



Divergent responses of leaf herbivory to simulated hurricane effects in a rainforest understory



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ABSTRACT

Hurricanes are major disturbances in many forests, but studies showing effects of natural hurricanes on herbivory rates have yielded mixed results. Forest managers could benefit from a better understanding of the effects of disturbances on herbivory to manage for particular recovery or restoration goals after anthropogenic or natural disturbances, such as logging and windstorms. I measured herbivory on eight understory plant species that are common pioneer and non-pioneer species in a rainforest in Puerto Rico, following experimental manipulation of forest plots to simulate the two major effects of a hurricane (canopy opening and a detrital pulse). I expected that greater leaf production and leaf quality would result from canopy trimming and detritus (debris) addition to the forest floor, respectively, and that both treatments would enhance herbivory rates independently and especially in combination. I found a significant interaction of trim and debris treatments that affected plant species within pioneer and non-pioneer plant groups differently: a debris pulse or canopy trimming alone stimulated understory herbivory over time on non-pioneer and pioneer plants, respectively, but the combination of these two treatments had no effect on herbivory rates. Specifically, herbivory was higher on pioneer plants in plots where the canopy was trimmed but debris had not been added, whereas herbivory was higher on non-pioneer plants in plots where debris was added to the forest floor under intact canopy conditions. Therefore, different mechanisms apparently controlled herbivory of pioneer and non-pioneer species. Pioneer plants likely experienced enhanced herbivory in trimmed plots in part because of the increased densities of pioneer plants responding to canopy trimming; pioneer plants were temporarily less abundant in debris addition plots. Non-pioneer species may have experienced greater herbivory in debris addition plots in part because of increased foliar quality resulting from enhanced nutrient availability associated with the debris pulse. Future, complementary greenhouse and field mesocosm experiments that manipulate the factors likely contributing to these results would help to reconcile results from previous studies that have documented both increases and decreases in herbivory or certain herbivore taxonomic groups resulting from natural hurricanes. Understanding the mechanisms that affect herbivory after hurricanes is important because herbivory can affect nutrient cycling, plant community structure, and ultimately forest recovery after disturbance.

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1. Introduction

Globally, herbivores influence how ecosystems function (Huntly, 1995; Weisser and Siemann, 2004; Prather et al., 2013), and it is therefore important to understand the factors that control herbivory. Many factors are known to influence herbivory rates, including: food availability (the higher the levels of primary production, the more food available for herbivores; Lawton, 1983; Lewinsohn et al., 2005); food quality (differences

in the concentration of leaf nitrogen and phosphorus or secondary compounds influence herbivory rates; White, 1984; Huberty and Denno, 2004); the strength of competition (competitors can alter feeding rates and behavior; Bonser and Reader, 1995); and strength of top-down pressures (the greater the pressure from predators and parasites, the lower the herbivory; Siemann et al., 1998). All of these factors may interact with one another, and each can be altered by disturbances, such as hurricanes.

Hurricanes are common disturbances in many forested ecosystems, especially in the Caribbean (Walsh, 1997). Hurricanes result in two major, and simultaneous, changes in forest structure: the opening of a usually closed canopy (Fernandez and Fetcher, 1991), and a pulse of non-senescent detritus to the forest floor

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(Lodge et al., 1991; Ostertag et al., 2003), which decomposes very rapidly and acts as a nutrient pulse. These two physical effects can both directly and indirectly influence all the major factors that affect herbivory described above. Previous studies looking at the effects of hurricanes on herbivory rates in forests have had mixed results, including both increases in herbivory and the abundance of certain herbivore taxonomic groups (Torres, 1992; Schowalter, 1994; Schowalter and Ganio, 1999; Hunter and Forkner, 1999), and reductions in herbivory and the abundance of certain herbivore groups (Willig and Camilo, 1991; Spiller and Agrawal, 2003; Angulo-Sandoval et al., 2004). Increases in herbivory after hurricanes, however, have mostly been observed in forest canopies (Schowalter, 1994; Schowalter and Ganio, 1999), while reductions in herbivory rates have mainly been observed in forest understories (Willig and Camilo, 1991; Spiller and Agrawal, 2003; Angulo-Sandoval et al., 2004). No studies, however, have determined the relative effects of debris addition and canopy trimming on levels of herbivory, either static or in terms of rates, for a community of plants in a rainforest understory.

I utilized a large experiment (the Canopy Trimming Experiment, CTE) that simulated the main effects of natural hurricanes (canopy opening and debris pulse) in a Puerto Rican rainforest to test the following questions: (1) How do the independent and combined effects of canopy opening and debris addition to the forest floor affect understory herbivory? (2) Are the effects of canopy opening and debris addition on herbivory different for pioneer non-pioneer species? I predicted that (H1a) both increases in light and debris would have positive effects on understory herbivory through (H1b) increases in light to the understory causing increasing food availability in the form of greater new leaf production, and (H1c) a nutrient pulse from decomposing debris increases food quantity and quality for understory herbivores. I further expected that (H2) these two factors (canopy openness and debris deposition) combined would have even greater positive effects on herbivory than independently.

2. Material and methods

2.1. Site description

This study was conducted at the Luquillo Experimental Forest (LEF), located in the northeastern corner of Puerto Rico (18°19'N, 65°45'W). Animal diversity in this insular forest is generally lower than mainland tropical sites (Reagan and Waide, 1996). Invertebrates are the major folivores in this forest, and there are no extant folivorous mammals. Rates of herbivory in the understory of this forest are generally lower than other tropical forests—about 16% of leaf material a month is eaten by folivores—and herbivory rates are relatively constant throughout the year (Angulo-Sandoval and Aide, 2000a). This site is frequently disturbed by hurricanes (every 6–60 years depending on intensity, Scatena and Larsen, 1991) during months with generally higher precipitation (May through December), and the effects of natural hurricanes on abiotic and biotic processes at this site have been extensively studied (Brokaw et al., 2012). This study took place in Tabonuco forest, the dominant and lowest vegetation type along an elevational gradient at LEF. The dominant, non-pioneer trees in the Tabonuco forest are *Dacryodes excelsa*, *Sloanea berteriana*, and the palm, *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*). The study site is described more fully in Shiels and González (2014).

2.2. Experimental design

To test the effects of a simulated hurricane on understory herbivory, I utilized the CTE, which was designed to differentiate the two main effects of hurricanes (the opening of the canopy, and

the influx of debris onto the forest floor). This experiment has been extensively described (Richardson et al., 2010; Shiels et al., 2010; Shiels and González, 2014). Briefly, this experiment used a completely randomized block, fully factorial design where three replicate blocks in Tabonuco forest with similar land use history had two main factors (canopy trimmed = trim, or debris added to forest floor = debris) that were combined factorially to result in a total of four treatments (trim + no debris, no trim + debris, trim + debris, and no trim + no debris [control]). There were a total of 12–30 × 30 m plots ($n = 3$ per treatment) with plots located no closer than 20 m from each other. Although each 30 m × 30 m plot was treated, only the core 20 × 20 m area within each plot was used for measurements, with 10 m of buffer zone along each side. The core measurement area was divided into 16 subplots (each ca. 4.7 × 4.7 m) designated for measuring different variables and to minimize the amount of disturbance to any one plot (see Shiels and González, 2014). Understory herbivory measurements described in my study utilized four subplots dedicated to plant measurements for a total of 48 subplots.

Treatment application took place from October 2004 through June 2005. Light levels and canopy cover were reduced to levels that mimicked levels after Hurricane Hugo (Shiels et al., 2010). For the trim treatment plots, all branches ≤10 cm diameter that were above 3 m height were cut and removed from all non-palm trees that were >10 cm diameter at 1.3 m height. The fronds on all palm trees over 3 m in stem height were also removed. Material that was clipped from trimmed plots was used as the detritus added to debris-addition plots. This debris was separated into wood, leaves and twigs, and palm fronds. It was subsequently weighed, and a subsample was dried and reweighed to establish a wet to dry conversion rate. All material was piled along sides of the plots until trimming was complete, and subsequently the debris was added to respective plots. The process resulted in about 1 month of decomposition before treatment deposition. On average, 6500 kg (dry weight) was added to each debris-addition plot, an amount that mimicked debris that fell during Hurricane Hugo (Shiels et al., 2010).

2.3. Sampling methods

In all 12 plots, I measured herbivory in the summer before the experiment began in 2004, and annually for three summers after treatment application (2005–2007). I chose to measure herbivory on eight species of common understory plants that represented the most common pioneer and non-pioneer species in the CTE plots (Shiels et al., 2010) and in the Tabonuco forest in general (McDowell et al., 2012). The pioneer species included four trees (*Cecropia schreberiana*, Cecropiaceae; *Miconia prasina*, Melastomataceae; *Miconia racemosa*, Melastomataceae; *Schefflera morototoni*, Araliaceae), and one perennial herb (*Piper glabrescens*, Piperaceae). The non-pioneer species included three trees (*Casearia arborea*, Flacourtiaceae; *S. berteriana*, Elaeocarpaceae; *Manilkara bidentata*, Sapotaceae). I used methods previously used at this and other field sites to measure leaf area missing and leaf production (Aide, 1993; Angulo-Sandoval and Aide, 2000a, 2000b; Angulo-Sandoval et al., 2004), but leaf area missing was quantified digitally using ImageJ shareware (Schneider et al., 2012) instead of a grid system for higher accuracy.

I flagged all individuals of my focal plant species between 0.5 and 2.5 m tall within the four plant measurement subplots in each plot of the experiment annually (2004–2007) during the peak time of leaf production (late May/early June; Angulo-Sandoval and Aide, 2000a). Using colored wire tied around leaf petioles, I randomly marked up to 10 emerging leaves spread throughout the plant (most understory plants had fewer than 10 emerging leaves; median number of new leaves on pioneer species = 7.3; median

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