hollow circles*), nitrogen (*solid triangles*), and lignin (*hollow triangles*) during the first 3 years of decomposition, expressed as a percentage of the original mass, carbon, nitrogen, and lignin present. Decomposition rates were calculated using only the subset of lupine logs analyzed for carbon, nitrogen, and lignin, averaging over all treatments.

21.73 ± 0.59% of the mass remaining. By the end of the experiment, lignin accounted for almost a third (32.6 ± 1.12%) of the remaining mass. Neither isopod access nor simulated ghost moth boring affected the lignin content of lupine wood. Lignin, expressed as a percent of original lignin present, did not change over 3 years (Figure 5). This suggests that although the wood had lost over half of its mass by the end of the experiment, none of the original lignin had been broken down.

Lupine Decomposition and Nitrogen Loss Following the 2002 Die-Off

Lupine mortality during the 2002 die-off exceeded 90% at three sites (Lower Draw, Bay Shore, and Mussel Point) and produced between 78 and 1,350 g m^{-2} of dead lupine wood, depending on the density of lupines and the level of mortality (Table 2). The initial nitrogen content of dead lupine wood (1.04 ± 0.08%) is comparable to that in senescent annual grass litter (0.96 ± 0.18%). Dead lupine wood in the densest lupine stand (Lower Draw) contained almost three times as much nitrogen per area as the senescent grass litter in the surrounding prairie. Nitrogen per area of dead lupine wood was comparable to that of senescent grass litter at two of the other sites (Bay Shore and Mussel Point) and considerably less in the two sites that experienced relatively little mortality (Dune and Upper Draw). Because lupine wood decomposes more slowly than annual grass litter (29.1% mass loss for lupine wood and 66.7% for grass litter over the first year), nitrogen loss was much slower from lupine wood than loss from grass litter. Only during the third year of decomposition had lupine wood in the Lower Draw site released as much nitrogen per area as senescent grass litter releases during its first year of decomposition. Nitrogen loss from lupine wood at the other sites was not detectable given the large errors associated with these estimates.

Discussion

The Effect of Ghost Moth Boring on Lupine Wood Decomposition

Simulated boring by the ghost moth, *H. californicus*, increased the decomposition rate of lupine wood. Contrary to our hypotheses, the isopod, *P. scaber*, had no effect on the decomposition of lupine wood, and the effect of ghost moth boring was independent of the presence of isopods. Our simulated ghost moth boring increased the average surface area of *L. arboreus* logs by almost one-third (from 311 to 413 cm^2) and probably increased mass loss by increasing the surface area accessible to microbial decomposers.

This effect of herbivory has not been explicitly incorporated into previous studies of herbivore effects on decomposition, although many herbivores, including leaf- and stem-boring insects, increase the surface area of uningested litter. Although the difference in mass loss between drilled and intact lupine wood was relatively small after 3 years, simulated ghost moth boring is predicted to reduce the longevity (that is, time until 95% mass loss, or $3/k$) of dead wood from 11.5 to 9.4 years. Wood-boring insects may be predicted to have a larger impact on decomposition rates in systems where surface area-to-volume ratios of wood are initially lower, such as

Table 2. Dynamics of Dead Lupine Wood Following the 2002 Lupine Die-Off

	Year	Lower Draw	Bay Shore	Mussel Point	Dune	Upper Draw	Annual grass senescence
Biomass (g m^{-2})	0	1350 ± 120	698 ± 222	461 ± 156	92 ± 36	78 ± 47	534 ± 51
	1	988 ± 95	510 ± 164	337 ± 115	67 ± 26	57 ± 34	178 ± 20
	2	745 ± 74	385 ± 124	254 ± 87	51 ± 20	43 ± 26	
	3	589 ± 71	304 ± 100	201 ± 70	40 ± 16	34 ± 21	
Nitrogen (per mass remaining)(%)	0	1.04 ± 0.08	1.04 ± 0.08	1.04 ± 0.08	1.04 ± 0.08	1.04 ± 0.08	0.96 ± 0.18
	1	1.34 ± 0.07	1.34 ± 0.07	1.34 ± 0.07	1.34 ± 0.07	1.34 ± 0.07	1.80 ± 0.08
	2	1.64 ± 0.06	1.64 ± 0.06	1.64 ± 0.06	1.64 ± 0.06	1.64 ± 0.06	
	3	1.68 ± 0.09	1.68 ± 0.09	1.68 ± 0.09	1.68 ± 0.09	1.68 ± 0.09	
Nitrogen (g m^{-2})	0	14.0 ± 1.7	7.3 ± 2.4	4.8 ± 1.7	1.0 ± 0.4	0.8 ± 0.5	5.1 ± 1.1
	1	13.2 ± 1.5	6.8 ± 2.22	4.5 ± 1.56	0.9 ± 0.4	0.8 ± 0.5	3.2 ± 0.4
	2	12.2 ± 1.3	6.3 ± 2.04	4.2 ± 1.43	0.8 ± 0.3	0.7 ± 0.4	
	3	9.9 ± 1.3	5.1 ± 1.70	3.4 ± 1.19	0.7 ± 0.3	0.6 ± 0.3	
Nitrogen loss (g m^{-2})	0–1	0.80 ± 2.20	0.41 ± 3.25	0.27 ± 2.28	0.05 ± 0.52	0.05 ± 0.68	1.92 ± 1.14
	1–2	1.02 ± 1.94	0.53 ± 3.02	0.34 ± 2.12	0.07 ± 0.49	0.06 ± 0.63	
	2–3	2.33 ± 1.83	1.21 ± 2.66	0.80 ± 1.86	0.16 ± 0.43	0.13 ± 0.55	
	Total (0–3)	4.15 ± 2.10	2.15 ± 2.92	1.42 ± 2.04	0.28 ± 0.47	0.24 ± 0.60	

Biomass and nitrogen dynamics of dead lupine wood at five sites at BMR following the 2002 lupine die-off. Biomass of dead wood was measured in March 2003. The nitrogen content and decomposition rates were estimated using data from the litterbag experiment. Biomass and nitrogen dynamics of senescent annual grasses at BMR from a previous study is presented for comparison. Data for annual grass litter biomass, following senescence, and first year decomposition from Bastow and others (2008) (nitrogen content, J.L. Bastow, unpublished data).

forests. Given the abundance and ubiquity of wood-boring herbivorous insects in many forests (including Cermabycidae, Buprestidae, and Scolytinae), such changes to wood surface area-to-volume ratios may affect the long-term dynamics of coarse woody debris in these systems (Edmonds and Eglitis 1989).

If ghost moth herbivory alters the quality (for example, nutrient or lignin content) of *L. arboreus* wood, these effects on quality may be more important in determining the rate of lupine decomposition than ghost moth effects on wood surface area. Because this study used simulated ghost moth boring, the effects of herbivory on wood quality were not included in these results. It is well known that herbivore-induced changes in leaf quality can affect decomposition (Findlay and others 1996; Harrison and Bardgett 2003; Chapman and others 2003, 2006; Fonte and Schowalter 2005; Schweitzer and others 2005), but comparable studies on wood have not been performed, presumably because of the importance of leaf litter decomposition in nutrient cycling, the long time periods required to study wood decay, and the difficulty in applying and maintaining herbivore treatments on long-lived woody species.

Nitrogen and Lignin Control of Lupine Wood Decomposition

The carbon:nitrogen (C:N) ratio of litter is a good predictor of its decomposition rate; an inverse relationship between C:N ratio and decomposition rate was first noted by Tenny and Waksman (1929) and has since been confirmed for a wide variety of litters (Enríquez and others 1993). Melillo and others (1982) found that the lignin:nitrogen ratio was a good predictor of the decomposition rates of hardwood leaf litter with high lignin concentrations (10.1–24.1%), although Taylor and others (1989) found that the C:N ratio was a better predictor for litters with a wide range of lignin contents. The influence of both nitrogen and lignin is apparent in the decomposition of lupine wood. *L. arboreus* wood is comparable to annual grass litter from BMR in its C:N ratio (47.74 for lupine, 47.36 for annual grasses; (J.L. Bastow, unpublished data)), but the decomposition of lupine wood is considerably slower. This is likely the result of the higher concentrations of lignin and other recalcitrant compounds in lupine wood (14.7% lignin in lupine, 3.6–7.4% in annual grass litter (Bastow *unpublished data*)). Lupine wood decomposes considerably faster, however, than the wood of other trees and shrubs (Harmon and others 1986; Laiho and Prescott 2004). Although differences in climate and decomposer food webs may account for some of this difference, the high nitrogen content of lupine wood, compared to other woods (Whittaker and others 1979; Laiho and Prescott 2004), likely contributes as well. Berg (1984) proposed that the nutrient content of litter controls the rate of decomposition early during the

decomposition process, whereas the lignin content becomes more important as decomposition progresses. Although a larger range of litters and shorter sampling intervals would be necessary to rigorously test this model, lupine wood and annual grass litter differ considerably in their mass loss during even the first 6 months of decomposition at BMR (28.2% mass loss for lupine wood over the first winter, 43.7% mass loss for annual grass litter (Bastow and others 2008)). This suggests that the high lignin content of lupine wood slows its decomposition even during the early phases of decomposition.

The Contribution of Nitrogen from Lupine Wood Following the 2002 Die-Off

The quantity of nitrogen in nutrient poor litter often increases during the early stages of decomposition, as microbial decomposers transport nitrogen into the litter (immobilization, Melillo and others 1982). We saw no evidence of net nitrogen immobilization in this study; the quantity of nitrogen in lupine wood decreased during all time periods during which decomposition occurred. The nitrogen concentration of the remaining wood increased during decomposition, however, indicating that nitrogen loss from the litter was slower than overall mass loss. This may indicate that the most labile compounds in lupine wood contain relatively little nitrogen. Alternately, nitrogen may have been immobilized into lupine wood, but at a slower rate than decomposition, resulting in net nitrogen loss. In either case, the slow decomposition of lupine wood appears to limit the rate at which nitrogen is released, such that two-thirds of the original nitrogen in lupine wood was still present after 3 years.

Estimates of nitrogen release from decomposing lupine wood during the 3 years of this study ranged from 0.24 to 4.15 gN m^{-2}, but net release was only statistically detectable at one of the five sites (Lower Draw). At this site, woody debris from the 2002 die-off is estimated to have lost 0.80–2.33 gN m^{-2} during each of the 3 years following the die-off (4.15 ± 2.10 gN m^{-2} total). This is comparable to the rates of nitrogen input that are known to be ecologically significant in other systems, such as anthropogenic nitrogen deposition in the northeastern United States (1–2 gN m^{-2} y^{-1}, Chapin and others 2002) and nitrogen fixation by invasive *Myrica faya* in Hawai'i (1.8 gN m^{-2} y^{-1}, Vitousek and Walker 1989). The nitrogen contribution of decomposing lupine wood is likely to be small, however, compared to other effects of *L. arboreus* on soil nitrogen in this system, including nitrogen fixation by live bushes and the rapid decomposition of nitrogen-rich leaf litter. Maron and Jefferies (1999) found that soils under live lupine stands at BMR contained almost twice as much nitrogen as coastal prairie soils away from lupines and estimated that it would take 25 years without additional nitrogen inputs for this pool to be depleted by 50%. Of the total soil nitrogen pool, however, only 2.5–4.0% (11.0–17.5 gN m^{-2}) is mineralized annually (Maron and Jefferies 1999), suggesting that much of this nitrogen pool is not very labile. Depending on the lability of nitrogen released from woody debris, lupine wood may, therefore, make a detectable contribution to this pool in the years following severe die-offs.

Isopod Habitation of Lupine Wood: Seasonal or Successional?

Given that *P. scaber* is frequently found inhabiting ghost moth tunnels in both living and dead lupine woods in BMR, we were surprised at the scarcity of isopods in litterbags left in the field for 12 months or longer. The fact that isopods were abundant in the litterbags collected in April 2005, after 6 months in the field, indicates that there were still isopods in the vicinity of the experiment in October 2004, when *P. scaber* were virtually absent in collected litterbags. There are two possible explanations for the temporal pattern of isopods in litterbags. The first is that isopods only inhabit living and recently dead lupines, and that lupine wood becomes an inhospitable or undesirable habitat after less than a year of decomposition. This could explain why isopods had no effect on the decomposition of lupine wood. Because only the 6-month samples were collected in the spring, however, it is also possible that isopods inhabit the lupine wood in the spring, when the wood is still moist from winter rains and vacate the wood during the summer as it dries out. Lupine wood in litterbags collected in April, at the end of the wet, Mediterranean winter, had a gravimetric water content of 1.08 (g water/g dry weight, SD 0.40), whereas wood collected in October after the summer drought had a moisture content of 0.12 (SD 0.03). Litterbags collected after 12, 24, and 36 months in the field were all collected in October. An additional experiment, in which litterbags are collected in the spring after more than a year of decomposition, would be necessary to distinguish between these two explanations for the abundance of *P. scaber* in litterbags.

The Seasonality of Lupine Decomposition

Lupine mass did not decrease between 6 and 12 months in either the 2003 or the 2004 cohorts of litterbags. This indicates that first year decomposition occurred primarily between October and April (over-winter), and that little or no decomposition occurred between April and October (over-summer). Litterbags were only collected once a year after the first year of decomposition, so the seasonal pattern of decomposition in older debris is unclear. The availability of moisture is known to limit the activity of microbial decomposers (Swift and others 1979), however, so it is likely that decomposition of lupine wood occurred primarily during the wet over-winter periods throughout this study. The decomposition of annual grass litter at BMR is highly seasonal, with microbes and microfauna contributing to decomposition during the winter, and *P. scaber* contributing to decomposition during the summer (Bastow and others 2008). Because *P. scaber* did not contribute to the decomposition of lupine wood, it is likely that wood decomposition was restricted to the winter.

Conclusion

Woody debris is known to store nutrients and energy for many years in forest ecosystems (Whittaker and others 1979; Harmon and Hua 1991; Laiho and Prescott 2004). Although such debris is also a conspicuous feature of other ecosystems, including shrublands, deserts, and grasslands, the magnitude and dynamics of nutrients in woody debris have rarely been studied in such ecosystems (but see Ebert and Zedler 1984). This study showed that even rapidly decomposing wood stores nutrients for several years. Simulated ghost moth herbivory reduced the longevity of woody lupine debris by increasing its surface area. This demonstrates that herbivores may accelerate decomposition by increasing the surface area of uningested litter and that herbivores may affect the decomposition of woody detritus. The importance of these effects in a broader range of communities is a promising topic for future research.

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