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Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon

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Abstract Decomposing coarse woody debris (CWD) is a conspicuous and important component of forest ecosystems. Seasonal temperature and precipitation patterns influence heterotroph activity, which determines the rate of CWD decomposition. We tested the hypothesis that moisture content and heterotroph community composition influence carbon flux in freshly-cut Douglas fir (*Pseudotsuga menziesii*) logs. To evaluate the effects of physical penetration of bark and wood and transmission of basidiomycete compared with ascomycete fungi by insects, 360 experimental logs were assigned to five replicate sites, each with 12 heterotroph×moisture treatment combinations in 1995. Half of the logs in each heterotroph treatment received normal rainfall and half were placed individually under elevated clear plastic tents to reduce water inputs. Respiration was measured every 1–3 months. In 1996 and 1997 a different log representing each treatment combination was harvested from each replicate and analyzed for the presence of inoculated and colonizing fungi. Logs inoculated with decay fungi had higher respiration than uninoculated logs but this effect only approached significance (P=0.08) during the first season. Respiration was significantly higher in sheltered than in exposed logs. Our results indicate that respiration and wood decomposition rates may be depressed by high moisture content in the wet forests of the coastal Pacific Northwest.

Key words *Pseudotsuga* · Insect · Fungi ·*Stereum* · Decomposition

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Introduction

Coarse woody debris (CWD) is a conspicuous feature of forest ecosystems that has a number of long-term effects on ecosystem processes, including water, carbon, and nutrient fluxes, and community dynamics of associated organisms (Harmon et al. 1986; Rayner and Boddy 1988; Schowalter et al. 1992). Carbon flux from decomposing wood could be a significant contributor of atmospheric carbon, especially under warming atmospheric conditions. Ecologists and forest managers have long recognized the importance of decomposing CWD, but factors influencing seasonality and rates of decomposition, especially carbon and nutrient fluxes, remain poorly understood.

Several factors may affect decomposition processes of CWD. Seasonal temperature and precipitation patterns affect litter moisture content and heterotroph activity which in turn determine decomposition rates (e.g., Meentemeyer 1978; Whitford et al. 1981), but the effect of manipulated moisture content on decomposing CWD has not been reported. Carpenter et al. (1988) and Schowalter et al. (1992) suggested that the initial composition of heterotroph communities might affect seasonal and long-term decomposition processes. For example, seasonal patterns of colonization by bark- and wood-boring insects can affect initial establishment of microbial communities (Carpenter et al. 1988). Insect penetration of the chemical and physical barrier provided by bark facilitates microbial colonization (e.g., Ausmus 1977; Dowding 1984; Swift 1977). Communities initially dominated by ascomycetes or Fungi Imperfecti might delay colonization by basidiomycetous fungi responsible for degradation of lignin and cellulose (Käärik 1974). On the other hand, so called non-decay fungi may detoxify and condition the wood, making it more suitable for basidiomycete colonization (Barz and Weltring 1985; Blanchette and Shaw 1978; Rayner and Boddy 1988; Rayner and Todd 1979).

Wood moisture content may play a key role in determining which fungi initially dominate the community.

Although decomposition rate generally is positively related to moisture content (Meentemeyer 1978; Whitford et al. 1981), saturated wood inhibits decay by obstructing fungal growth and by limiting available oxygen, decreasing respiration rates in CWD (Rayner and Boddy 1988). Carpenter et al. (1988) suggested that the peak respiration rates from conifer CWD during late summer in western Oregon reflected sufficient drying of CWD to inhibit mold fungi and promote growth and cellulytic activity by decay fungi. However, the Carpenter study was not designed to test effects of different initial microbial communities or moisture contents on carbon flux from CWD, nor to assess seasonal shifts in microflora.

We tested the hypothesis that moisture content and heterotroph community composition influence carbon flux in decomposing CWD by manipulating these factors in freshly-cut Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, logs at the H.J. Andrews Experimental Forest Long Term Ecological Research (LTER) site in western Oregon. Respiration was measured seasonally in these logs over a 2-year period to assess the effects of bark and wood penetration, initial microflora, and moisture content on patterns of carbon flux as respiration from these logs.

Materials and methods

Site description

This study was conducted during 1995–1997 at the 6400-ha H.J. Andrews Experimental Forest located 80 km east of Eugene, Oregon in the central western Cascade Mountains (44°N, 122°W). The Andrews Forest is a Long Term Ecological Research (LTER) site and Man and the Biosphere (MAB) Reserve administered jointly by the USDA Forest Service (Willamette National Forest and Pacific Northwest Research Station) and Oregon State University.

Elevation at the Andrews Forest ranges from 400 to 1500 m. A maritime climate prevails, with wet, relatively mild winters and dry, warm summers. Precipitation averages 223 cm year^{-1} and is strongly seasonal, with 75% occurring from November through March. Precipitation during 1996 and 1997 exceeded long-term averages with 307 cm in 1996 and 331 cm in 1997 (rainfall data available at www.fsl.orst.edu/lterhome.html). Winter storms during January, February, and November 1996 brought record rainfall, causing flooding and landslides that limited access to the sites.

Vegetation at the Andrews Forest is dominated (40% of land area) by old-growth forest, composed primarily of emergent Douglas fir and a subcanopy of western hemlock, *Tsuga heterophylla* (Raf.) Sarg., and western red cedar, *Thuja plicata* Donn, with dominant trees about 500 years old and often exceeding 70 m in height and 125 cm diameter at breast height (dbh). Douglas fir and western hemlock represent 70% of stand biomass in old-growth stands (Grier and Logan 1977). Younger naturally regenerated and harvested-and-replanted stands occupy the remainder of the land area of the Andrews Forest.

Experimental methods

Harvest restrictions prevented acquisition of freshly cut logs within the Andrews Forest for this study. Instead, mature Douglas fir were cut from McDonald-Dunn Forest, operated by the College of Forestry at Oregon State University, north of Corvallis, Benton Co., Oregon, during June and July 1995 to provide 360 experimental logs (25–35 cm diameter, 1.5 m long). The logs were end-sealed with Gaco-Flex (elastomeric paint) to simulate longer logs (Smith et al. 1987), leaving the bark surface and simulated galleries as primary entry points. These logs were randomly assigned to five replicate sites at the Andrews Forest and placed horizontally on the ground during June–July 1995. All sites were under old-growth forest canopies (i.e., shaded) at 700–1000 m elevation and represented north and south aspects. The 72 logs at each site were randomly assigned to 12 treatment combinations (6 heterotroph treatments×2 moisture contents).

The six heterotroph treatments were selected to represent the combinations of bark beetles, ambrosia beetles, mold fungi and decay fungi observed in earlier studies of decomposition of four conifer species (see Carpenter et al. 1988; Schowalter et al. 1992). We designed our treatments to separate the effects of physical penetration of bark and wood by insects from the effects of inoculation of wood with insect-vectored fungi. Three treatments simulated insect penetration. One set of 12 logs had no bark penetration. A second set of 12 had holes (3 mm diameter, 10 mm deep, 50 m^{-2} of log surface area) drilled into the phloem (using a drill bit flame-sterilized between holes) to simulate colonization by bark beetles. The remaining 48 logs had sterile holes drilled into the sapwood (3 mm diameter, 37 mm deep, 50 m^{-2} of log surface area) to simulate colonization by ambrosia beetles. Holes in 12 of these logs were not treated further. In a second set of 12, the holes received 100 µl per hole of a blend of microfungi [*Ophiostoma picea* (Münch) Syd. & Syd. (isolate #387G), *Penicillium thomii* Maire (isolate #655A), and *Trichoderma viride* (Pers.: Fr.) (isolate #121ES)] and bacteria as described below. In a third set of 12, these holes received 100 µl per hole of a blend of basidiomycete fungi [*Stereum sanguinolentum* (Albertini and Schwein: Fr.) Fr. (isolate #10M2), *Heterobasidion annosum* (Fr.: Fr.) Bref. (isolate #10MB), and *Peniophora* sp. (isolate #Z1B10)]. In the last set of 12, the holes received 100 µl per hole of a blend of both groups of microorganisms. These fungi are representative of initial communities in decomposing logs with microfungi dominating logs colonized by ambrosia beetles and basidiomycetes dominating logs colonized by bark beetles (Carpenter et al. 1988; Schowalter et al. 1992). These treatments should indicate the degree to which initial penetration of the bark barrier, depth of penetration, inoculation of two beetle-vectored saprophyte functional groups, and the increasing level of functional diversity influence decomposition processes.

The inocula were prepared by placing a 3-mm-diameter agar disc cut from the actively growing edge of a 2% malt extract agar (MEA) culture of the desired test fungus in a flask containing 50 ml of a 1% malt extract. The cultures were incubated for 7–14 days for basidiomycetes and 3–5 days for microfungi until abundant mycelium was present. Spores and mycelium were collected on sterile filter paper by vacuum filtration, rinsed with sterile distilled water, and back washed into 50 ml of sterile distilled water. The resulting suspension was briefly macerated in a Waring blender and used directly for log inoculation. Aliquots of this mixture were also removed and applied to the surface of 2% malt agar in Petri dishes. These plates were incubated for 28 days at room temperature (23–25°C) and observed for evidence of growth of the test fungus and for the presence of contaminating organisms.

Half (6) of the logs in each of the above heterotroph treatments received normal water input (i.e., rainfall) and the other half were placed individually under elevated clear plastic tents (triangular cross-section, 1 m tall×2 m long, plastic extending down both sides to 40 cm above the ground, Fig. 1) to reduce water inputs while permitting normal light penetration and air flow over the logs. Because all logs lay horizontally on the ground, they received additional unmeasured amounts of water input via absorption from the ground, condensation, and rain splash. This moisture manipulation was designed to assess the effect of wood moisture content on heterotroph interactions and log decomposition processes. Moisture content was later measured gravimetrically by comparing fresh and dry weights of increment cores taken from each log at two accessible sites in March 1996, and from all sites in June 1998.

We installed one respiration chamber (20 cm diameter×20 cm high PVC) near the top-center of one log (Fig. 1) from each of the 12 treatment combinations during September 1995. Chambers were cut to fit the logs and sealed to the bark with silicone sealant. Respiration was measured seasonally (1–3 times per season, as sites were accessible) by placing an open jar (10 cm diameter×8 cm high) containing 30 g of soda-lime in each chamber, and capping and sealing the chamber for a 24-h period to absorb CO_2 (Edwards 1982). The jars were then dried, reweighed, and CO_2 evolved (grams) was measured by subtraction.

In June 1995, prior to treatment, we collected sterile increment core samples 25 cm from each end and from the center of each log. These samples were placed on MEA in order to ascertain that logs were not colonized by fungi prior to treatment. Fungal cultures were isolated and identified. In July of 1996 and 1997, three 50- to 75-mm discs were cut from a single log (25 cm from each end and from the center) representing each treatment combination at each of the five test sites. Logs used for respiration measurement were not sampled. Increment cores were then removed from four equidistant locations around each disc. These cores were divided into inner bark, outer bark, sapwood and heartwood, and placed on MEA in a separate Petri dish. The cores were incubated at 23–25°C, and only fungi growing from the wood were subcultured to 1.5% MEA slants for identification.

Fig. 1 Experimental log with attached respiration chamber and adjacent tented log

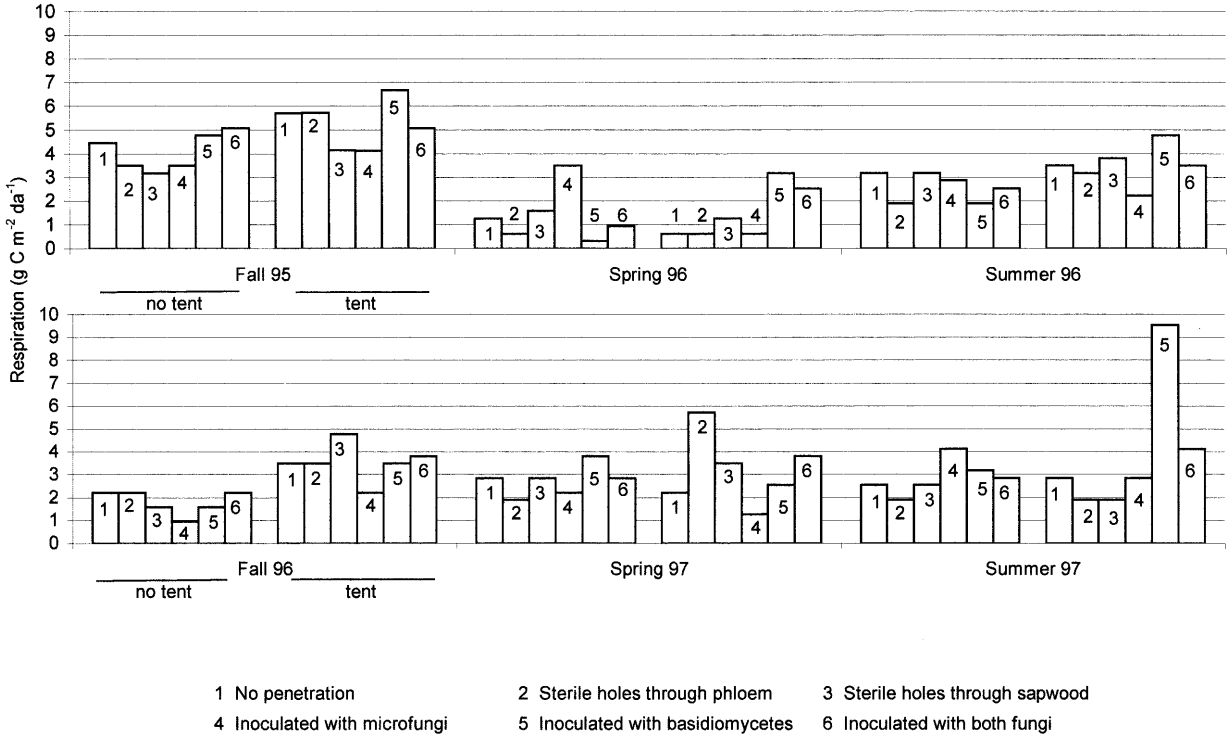
Fig. 2 Effect of fungal inoculation and moisture manipulation on mean respiration in experimental Douglas fir logs at the H.J. Andrews Experimental Forest, western Oregon

Data analyses

Respiration data for each log were combined as necessary to provide seasonal averages (September–November, December–February, March–May, and June–August). These time periods represent early, mid and late wet season, and dry season, respectively. The data were transformed to their square roots to better meet assumptions of normality for two-way analysis of variance (ANOVA) (Sokal and Rohlf 1981) and analyzed for each season using two-way ANOVA, with heterotroph and sheltering treatments as main factors and sites as replicates, and for the 2-year period using three-way ANOVA with season as an added factor (Steel and Torrie 1980). SAS software (SAS Institute 1982) was used for all analyses.

Results

Analysis of respiration data (Fig. 2) Showed that moisture content (tenting) had an important effect on respiration (F=7.87; df=1,44; P=0.007) and that fungal groups may have also influenced respiration rate (F=2.08; df=5,44; P=0.08) during the first measurement period. The interaction between these main effects was not significant (P=0.67). Respiration rates were highest in unpenetrated logs and in logs inoculated with decay fungi.



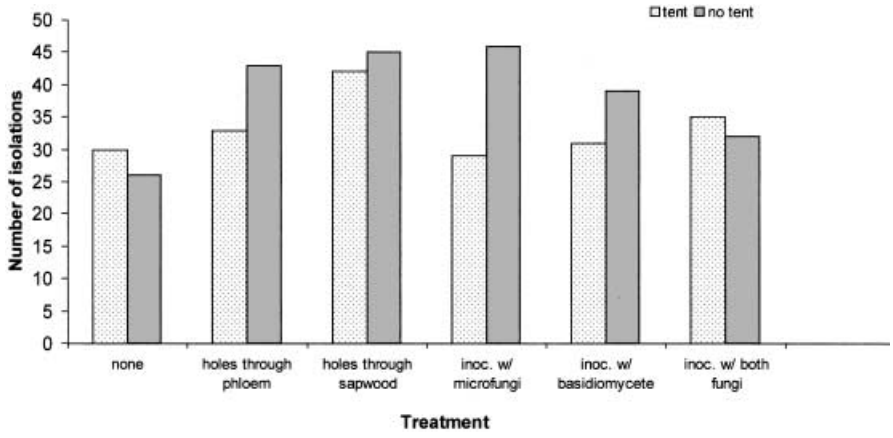


Fig. 3 Frequency of basidiomycete isolation from experimental Douglas fir logs subjected to varying drilling and fungal inocula and 2 years exposure after treatment at the H.J. Andrews Experimental Forest, western Oregon

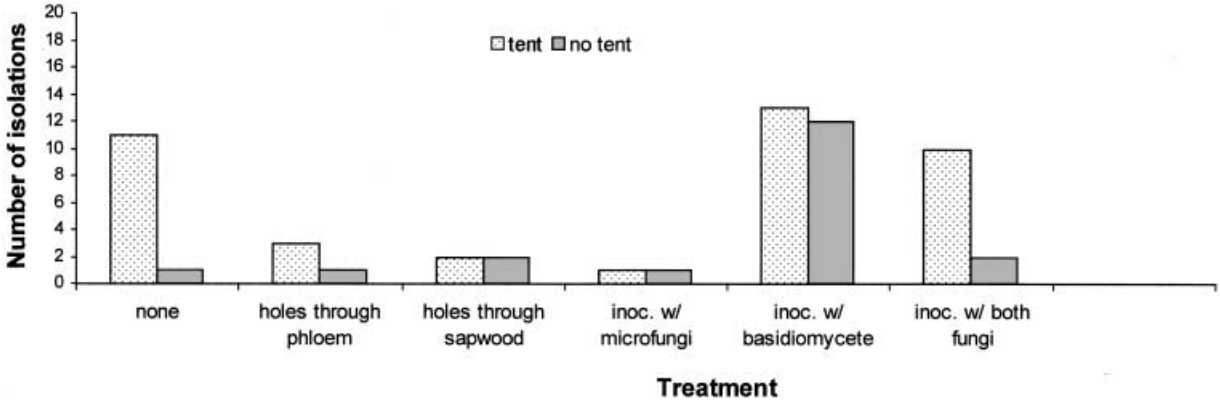


Fig. 4 Frequency of *Stereum sanguinolentum* isolations from Douglas fir logs subjected to varying drilling and fungal inocula and 2 years exposure after treatment at the H.J. Andrews Experimental Forest, western Oregon

Logs inoculated with decay fungi alone had higher respiration rates when under tents than when unsheltered. Logs inoculated with mold fungi alone had higher respiration rates when unsheltered. Heterotroph treatment effect was not significant for subsequent seasons nor for longer periods, although the logs inoculated with decay fungi generally had higher respiration rates.

Only *Penicillium* and *Trichoderma* were isolated in small numbers from fresh logs. Presence of inoculated fungi in logs did not appear to be consistent with respect to inoculation. Treatments initially inoculated with *S. sanguinolentum* and *Peniophora* sp. contained only slightly higher frequencies of these fungi after one year (Figs. 3, 4). Both of these fungi are among the initial colonizers most frequently found on Douglas fir logs shortly after felling. Thus, the natural inoculum present in the forest and its ability to colonize wood may have overwhelmed our initial treatments. We also collected fungal fruiting bodies from selected logs at each test site. While a variety of fungi were collected, *S. sanguinolentum* was the most abundant species and was more abundant on logs into which it had been inoculated. Fruiting bodies are a poor indicator of overall abundance of a given fungus, but are a relative indicator of substrate suitability (Zabel and Morrell 1992), and provide a linkage for comparison with previous studies.

Respiration rate was significantly higher ($P<0.004$) in sheltered than in unsheltered logs for each season (except spring 1996), and for longer periods. Sheltered logs appeared to have slightly larger numbers of *S. sanguinolentum*, but not other decay fungi (Figs. 3, 4). Winter storms during 1996 and 1997 tore or overturned many tents and restricted access to several of the sites, potentially confounding moisture manipulation and preventing measurement of the extent of moisture reduction in sheltered logs. During this period, moisture content of sheltered logs at two accessible sites in March 1996 (following the storms) was only slightly and non-significantly lower (39%) than that of unsheltered logs (41%). Reliable measurement at all sites in early June 1998, following a period of heavy precipitation, indicated significantly higher ($P=0.01$) moisture content in unsheltered logs (57±3%) than in sheltered logs (45±3%) indicating a 20% reduction in moisture content when tents were functional.

Respiration was significantly higher ($P<0.01$) in logs at the two south-facing sites (4 and 5), compared to logs at the three north-facing sites for each season (except spring 1996), and overall. Moisture content among logs was not significantly different between north and south facing slopes ($P=0.12$). As expected, respiration rate also was higher during warmer seasons.

When all data were combined and analyzed, with season as an added factor, respiration differed significantly

among blocks (F=8.77; df=4, 374; P<0.0001, sites 4 and 5>sites 1–3), seasons (F=23.63; df=3, 374; P<0.0001, summer and fall>winter and spring), and sheltering treatment (F=8.51; df=1, 374; P<0.004, sheltered>unsheltered). Respiration was progressively greater from microfungus-inoculated to non-inoculated and finally to decay fungus-inoculated, but the heterotroph treatment effects were not significant.

Discussion

In most studies, the effects of fungal colonization or insect attack are assessed in naturally colonized logs. This study addressed the effects of manipulated heterotroph communities and moisture content on respiration rates of CWD. We expected carbon flux in these experimental logs to reflect activity of inoculated microorganisms as affected by moisture content, i.e., higher rates in logs inoculated with decay fungi and in drier logs that favor decay fungi (hence, greater cellulytic activity) over mold fungi. We also expected that the inoculation treatments would provide a substantial advantage to the fungi selected with regard to successful colonization.

Our data indicate that the initial heterotroph community, composed of common, early successional species at this site, may influence respiration rate, but only for a short period. Note that our treatments penetrated only 1% of the log surface. Logs inoculated with decay fungi generally had higher respiration rates than did other treatments. However, logs inoculated with both decay and mold fungi did not have the highest respiration rate, suggesting that these groups may be antagonistic rather than synergistic (Barz and Weltring 1985; Blanchette and Shaw 1978; Rayner and Todd 1979). Antagonism is also indicated by the greater respiration of sheltered logs with decay fungi alone than when mold fungi also were present (Fig. 2). Respiration rate and decay fungus population levels in logs with unpenetrated bark were unexpectedly high, given indications from previous studies that bark penetration facilitates microbial colonization of CWD (Ausmus 1977; Dowding 1984; Swift 1977; Schowalter et al. 1992). This suggests other avenues of microbial colonization, even though the log ends were sealed to preclude colonization via cut ends. The effect of initial heterotroph community composition on carbon flux disappeared relatively quickly from logs in this study. The isolation data indicate that differences in the microbial community also disappeared after 1 year (e.g., Figs. 3, 4). These results suggest that early colonization by basidiomycetes may not affect subsequent microbial community structure in CWD, although it may accelerate decomposition processes. For example, inoculation of *S. sanguinolentum* into our logs was not the only avenue of colonization for this species, but inoculated logs had greater sporocarp production (indicating more growth and development) early in the decomposition process.

Respiration rate was higher in logs sheltered to reduce moisture content, supporting our hypothesis that drier conditions promote decay in wet forests of the Pacific Northwest. The effect of sheltering on respiration rate was significant for each time period analyzed (except for spring 1996, when many shelters had been ineffective), indicating that water content influences the decay rate of these logs. Unfortunately, winter storms compromised the tents and limited access to our sites during a portion of the study period. Nevertheless, moisture content was generally reduced in sheltered logs, and decay fungi were more abundant, further suggesting reduced moisture. Because sheltering simulated effects of a drier environment, we predict that respiration and overall decomposition rates will be higher under the warmer, drier conditions predicted by climate change models for this region (Schneider et al. 1992; Hansen et al. 1988).

Although our study was not designed to test effects of temperature, respiration rates were higher for logs at the two south-facing sites than for logs at the three north-facing sites and were higher during warmer seasons of the year, similar to results reported by Marra and Edmonds (1994). These results could have implications for decomposition rates under differing disturbance regimes that create varying degrees of openings in the forest (Marra and Edmonds 1994, 1996). Larger openings could increase summer warming and drying, increasing decomposition rates of CWD, provided that the moisture levels in the wood remained high enough to support growth of decay fungi (>20% moisture content). Over time, these increased rates could affect the volumes of CWD in a stand, particularly in managed second growth stands with smaller log diameters. Given the potentially important roles of CWD, these changes may require that an increased level of CWD be left to maintain a stable ecosystem.

In conclusion, we demonstrated that moisture content significantly affect carbon flux in experimental conifer logs in western Oregon. Initial heterotroph community composition may have had a short-term effect on respiration. These data indicate that respiration and decomposition rates should be higher under warmer, drier conditions that promote the activity of basidiomycetous decay fungi, e.g., in clearcuts and under climate change scenarios.

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