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Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest

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ABSTRACT

Humid tropical forests have the highest rates of litterfall production globally, which fuels rapid nutrient recycling and high net ecosystem production. Severe storm events significantly alter patterns in litterfall mass and nutrient dynamics through a combination of canopy disturbance and litter deposition. In this study, we used a large-scale long-term manipulation experiment to explore the separate and combined effects of canopy trimming and litter deposition on litterfall rates and litter nutrient concentrations and content. The deposition of fine litter associated with the treatments was equivalent to more than two times the annual fine litterfall mass and nutrient content in control plots. Results showed that canopy trimming was the primary driver of changes in litterfall and associated nutrient cycling. Canopy trimming reduced litterfall mass by 14 Mg ha^{-1} over the 2.5 year post-trim period. Nutrient concentrations increased in some litter fractions following trimming, likely due to a combination of changes in the species and fractional composition of litterfall, and increased nutrient uptake from reduced competition for nutrients. Declines in litterfall mass, however, led to large reductions in litterfall nutrient content with a loss of 143 ± 22 kg N ha^{-1} and 7 ± 0.2 kg P ha^{-1} over the 2.5 year post-trim period. There were no significant effects of litter deposition on litterfall rates or nutrient content, contrary to results from some fertilizer experiments. Our results suggest that large pulsed inputs of nutrients associated with tropical storms are unlikely to increase litterfall production, and that canopy disturbance has large and lasting effects on carbon and nutrient cycling.

1. Introduction

Litterfall is a key conduit for carbon (C) and nutrient recycling in terrestrial ecosystems. Humid tropical forests have the highest rates of litterfall production globally (Raich and Tufekcioglu, 2000; Clark et al., 2001). These ecosystems also have the fastest rates of litter decomposition (Parton et al., 2007; Cusack et al., 2009), leading to rapid turnover of litterfall C and nutrient stocks. Fast rates of litterfall production and decomposition contribute to the high net ecosystem production typical of humid tropical forest ecosystems (Melillo et al., 1993; Malhi et al., 1999).

Canopy disturbances associated with severe storms dramatically alter patterns in litterfall and associated nutrient cycling (Lugo and Scatena, 1996; Scatena and Lugo, 1995). Current estimates from global circulation models suggest that severe tropical storms (i.e., hurricanes, cyclones, and typhoons) are likely to increase in intensity and/or frequency with elevated greenhouse gas emissions and climate change (Zhao and Held, 2012; Villarini and Vecchi, 2013). Declines in litterfall production following severe storms can persist for many years (Scatena et al., 1996, although see Lugo et al., 2011), and thus are likely to decrease nutrient transfers from the canopy to the forest floor, and slow rates of nutrient recycling between plants and soils during the post-storm period. Lower nutrient inputs could ultimately feed back on the tropical forest C cycle over the long term, resulting in lower plant C uptake and higher atmospheric CO_2 concentrations.

The effects of tropical storms on litterfall dynamics result from a combination of canopy reduction and litter deposition. High winds defoliate and break fine and coarse branches in upper and mid-canopy trees, temporarily decreasing litterfall production. Canopy reduction and tree falls create gaps that increase understory light levels (Fernández and Fetcher, 1991) and decrease competition for light and other resources for survivors (Silver et al., 1996), which could in turn increase the growth and litter

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production of surviving vegetation (Fernández and Fetcher, 1991; Lin et al., 2011; Plotkin et al., 2013). Changes in ecosystem structure associated with disturbance can lead to changes in the composition and distribution of litterfall. For example, surviving understory vegetation and new recruitment may differ in the seasonality of litter production (Angulo-Sandoval et al., 2004), the distribution of litterfall fractions (leaves, wood, fruits and flowers, and miscellaneous material), as well as litterfall nutrient concentrations relative to canopy species (Lugo, 1992). Litter deposition associated with severe storms can reduce understory litter production, at least initially, if understory plants are physically damaged or buried by falling debris (Basnet et al., 1992). A large influx of nutrient-rich green plant material can stimulate plant growth and associated litter production through a fertilization effect (Wood et al., 2009), although woody litter can immobilize added nutrients and slow nutrient recycling (Zimmerman et al., 1995).

The different and potentially confounding effects of canopy opening and litter deposition make it difficult to predict the effects of severe storms on C and nutrient cycling during ecosystem reorganization in tropical forests. Here we report on the Canopy Trimming Experiment (CTE), a large-scale long-term experiment in the Luquillo Experimental Forest (LEF), Puerto Rico (Richardson et al., 2010). The CTE included a canopy disturbance treatment, as well as treatments designed to allow us to explore the separate effects of canopy disturbance and litter inputs associated with strong tropical storms. We tested the hypothesis that litter deposition associated with severe storms partially offsets the negative effects of canopy disturbance, leading to greater litterfall production in sites with litter deposition and canopy trimming than with canopy trimming alone. We also tested the hypothesis that patterns in litterfall nutrient inputs would be driven primarily by effects on litterfall mass and not by changes litterfall nutrient concentrations, which were predicted to be relatively insensitive to the manipulations. Finally, we used the CTE to explore seasonal dynamics in litterfall and litterfall nutrients in this relatively aseasonal humid tropical forest.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted in the El Verde research area of the Luquillo Experimental Forest (LEF), Puerto Rico, part of the Long Term Ecological Research program (18°20′N, 65°49′W). The sites were located in the tabonuco forest type at approximately 350 m elevation above sea level. Mean annual air temperature during the study (2003–2009) was 24.2 (±0.1) °C and mean annual precipitation was 3105 (±70) mm (range from 2885 to 3405 mm y^{-1}). January through April are drier months, with average monthly rainfall 275 mm mon^{-1} (Heartsill-Scalley et al., 2007).

Soils in the research area are dominantly Oxisols in the Zarzal complex, derived from volcanoclastic sediments. These soils are clay rich, deeply weathered, and depleted in most primary minerals (Soil Survey Staff, 2002). The tabonuco forest type is characterized by approximately 190 tree species (Scatena, 1989). Vegetation at the site was dominated by *Dacryodes excelsa* (Vahl), *Prestoea montana* (Vahl), *Manilkara bidentata* ((A.DC.)A.Chev.) and *Sloanea berteroana* (Choisy) (Shiels et al., 2010). There are two main peaks of leaffall observed in this forest, which coincide with the periods of major solar radiation at this latitude (Zalamea and González, 2008).

We used a complete randomized block design with three replicate blocks each containing four 30 × 30 m treatment plots separated by approximately 20 m buffers. Within each plot, a 20 × 20 m sampling area was defined and furthered divided into 16 subplots to minimize the effects of destructive sampling on long-term measurements. Treatments consisted of: (1) canopy trimming and litter deposition (trim + debris), (2) canopy trimming with the litter removed (trim + no debris), (3) intact canopy with litter added from the removal treatment (no trim + debris) and (4) no manipulation (no trim + no debris). Pre-treatment litterfall measurements began in November 2002. The manipulations spanned from late October 2004 to June 2005. Each treatment was completed within a given plot and block before the subsequent block was treated. Details of the treatments, plots, and timing are given in Shiels et al. (2010) and Richardson et al. (2010). Trimmed material was weighed using tarps and spring balances. Canopy trimming generated approximately 72 ± 2 Mg ha^{-1} of necromass. The necromass was not immediately distributed on the plots resulting in some loss of mass (Richardson et al., 2010; Shiels et al., 2010), and associated nutrient changes (Shiels and González, 2014). To determine the nutrient deposition from fine litter generated from trimming, we multiplied the dry mass (1.6 Mg $plot^{-1}$) of leaves (which were pooled with fine twigs) by the mean annual nutrient concentrations in leaf litterfall in the same forest, using data generated from the unmanipulated plots (no trim + no debris) (Table 1). We used litterfall concentrations as opposed to values for fresh plant fractions because of potential nutrient loss prior to placement on the experimental plots (Shiels and González, 2014). This resulted in an estimated minimum nutrient deposition rate of 164 kg N ha^{-1}, 5 kg P ha^{-1}, 34 kg K ha^{-1}, 157 kg Ca ha^{-1}, and 40 kg Mg ha^{-1}. These are minimum values because additional nutrients were added in other litter fractions (fine and coarse wood, fruits and flowers, and miscellaneous material) that were not quantified during the trimming events but were deposited on the plots.

Litterfall was collected every 14 days from 10 baskets (dimensions 43 × 43 cm) distributed in a stratified random fashion (to ensure plot coverage) inside each 20 × 20 m core area of each treatment plot. Baskets were leveled and fastened to poles at 1 m height. Baskets were removed during the trimming of respective treatment plots in order to prevent the baskets from getting broken by dropped branches, and replaced as soon as the canopy trimming was completed.

We separately report the pretreatment (November 2002–October 2004) and post-treatment (July 2005–December 2007) data, recognizing that this excludes a small amount of data during the establishment of the experiment. Litterfall mass associated with the trimming events was estimated by weighing the litter generated during the canopy manipulation using tarps and spring balances. Following each litter collection, litter was dried at 40 °C for at least one week, and kept in a heated room until samples could be sorted into the following categories: leaves, wood, fruits and flowers (including seeds), miscellaneous (unidentifiable material >2 mm). We re-dried subsamples of litterfall at 65 °C and weighed them to establish a conversion to oven dry weight. Litterfall was pooled by fraction within each plot quarterly for chemical analyses. In this paper we report quarterly mass to compare with nutrient concentrations and nutrient content.

2.2. Laboratory procedures

Litterfall samples were ground to pass through an 18 mesh sieve. Total C and N were determined using the macro dry combustion method on a LECO TruSpec CN Analyzer or LECO CNS-2000 Analyzer. The LECO CNS-2000 Analyzer was used to determine total C and N of litterfall in 2002–2004. The remaining total C and N analyses were determined utilizing the LECO TruSpec CN Analyzer. Blanks and reference materials were analyzed with each run at a rate of 1 per 10–20 samples to insure that the samples were directly comparable.