disturbance) between the ridge and slope sites. Under equal conditions, it could be expected that slope would be a major factor in causing tree falls, due to decreased soil stability and the asymmetry of tree support structures. However, our data seem to suggest that wind and slope contribute to disturbance equally in the two sites we examined. Similar rates of disturbance should produce similar forest structure at both sites. Indeed, the mean DBH of canopy trees, the density of canopy and sub-canopy trees, and the ratio of canopy to sub-canopy tree abundance did not differ between sites. These similarities suggest that the processes that determine *Quercus* forest structure, recruitment, growth rate, and/or mortality, may be similar at both sites.

Sub-canopy DBH and the overall DBH distribution, however, varied significantly between sites. The ridge population structure was strongly biased towards trees with a DBH between 1 and 10 cm. The distribution at the slope site was more even than that of the ridge. These differences could be attributed to variation in timing of recruitment or growth rate. The timing of acorn masts could differ between sites, affecting the average age of the understory, or the growth rate of slope trees is higher than the growth rate on the ridge. Further, recruitment and growth rate are likely affected by the under-story composition and density.

Bamboo was more dominant in the slope under-story than on the ridge. Carlos Solano, the proprietor of the study site land, has proposed that *Quercus* undergoes a rapid increase in recruitment following the senescence of bamboo stands at the end of a flowering cycle (pers. comm.). Future research should quantify oak response to the bamboo cycle. Understanding the relationship between tree fall disturbance and oak recruitment and growth patterns is central to interpreting the Cerro forest population structure.

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Effects of varying amounts of oak leaf litter on microbial respiration in a tropical montane forest

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Abstract: The chemical compound tannin, found in *Quercus* leaf litter, slows decomposition and acidifies soil. We hypothesized that the organic soil horizon found directly below oak trees with no bamboo (*Chusquea*) understory would have lower microbial respiration, arthropod density, and pH, and a greater moisture accumulation than leaf litter from a large forest gap dominated by bamboo (*Chusquea*) with no oak canopy. Contrary to our predictions, we found that microbial respiration was higher in oak-dominated sites than bamboo-dominated sites. There was no difference in arthropod densities, soil moisture, or litter moisture between oak and bamboo sites. However, pH was slightly lower in the oak site. The greater overall mass of leaf litter in oak sites and/or the nutritive quality of the oak litter may account for the greater microbial activity in the oak site. Mechanisms related to microbial efficiency and/or litter input rates may help explain how oak systems maintain deeper litter horizons and higher microbial activity.

Key Words: arthropods, bamboo, litter moisture, pH, soil moisture, tannin

Introduction

Tannin is a complex, highly indigestible chemical compound in the leaves of many trees that slows the process of decomposition. Oak leaves (*Quercus*) contain high concentrations of tannins, and oak leaf litter has been shown to inhibit seedling recruitment in tropical montane forests (Dallison et al. 1999). We hypothesized that tannins from leaf litter comprised of dense layers of oak leaves would have effects throughout the organic soil horizon (leaf litter, partially-digested leaf fragments, and highly decomposed humic soil - see Osterling et al. 1995). We compared microbial respiration, arthropod abundance, pH, and soil and litter moisture from areas differing in quantity of oak leaf litter: an oak-dominated (canopy and understory) forest and a ~ 50 m^2 gap in that forest with no overstory trees but a dense bamboo (*Chusquea*) understory (hereafter referred to as the oak site and the bamboo site, respectively). We predicted that higher tannic acid concentrations, which we proposed would occur in the oak site, would lead to lower pH, lower microbial respiration rates, and lower arthropod densities compared to the bamboo site. We also predicted that slower decomposition due to high tannin levels would allow for greater soil and litter moisture accumulation in the oak site.

Methods

We used visual assessment of dominant vegetation to choose one site with an oak (*Quercus copeyensis* and *Q. costaricensis*) canopy and one site dominated by bamboo with no oak canopy directly overhead. We found oak leaves in the litter at both sites, presumably because oak leaves drift into the bamboo site from nearby oak canopies. Both sites were at similar elevations (2770 m and 2755 m respectively) along the Mirador Trail at the Estación Biológica de Cuericí in Cerro de la Muerte, Costa Rica. Using a 25 m section of the trail as a transect, we haphazardly selected nine 30 x 30 cm sampling plots in each site, 2-6 m from the trail, on 27 January 2001. We collected all leaf litter from each plot, and measured soil temperature (taken at ~ 5 cm depth) and ambient temperature using a Physitemp Thermometer™, and humic soil pH measurement using a Demetra™ soil tester. We also collected a humic soil sample (~ 100 ml) at each plot.

Oak leaves in the litter from each plot at both sites were manually sorted from the non-oak leaves, and all leaf litter was in-

spected for arthropods. We measured oak leaf mass before and after drying to calculate moisture content and to assess the abundance of oak leaves in each plot's litter. We quantified microbial respiration in the soil samples using soil respirometers: nine replicates from each site were run for 1 h, in blocks of three samples from each site and one control (Eaton et al. 1998). The three respirometer blocks were run at approximately equal and constant temperatures. Soil respiration sample weights were recorded before and after drying to calculate soil moisture content.

We used t-tests to compare oak leaf litter dry mass, microbial respiration, litter moisture, soil moisture, pH, temperature, and arthropod density between oak and bamboo sites. Linear regression was used to investigate the relationship between these same variables and oak leaf litter mass. We normalized the pH data by anti-log transformation.

Results

Mean oak leaf mass was over three times greater in oak plots (60.3 g dry mass, SE = 7.6, n = 9) than bamboo plots (17.1 g dry mass, SE = 3.9, n = 9) (t = 3.72, df = 16, P = 0.002). The mean microbial respiration rate was significantly greater in soil from the oak plots (52.27 µL/g, SE = 5.62) than bamboo plots (35.12 µL/g, SE = 4.99) (t = 2.28, df = 16, P = 0.04). The respiration rate increased with dry mass of oak leaf litter (r^2 = 0.23, df = 1, P = 0.025, Fig. 1), and with soil moisture (r^2 = 0.19, df = 1, P = 0.04). However, the mean soil moisture contents of oak plots (51.07% of total dry mass, SE = 4.02) and bamboo plots (51.26% of total dry mass, SE = 3.54) were almost identical. Mean soil temperatures at the oak plots (11.74 °C, SE = 0.45) and the bamboo plots (11.39 °C, SE = 0.56) were also similar (t = 0.496, df = 16, P = 0.63). The mean pH of oak plots was significantly lower (6.7, SE = 0.062) than that of bamboo plots (6.9, SE = 0.045) (t = 0.36, df = 16, P = 0.03). Arthropod density did not differ significantly between the oak and the bamboo plots (t = 1.085, df = 16, P = 0.29). Arachnids, coleopterans and dipterans were the most common orders. Because of the overall low arthropod abundance (2.3 individuals/plot, SE = 0.46), we did not calculate a diversity index.

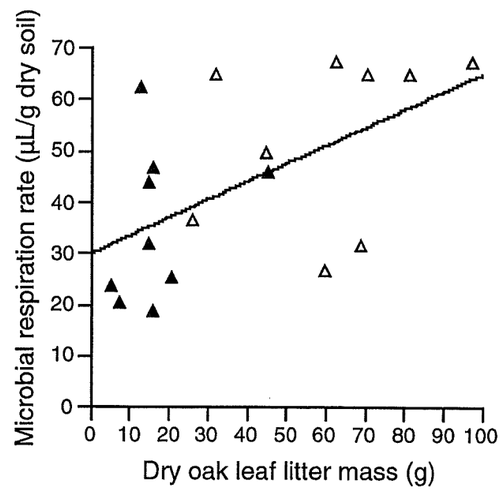

Fig. 1. Microbial respiration rate correlated with dry oak leaf litter mass from 30 cm^2 plots on Mirador Trail in Estación Biológica de Cuerici, Costa Rica (n = 18). Closed triangles represent sites dominated by bamboo understory with no oak canopy cover; open triangles represent oak forest with no bamboo understory.

Discussion

We predicted a decrease in microbial respiration with oak litter mass, but found the opposite relationship. Humic moisture content and temperature have been shown to affect microbial activity (Braden et al. 2001), yet do not explain the variation in microbial respiration rate with oak litter mass in this study because their values were statistically similar across our habitat types. The small statistical difference in mean pH between bamboo and oak sites does not help explain the variation either, because pH values were close to neutral and within the optimal range of microbial activity (D.R. Peart, pers. comm.). It therefore appears that the relationship between oak leaf litter mass and microbial activity in these tropical montane sites is independent of moisture, temperature, pH and arthropod density. Our study does not reject the hypothesis that tannin from oak leaves deters microbial activity; in nutrient-limited systems such as montane tropical forests, oak leaves may simply have sufficient nutritive quality to outweigh the cost to microbes of digesting tannin. Further study comparing more leaf litter types of varying abundances and nutritive qualities could determine the importance of oak leaf litter mass and quality in the rate of microbial respiration in the humic soil.

A second paradox stems from our observation that the humic layer was thicker in oak areas than bamboo areas. Two mechanisms could explain the accumulation of this decomposing material, given the higher microbial respiration rate in oak areas. Either leaf litter input is greater in oak areas than bamboo areas, or leaf litter inputs and outputs are equal in oak and bamboo areas, but oak leaves (due to tannins) require greater microbial effort and time for digestion. The first proposed mechanism implies that decomposition (i.e. microbial output) is faster in oak areas than in bamboo areas, conflicting with the widely-held notion that tannins slow decomposition. The second mechanism, in which the ratio of microbial output to microbial activity is decreased by the inefficiency of digesting tannins, could help explain why decomposition may be slower in oak leaf litter. Of course, these two explanations are neither mutually exclusive nor an exhaustive list of possible mechanisms. In this study we have assumed that bamboo litter neither contains tannins nor affects decomposition in any significant way; this may not be the case. However, oak litter input rates and the efficiency of microbial digestion of tannins may play significant roles in oak forest dynamics, and provide fertile ground for future studies.

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