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Canopy arthropod responses to experimental canopy opening and debris deposition in a tropical rainforest subject to hurricanes

Timothy D. Schowalter [a,*], Michael R. Willig [b], Steven J. Presley [b]

[a] Department of Entomology, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, United States
[b] Center for Environmental Sciences & Engineering and Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT 06269, United States

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ABSTRACT

We analyzed responses of canopy arthropods on seven representative early and late successional overstory and understory tree species to a canopy trimming experiment designed to separate effects of canopy opening and debris pulse (resulting from hurricane disturbance) in a tropical rainforest ecosystem at the Luquillo Experimental Forest Long-Term Ecological Research (LTER) site in Puerto Rico. We expected that either canopy opening or added debris would result in increased abundances of certain scale insects and other hemipterans, and thereby affect arthropod diversity.

Six of thirteen arthropod taxa tested showed significant responses to treatments as main effects or interactions. No taxon responded significantly to trim treatment alone. The red wax scale, *Ceroplastes rubens* (on *Manilkara bidentata*), was significantly less abundant in treatments with added debris than in treatments without added debris, and salticid spiders (on *Sloanea berteroana*) were significantly more abundant in treatments with added debris than in other treatments. Canopy trimming generally did not have a significant effect on assemblage diversity, whereas debris deposition significantly increased diversity on three late successional tree species. A number of significant treatment interactions were observed. Overall, the debris pulse had a greater effect on canopy arthropods than did canopy opening, suggesting that changes in plant condition resulting from nutrient availability associated with debris deposition have a greater effect on canopy arthropods than do the more direct and immediate changes in abiotic conditions resulting from canopy opening.

1. Introduction

Cyclonic storms are a major factor affecting the structure and dynamics of forests in many parts of the world (Mabry et al., 1998; Whigham et al., 1999; Stork, 2007; Lee et al., 2008; Turton, 2008; Li and Duan, 2010). While such disturbances have obvious and widely-studied effects on vegetation (Brokaw and Grear, 1991; Walker, 1991; Scatena et al., 1996; Whigham et al., 1999; Stork, 2007), relatively few studies have addressed responses of forest fauna to direct and indirect effects of these disturbances.

Disturbances that open forest canopies directly alter gradients of light, temperature and moisture that affect abundance and distribution of arboreal arthropods (Gram et al., 2001; Schowalter, 1995, 2011, 2012; Marquis et al., 2002; Schowalter and Ganio, 2003; Madigosky, 2004; Grimbacher and Stork, 2007, 2009). In addition, foliage and branches stripped from trees add a pulse of detrital material to the forest floor (Lin et al., 2003; Richardson et al., 2010). This pulse has obvious effects on habitat conditions and resource availability for litter fauna (Richardson et al., 2010), but decomposing litter also promotes primary production (Wood et al., 2009), thereby indirectly affecting habitat conditions and resource availability for canopy fauna. Canopy arthropod responses to disturbances have the capacity to alter patterns of biogeochemical cycling and ecosystem recovery, including adding pulses of detrital inputs to the forest floor during outbreaks (Schowalter et al., 2011; Schowalter, 2012).

A few manipulative studies in temperate forests have provided the opportunity to compare arboreal arthropod abundances before and after tree harvest in replicated experimental plots (e.g., Shure and Phillips, 1991; Gram et al., 2001; Marquis et al., 2002; Schowalter et al., 2005). However, tree harvest removes, rather than adds, much debris and thereby fails to imitate conditions created by natural disturbances, such as hurricanes that cause a pulse of treefall and other detrital input to the forest floor. Given the difficulty of anticipating where and when natural disturbances will occur, most research on effects of canopy disturbances on invertebrates has been restricted to comparisons of abundances among plots varying in post-disturbance severity (e.g., Schowalter and Ganio, 2003; Hirao et al., 2008; Grimbacher and Stork, 2009). Such research is potentially confounded by pre-disturbance spatial variation and post-disturbance spatial and environmental variation

* Corresponding author. Tel.: +1 225 578 1628; fax: +1 225 578 2257.
E-mail address: tschowalter@agcenter.lsu.edu (T.D. Schowalter).

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(e.g., topography, wind damage). Furthermore, no previous studies have separated the effects of canopy opening and debris deposition on forest canopy fauna.

In 2004, a canopy trimming experiment (CTE) was initiated in a hurricane-structured tropical rainforest ecosystem at the Luquillo Experimental Forest Long-Term Ecological Research (LTER) site in Puerto Rico. This experiment was designed to separate effects of canopy opening and debris deposition in replicated plots of sufficient size to simulate the effects of recent major hurricanes, e.g., Hugo in 1989 and Georges in 1998 (Brokaw and Grear, 1991; Walker, 1991; Schowalter and Ganio, 2003). Previous papers have reported treatment effects on plants and litter invertebrate communities (Richardson et al., 2010; Shiels et al., 2010).

This paper describes responses of canopy arthropods to experimental canopy opening and debris deposition treatments. Based on previous canopy arthropod responses to hurricane disturbance in this ecosystem (Schowalter and Ganio, 2003), we expected that either canopy opening or debris deposition would result in increased abundances of certain scale insects and other hemipterans.

2. Materials and methods

2.1. Site description

El Verde Field Station, Luquillo Experimental Forest LTER Site, is located 10 km south of Rio Grande, Puerto Rico (18°10′N, 65°30′W) at 500 m above sea level (McDowell et al., 2012). This site is administered by the USDA Forest Service Caribbean National Forest and Southern Forest Research Station and by the University of Puerto Rico. Mean monthly temperatures range from 21 °C in January to 25 °C in September (Brown et al., 1983). Annual precipitation averages 370 cm and varies seasonally, with 20–25 cm per month in January–April (dry season) and 35–40 cm per month in the remainder of the year (wet season) (McDowell and Estrada-Pinto, 1988; Heartsill-Scalley et al., 2007).

The forest is subject to frequent disturbances that alter the composition of forest communities (Scatena et al., 2012). During the past 25 years, this site experienced two major hurricanes (Hugo 1989 and Georges 1998) that broke or toppled trees on windward slopes over large areas, several moderate hurricanes (Luis and Marilyn 1995, Bertha and Hortense in 1996, Erika in 1997, Jose in 1999 and Debby in 2000) that caused substantial defoliation and flooding, a number of minor hurricanes and tropical storms (Heartsill-Scalley et al., 2007), and hundreds of landslides resulting from rainstorms. A significant drought occurred during 1994–95, when precipitation was only 41% of the long-term annual average, and minor droughts occurred in 1991, 1996, 2001 and 2003 (Heartsill-Scalley et al., 2007). Previous studies have shown similar responses by canopy invertebrates to hurricanes and droughts (Schowalter and Ganio, 2003), suggesting that abiotic changes resulting from experimental canopy opening should have significant effects.

Vegetation surrounding the field station is dominated by tabonuco, *Dacryodes excelsa* (Burseraceae), which comprises 35% of the forest canopy below 600 m elevation (Brown et al., 1983). Other canopy dominants include *Manilkara bidentata* (Sapotaceae) and *Sloanea berteroana* (Elaeocarpaceae). *Prestoea acuminata* (Palmaceae), *Miconia prasina* (Melastomataceae) and *Psychotria brachiata* (Rubiaceae) are major subcanopy species. Canopy height averages 20 m, and small light gaps occur infrequently in the otherwise closed canopy of mature forests. *Cecropia schreberiana* (Cecropiaceae) is an important early successional tree species. *Heliconia caribaea* (Heliconiaceae), *Piper* spp. (Piperaceae) and other understory shrubs, vines and herbs form a dense understory in gaps.

At this site, Hurricane Hugo (1989) left severely disturbed patches (30–60 m diameter), with nearly complete tree-fall (gaps), interspersed with less disturbed patches where most or all trees remained standing but lost their foliage and smaller branches (non-gaps). Rapid sprouting, refoliation and seedling recruitment began during the wet season of early 1990 (Frangi and Lugo, 1991). Thickets of *C. schreberiana* saplings and other early successional plants, especially *H. caribaea*, developed in gaps, and some later successional species resprouted from stumps and fallen trees. *Cecropia schreberiana* largely disappeared from non-gaps by 1995, following canopy closure, but reappeared in gaps following canopy opening by Hurricane Georges in 1998. Hurricanes Bertha, Hortense, and Marilyn during 1996 and Debby in 2000 caused substantial defoliation but no significant canopy opening.

2.2. Experimental design

The CTE created replicate disturbed or undisturbed plots similar in severity and scale to disturbed patches resulting from Hurricanes Hugo and Georges at this site (see Schowalter and Ganio, 2003). Four 30 × 30 m plots with a 5 × 5 m grid designated by PVC pipe were established in each of three experimental blocks (Shiels et al., 2010). Each plot within a block was assigned randomly to one of four treatments: (1) canopy trimmed with debris removed, weighed, then redistributed throughout the plot to simulate conditions created by natural hurricanes (Trim + debris), (2) canopy trimmed, with trimmed material removed from the plot to simulate canopy opening without debris deposition (Trim + no debris), (3) canopy undisturbed, with trimmed material from treatment 2 weighed, then distributed throughout the plot to simulate debris deposition without canopy opening (No trim + debris), and (4) canopy undisturbed and no debris alterations occurred at the forest floor (No trim + no debris). Treatments were installed during October 2004–June 2005.

In trimmed plots, all non-palm trees ⩾15 cm diameter at 1.3 m height had branches <10 cm diameter removed (Shiels et al., 2010). For non-palm trees between 10 and 15 cm diameter, each tree was cut at 3 m height. For palms ⩾3 m tall (at the highest part of the leaf above ground), all leaves (fronds) were trimmed at the connection with the main stem, and the apical meristem was preserved. Therefore, except for some palms that had fronds attached to their stem below 3 m height, no vegetation of any type was trimmed below 3 m height. The trimming treatment reduced canopy cover and increased light levels at the forest floor by amounts similar to those caused by Hurricane Hugo (Shiels et al., 2010).

The debris from canopy trimming was sorted into three categories: wood (branches ⩾1.5 cm diameter), leaves and twigs (branches <1.5 cm diameter and all non-palm foliar material), and palm fronds (Shiels et al., 2010). Debris was immediately weighed to establish wet mass, then subsampled, weighed, dried at 45 °C to constant mass, and reweighed to establish wet–dry mass ratios. All debris was then piled by category outside of debris deposition plots until trimming and weighing in both plots within a block were completed. Therefore, debris experienced about one month of decomposition outside of plots before being placed in the treatment plots. Trimmed material totaled about 6500 kg dry weight per plot, similar to amounts deposited by Hurricane Hugo (Shiels et al., 2010).

2.3. Sampling methods

Canopy invertebrate abundances were measured as described by Schowalter and Ganio (1999, 2003). Briefly, seven tree species were selected for study to represent the dominant early (*C. schreberiana*, *P. acuminata*, *P. brachiata* and *M. prasina*) and late (*D. excelsa*, *M. bidentata* and *S. berteroana*) successional and overstory (*D. excelsa*, *M. bidentata*, *S. berteroana* and *C. schreberiana*) and understory (*P. acuminata*, *P. brachiata* and *M. prasina*) species