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ARTICLE

Special Feature: Tropical Forest Responses to Repeated Large-scale Experimental Hurricane Effects

Aboveground carbon responses to experimental and natural hurricane impacts in a subtropical wet forest in Puerto Rico

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Abstract

Climate change and disturbance make it difficult to project long-term patterns of carbon sequestration in tropical forests, but large ecosystem experiments in these forests can inform predictions. The Canopy Trimming Experiment (CTE) manipulates two key components of hurricane disturbance, canopy openness and detritus deposition, in a tropical forest in Puerto Rico. We documented how the CTE and a real hurricane affected tree recruitment, biomass, and aboveground carbon storage over 15 years. In the CTE treatments, we trimmed branches, but we did not fell trees. We expected that during the 14-year period after initial canopy trimming, regrowth of branches and stems and stem recruitment stimulated by increased light and trimmed debris would help restore biomass and carbon loss due to trimming. Compared to control plots, in the trimmed plots recruitment of palms and dicot trees increased markedly after trimming, and stem diameters of standing trees increased. Data showed that recruitment of small trees adds little to aboveground carbon, compared to the amount in large trees. Nevertheless, this response restored pretreatment biomass and carbon in the experimental period. In particular, the experimental additions of trimmed debris on the forest floor seemed to stimulate increase in aboveground carbon. Toward the end of the experimental period, Hurricane Maria (Category 4 hurricane) trimmed and felled some trees but reduced aboveground carbon less in the plots (including untrimmed plots) than experimental trimming had. Thus, it appears that the amount of regrowth recorded after experimental trimming could also restore aboveground carbon in the forest after a severe hurricane in the same time span. However, Hurricane Maria, unlike the trimming treatments, felled large trees, and it may be that with predicted, more frequent severe hurricanes, that the continued loss of large trees would over the long term decrease aboveground carbon stored in this Puerto Rican forest and likewise in other tropical forests affected by cyclonic storms.

KEYWORDS
aboveground carbon, biomass, hurricanes, Puerto Rico, subtropical wet forest

INTRODUCTION

Tropical forests have a strong influence on the global carbon cycle. Tropical forests contain about 553 Pg of carbon, which accounts for 40% of the total carbon in the terrestrial biosphere, with 58% in tropical forest vegetation, 41% in its soil, and 1% in its litter (Soepadmo, 1993). Moreover, nearly 20% of the CO_2 currently produced globally by industrial emissions and land conversion is absorbed by tropical forests (Lewis et al., 2009; Viswanath & Sandeep, 2019). However, it is uncertain whether tropical forests will continue to be carbon sinks or shift to being net carbon sources (Cavaleri et al., 2015), making understanding of their carbon flux and aboveground storage imperative.

Major climatic events affect tropical forest carbon sequestration (Feeley et al., 2011; Newbery & Lingenfelter, 2004). For instance, large cyclonic storms (hurricanes, typhoons, and cyclones) can quickly modify the structure and dynamics of an ecosystem (Lin et al., 2011; Navarro-Martínez et al., 2012). Hurricane disturbances increase rates of mortality, recruitment, and growth of trees and, consequently, can alter the composition, structure, biomass, and carbon storage of forests (Harmon et al., 1991; Navarro-Martínez et al., 2012; Zimmerman et al., 2014).

Hurricanes have two main impacts on forests. They create forest gaps in which light reaches the forest floor, and they drop debris that decomposes on the forest floor. Thus, hurricanes provide light and nutrients that can promote posthurricane plant recruitment and growth (Cházdon & Fetcher, 1984). This growth restores biomass and stores aboveground carbon (Seedre, 2014). Estimation of aboveground carbon is a fundamental to studies of carbon storage, since it is a major compartment in the global carbon balance (Seedre, 2014).

In the Luquillo Experimental Forest (LEF) of Puerto Rico, we are conducting a large-scale field experiment, the Canopy Trimming Experiment (CTE), in which canopy is trimmed and resulting debris is manipulated in order to simulate and compare the two main direct effects of hurricanes—increased light in gaps and debris deposition on the forest floor—on posthurricane forest regrowth (Shiels & González, 2014). Because the CTE includes measurements of tree density and size over 15 years, both before and after the experimental treatments, we can use the experiment to understand the potential effects of hurricane disturbance on biomass and aboveground carbon (Shiels et al., 2015). Moreover, Hurricane Maria in 2017 also affected the CTE experimental plots.

Therefore, we used the CTE to address the following questions. First, did recruitment and growth, after trimming in the CTE, compensate for aboveground carbon losses due to trimming in the 15 years of the study, and second: (1) which effect—canopy removal versus debris deposition—had more impact on carbon storage, and (2) how does a real hurricane affect aboveground carbon? Our hypothesis was that regrowth would compensate for carbon loss due to experimental trimming in the period of the study. If this is not true, it implies that a predicted increase in frequency of intense hurricanes (Knutson et al., 2010) could eventually reduce aboveground carbon over the long term in forests affected by hurricanes and other cyclonic storms.

METHODS

Study site

The study site was in the LEF of northeastern Puerto Rico (coterminous with El Yunque National Forest), near El Verde Field Station (EVFS; 18°20′ N, 65°49′ W), a research site of the Luquillo Long-Term Ecological Research Program. The elevation is 340–485 m above sea level, and the terrain is steep and rocky (24% average slope, 25% area covered by boulders; Soil Survey Staff, 1995). Soils at EVFS are Oxisols and Ultisols (Soil Survey Staff, 1995). The study site showed >80% forest cover in a 1936 aerial photograph (Shiels et al., 2010). Annual rainfall at the site averages 3500 mm (Shiels et al., 2010). The study site is in "tabonuco forest," which is a subtropical wet forest in the Holdridge System (Ewel & Whitmore, 1973). The most common large trees at the site are *Dacryodes excelsa* (Burseraceae; commonly named "tabonuco"), the palm *Prestoea acuminata* var. *montana* (Arecaceae), *Sloanea berteroana* (Elaeocarpaceae), and *Manilkara bidentata* (Sapotaceae) (Shiels et al., 2015).

As of 1989, the LEF had experienced major hurricanes on average every 50–60 years, including Hurricane Hugo in 1989 (based on records 1769–1989, Scatena & Larsen, 1991). But by 2017, it had experienced three severe hurricanes in 28 years (Hugo in 1989, category 5; Georges in 1998, category 3; and Maria in 2017, category 4).

Experimental design and treatments

The CTE is a 2×2 factorial randomized block design established in tabonuco forest sites of similar age and land-use history. Three blocks (A, B, and C) were established (within approximately 50 ha). Each of the three blocks had four 30×30 m treatment plots (each 0.09 ha; 12 plots in total). Plot size was chosen to reflect the apparent patch size of impacts to forest canopies observed in the LEF following Hurricane Hugo (Brokaw & Grear, 1991; Zimmerman et al., 2010, 2014). The 30×30 m plots within blocks were located at least 20-m distance from the edge of adjacent plots.

Each 30×30 m plot had a 20×20 m interior plot measurement area, leaving a 5-m margin around each plot to minimize edge effects. A 1.5-year monitoring period began in 2003, before applying treatments. Each of the four plots within a block was randomly assigned one of four types of treatment: (1) Trim, debris not removed; (2) Trim, debris removed; (3) No trim, debris added; and (4) Control (no trim, no manipulation of debris). Thus, each block had one of each treatment. Arborists applied these treatments during November 2004 to June 2005 for TRIM 1.

We defined the area trimmed as the vertical projection of the boundaries of the 30×30 m plot. All nonpalm trees ≥15 cm diameter at 1.3 m height (dbh) inside the 30×30 m area had their branches <10 cm diameter trimmed (cutoff). For nonpalm trees between 10 and 15 cm dbh, each tree was trimmed starting at 3 m height and continuing up the stem. For all palm trees ≥3 m height, fronds were trimmed at the connection with the main stem; however, the apical meristem was preserved. Vegetation below 3 m height was not trimmed, except that we trimmed palm fronds below 3 m. In trimmed plots, canopy openness increased to about 16% of pretrim openness (Shiels et al., 2010; Shiels & González, 2014; Zimmerman et al., 2014).

The debris resulting from the trimming was sorted into three types: wood (branches ≥ 1.5 cm diameter), leaves and twigs (branches < 1.5 cm diameter and all nonpalm foliar material), and palm fronds. To establish wet mass, the debris was weighed immediately after trimming; then, samples of debris were weighed and dried at 45°C until constant mass was achieved, to establish wet/dry mass ratios. Then, within each block, all detritus of each of the three types was spread evenly on Trim, debris not removed, and No trim, debris added plots (debris from Trim, debris not removed, plots was deposited back on the plot where it originated). On average, $11,157 \pm 362$ kg (mean ± SE) of wet mass detritus (6530 ± 186 kg dry mass) was cut on each of the six *Trim* plots.

We made TRIM 2 in 2014, with just one manipulative treatment: Trim, debris not removed. Thus, in 2014, we did not remove debris from any plots nor add debris to any plots. The same trimming protocol was used for Trim, debris not removed, plots in 2014 as in 2004. On average, 9379 ± 179 kg (mean ± SE) of wet mass detritus (3995 ± 170 kg dry mass) was trimmed.

Plant measurements

Pretreatment measurements were taken in March 2003 and October 2004. In all manipulative and Control treatments in all blocks, we measured the dbh ($H = 130$ cm) of all woody plants ≥1 cm dbh, including trees, shrubs, and lianas (hereafter termed "stems"). After TRIM 1, measurements were made in September 2007, October 2008, November 2009, February 2011, February 2012, and February 2014. Following TRIM 2, in October 2014, measurements were taken in October 2014, October 2015, and October 2016. Measurements were also taken in December 2017, after the passage of Hurricane Maria, and in November 2018.

We followed the Center for Tropical Forest Science protocol (Condit, 1998) for measuring stems. To minimize sampling error between subsequent measurements, we marked points of measurement with lumber crayons. Vernier calipers were used to measure stems with dbh <5 cm. Diameter tapes were used to measure stems with diameters ≥5 cm dbh.

Aboveground carbon calculations

Our study focused on live aboveground carbon. We did not consider belowground carbon nor litter in our analysis. To measure the effect of canopy trimming on the aboveground carbon dynamics, we estimated aboveground biomass and converted biomass to carbon. We used biomass equations previously used in the forests of the LEF. We separately estimated biomass of palms and nonpalm trees. For palms, we used: $Y = ax + b$, where Y is aboveground biomass, x is height in meter, and a and b are estimated parameters of the fitted models (Frangi & Lugo, 1985). For nonpalm trees, we used two equations: (1) for trees <5 cm dbh, $Y = 0.3210D^{1.3925}$, and (2) for trees >5 cm dbh, $Y = 4.7306–2.8566D + 0.5832D^2$, where Y is estimated biomass and D is the dbh in centimeter (Weaver & Gillespie, 2017). We then multiplied the aboveground biomass by 0.47 to obtain aboveground carbon (Macías et al., 2017). Our statistical analyses were made in R, SigmaPlot, and Excel. We made a general linear model to determine which hurricane effect—canopy removal versus debris deposition—had more impact on carbon storage.

Preliminary analysis suggested that using dbh to estimate biomass (and carbon) loss and gain in the *Trim* treatments was adequate for general trends and comparisons but not for a detailed comparison of biomass loss and gains due to experimental canopy trimming. This is because trees were not felled (thus not greatly changing biomass) in the experiment, and because using dbh does not accurately compare the biomass of branches and leaves that were trimmed with the biomass of branches and leaves that regrew on the trimmed trees. Therefore, we used the following method to estimate biomass loss and gain of leaves and branches in Trim, debris not removed (the only treatment for which this calculation was possible). As described in our methods, we weighed trimmed material to estimate biomass loss due to TRIM 1 and likewise to estimate biomass loss due to TRIM 2. Most important, we used the same guidelines (branches <10 cm diameter trimmed, etc.) to perform both trims. So, whatever biomass of leaves and branches we trimmed at TRIM 2 was what had regrown since TRIM 1. With this method, we can state accurately that the weight trimmed at TRIM 1 is biomass loss in leaves and branches, and the weight trimmed at TRIM 2 is biomass gained in leaves and branches in the TRIM 1 to TRIM 2 period in Trim, debris not removed. We will use both this accurate amount and the general trends shown using dbh to evaluate the loss and potential recovery of biomass and carbon in the experiment.

RESULTS

Our dataset contained a cumulative total of 24,678 individual stems of 83 species in all blocks for the whole study period. Among these 24,678 stems, 7545 were in Trim, debris not removed; 8490 were in Trim, debris removed; 3688 were in No trim, debris added; and 4955 were in Control.

Stem recruitment and dynamics

The total number of stems ≥1.0 cm dbh in all plots was decreasing before any treatments (Figure 1), perhaps due to natural thinning after previous hurricanes. But after TRIM 1 in 2004, stem number increased, respectively, by 65% and 151% of pretrim values in Trim, debris removed and Trim, debris not removed, where there were significantly more stems than in No trim, debris added, and Control (*$p < 0.05$). However, the increase was transitory; by 2009, the number of stems in both *Trim* plots had fallen (Figure 1), to reach 26% in Trim, debris removed, and 15% Trim, debris not removed, of the peak values of 2014. It increased again by 114% of lowest value in Trim, debris not removed, after TRIM 2 (not applied to Trim, debris removed) in 2016.

It was mainly the number of small stems that increased in the *Trim* treatments (Figure 2). These stems peaked in 2007–2008, then declined until increasing again after TRIM 2 in Trim, debris not removed. There were only slight changes in stems <10 cm dbh in No trim, debris added, and Control, until after Hurricane Maria, when small stems increased in all three manipulative treatments and in Control (Figure 2).

Aboveground carbon dynamics

Aboveground carbon, as determined from stem dbh, was increasing in all manipulative treatments and Control before any treatments (Figure 3), perhaps due to recovery after previous hurricanes. Between trims it increased in Trim, debris not removed; No trim, debris added; and Control; it decreased in Trim, debris removed 3 years after TRIM 1. It increased fastest in No trim, debris added. After Hurricane Maria, aboveground carbon declined in all treatments and Control (Figure 3). From 2016 to 2018 (from just before to after Hurricane Maria), aboveground carbon decreased in Trim, debris not removed, by 4689 kg/ha, in Trim, debris removed by 4949 kg/ha, in No trim, debris added by 7800 kg/ha, and in Control by 10,068 kg/ha.

Aboveground carbon increased significantly in No trim, debris added ($p < 0.001$) during the experimental period, 2004–2017 (general linear model, Figure 3). Aboveground carbon also significantly increased in Trim, debris not removed ($p < 0.01$), in this period. By contrast, in Trim, debris removed, there was a significant increase of aboveground carbon only in 2007 ($p < 0.01$). In the control plot, aboveground carbon significantly increased from 2015 to 2017 just before Hurricane Maria ($p < 0.03$).

The many small dbh stems recruited during the experiment in all treatments and Control contributed little to aboveground carbon, whereas the many fewer large dbh stems contributed greatly and disproportionately more (Figure 4). For instance, 17,215 trees with diameters ranging from 1 to 10 cm accounted for more than 73% of all stems but contributed only 3.27% of aboveground biomass, while 221 trees with diameters greater or equal to 50 cm accounted for 0.94% of stems contributed to 35% of aboveground biomass.

Based on trimmed material removed, the average aboveground carbon loss at TRIM 1 in Trim, debris not removed was 11,157 kg, and the average loss at TRIM

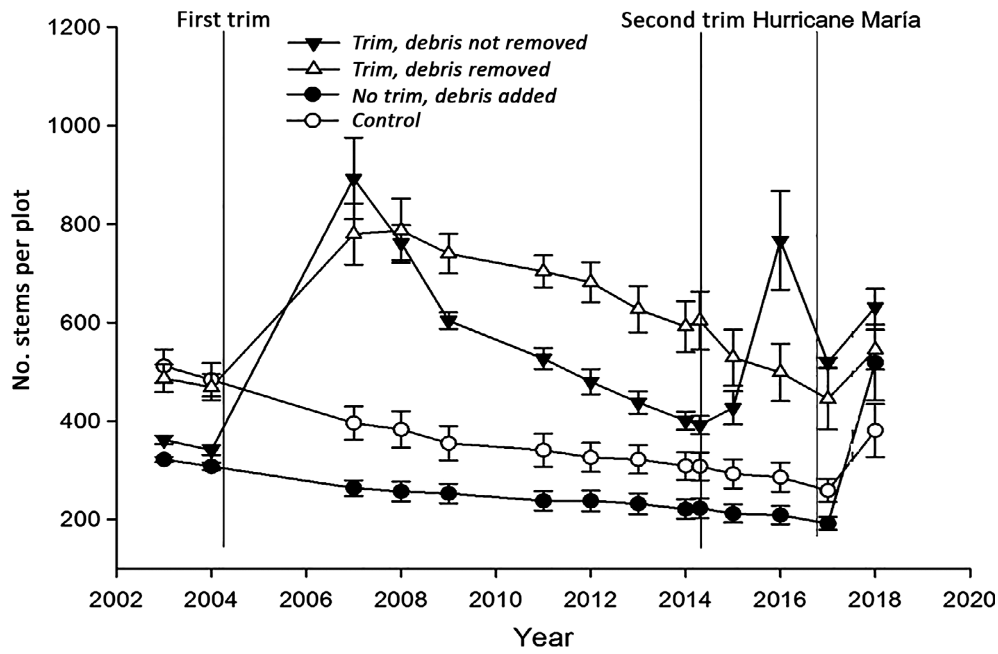

FIGURE 1 Stem (≥1 cm dbh) recruitment dynamics over time. The three vertical bars indicate the dates of TRIM 1, TRIM 2, and Hurricane Maria. The error bars are SDs. The two error bars in 2014 indicate the two censuses for that year (February and October, respectively). The number of stems is the mean and SD among three replicates of each treatment. TRIM 2 was performed only for Trim, debris not removed

2 was 9379 kg, using the same trim protocol in both trims. Therefore, Trim, debris not removed, had regained 9379 kg due to regrowth of branches <10 cm diameter and leaves between 2004 and 2014. Thus, in Trim, debris not removed, regrowth of branches and leaves in the 10-year interval between TRIM 1 and TRIM 2 had restored 84.1% of aboveground carbon lost due to trimming at TRIM 1. Hurricane Maria removed (based on dbh) 4684, 4949, 7800, and 10,068 kg/ha of aboveground carbon from Trim, debris not removed; Trim, debris removed; No trim, debris added; and Control, respectively. The amounts removed by Hurricane Maria for all three treatment plots were less than that removed at TRIM 1 in the two trim treatments.

DISCUSSION

This paper describes stem number and aboveground carbon dynamics through 15 years of pre- and post-treatments designed to simulate hurricane impacts, and it describes the effects of a true hurricane. Our results showed an increase of more than 60% in stem density (compared to pretrim density) 3 years after TRIM 1 in the two *Trim* treatments. However, this increase was transitory; after 3 years, stem density dropped, as found by Shiels et al. (2010) and Zimmerman et al. (2014). In both *Trim* treatments, recruitment of saplings after TRIM 1 (2004) seemed to end in 2007, and recruitment after the TRIM 2 (2014) seemed to end in 2017. It appears that canopy opening offered opportunity for seedlings and saplings to establish. Then, as the forest canopy closed, the light available declined rapidly at the forest floor (Shiels et al., 2010; Shiels & González, 2014), and recruitment diminished. In 2017, Hurricane Maria disturbed the canopy in all plots and induced stem recruitment.

Plant recruitment following TRIM 1, TRIM 2, and after Hurricane Maria had little effect on the dynamics of aboveground carbon, because recruited stems were small and mostly short-lived. Similarly, in the study by Mascaro et al. (2005) where aboveground biomass was measured after a hurricane in Nicaragua, trees ranging from 3.2 to 10 cm in dbh made up more than 89% of all stems but accounted for only 2.5% of aboveground biomass, while seven trees >70 cm dbh made up 1.4% of stems but accounted for 45% of aboveground biomass. Other studies in Nepal (Gautam & Mandal, 2016), in Ethiopia (Yohannes & Soromessa, 2015), and in Tanzania (Mwakisunga & Majule, 2012) all report that large diameter trees account for the bulk of aboveground carbon in forests (Lutz et al., 2018).

In No trim, debris added, aboveground carbon increased by 4% in 2007 and 9% in 2014, while in Trim, debris removed, there was a 2% increase by 2007, then a decrease of 5% in 2014, before the second trim, based on dbh measurements. Thus, adding debris seems to have

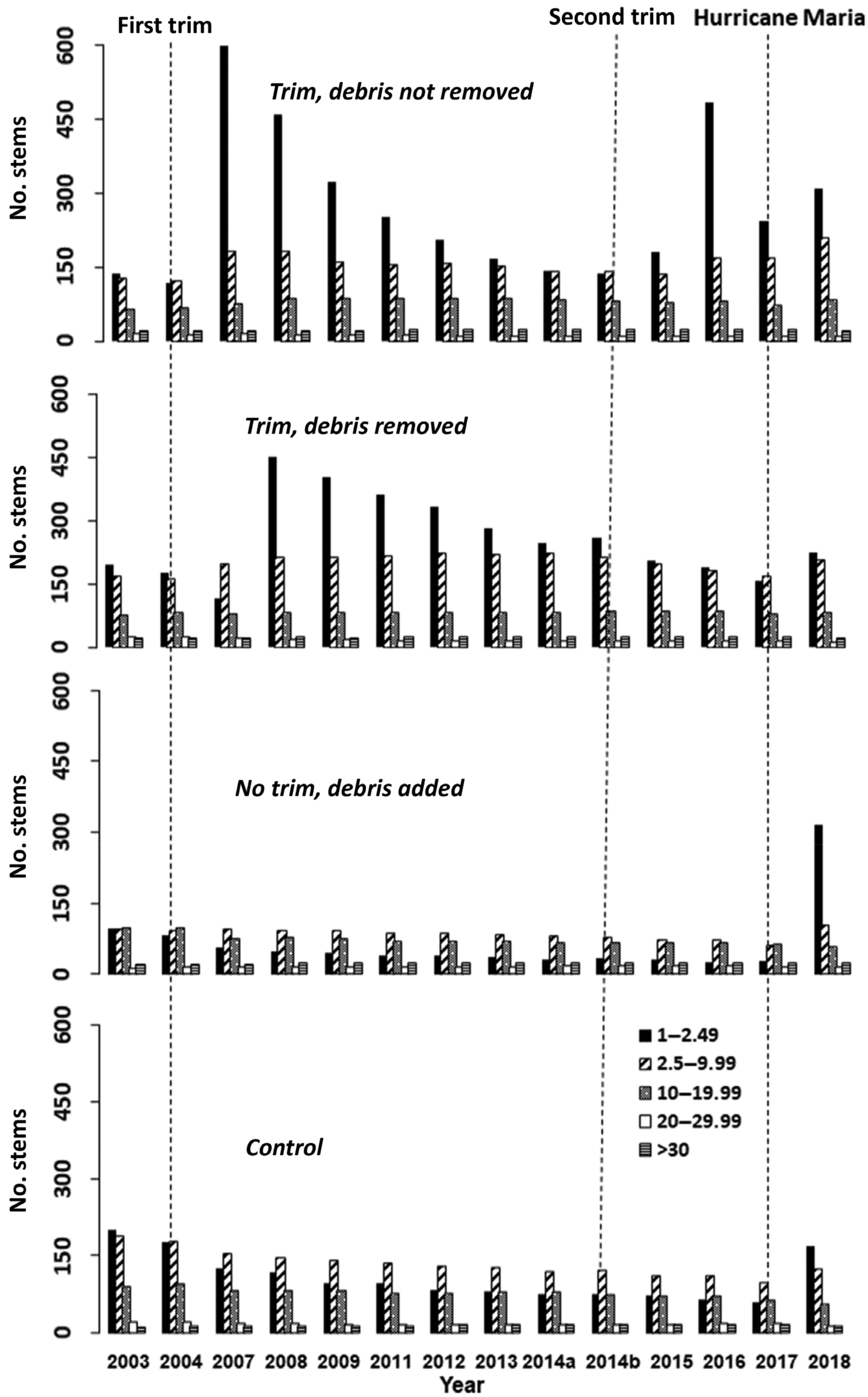

FIGURE 2 Diameter-class distributions of stems ≥1 cm dbh at each census date (2014a and 2014b) indicate the two censuses in 2014. TRIM 2 was performed only for Trim, debris not removed

increased aboveground biomass after 3 years or more after such hurricane debris deposition. In earlier analyses, debris added to No trim, debris added, appeared to increase basal area increment (Shiels et al., 2010). This increase was attributed to a fertilization effect, the benefits of increased soil moisture, or other unmeasured effects of decomposing debris on tree growth (Zimmerman et al., 2014). Consequently, CTE results suggest that adding debris as a hurricane effect had a greater effect on aboveground carbon than did canopy trimming and consequent increased light. Debris deposition also influences belowground carbon. In a previous study in the CTE,

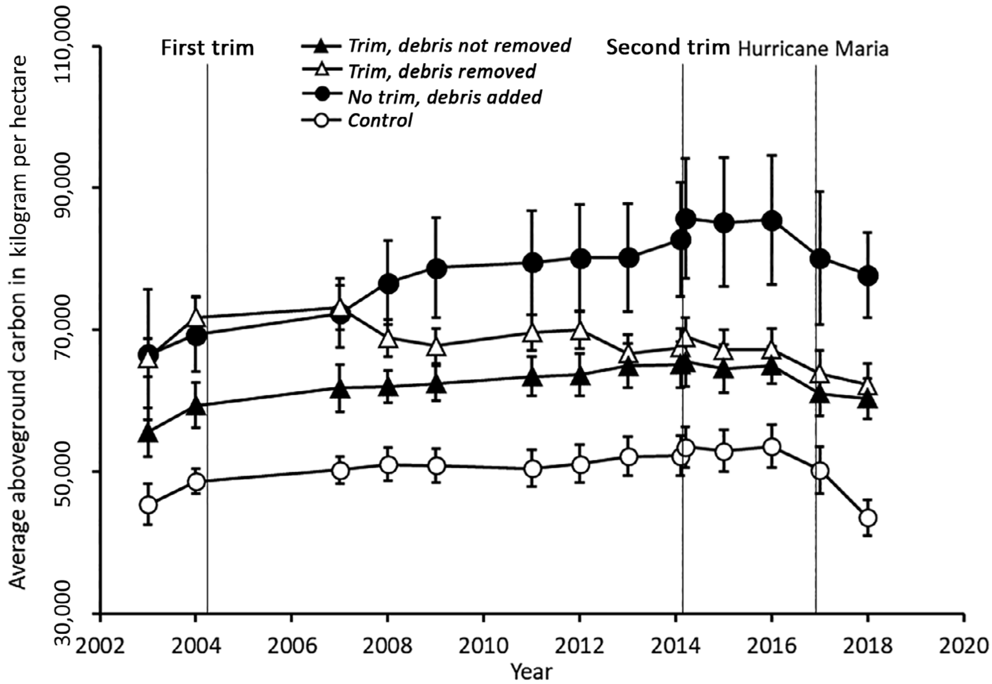

FIGURE 3 Aboveground carbon changes over time. The three vertical bars indicate the dates of TRIM 1, TRIM 2, and Hurricane Maria. The two error bars in 2014 indicate the two censuses for that year (February and October, respectively). The aboveground carbon is the mean and SD among three replicates of each treatment. TRIM 2 was performed only for Trim, debris not removed

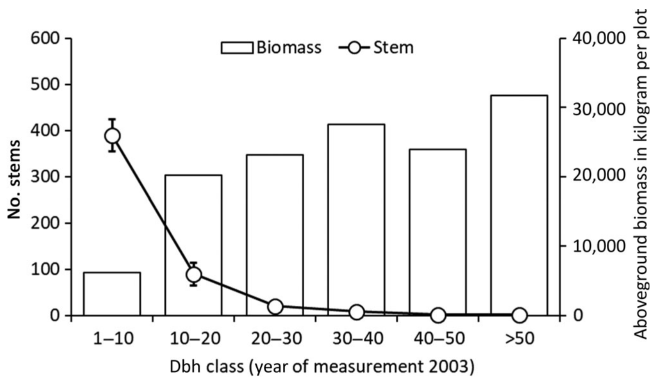

FIGURE 4 Relationship between stem size and aboveground biomass in *Control* (no manipulation) in 2003. The error bars are SDs

Gutiérrez del Arroyo and Silver (2018) found that belowground carbon significantly increased in No trim, debris added. They also argued that canopy opening as a treatment alone did not significantly affect carbon.

Over the first 14 years of the experiment (2003–2017), before Hurricane Maria, net aboveground carbon (based on dbh measurements) increased in all treatments including the control, except in Trim, debris removed. And, based only on branches and leaves trimmed and regrown, it had increased to 84.1% of pretrim aboveground carbon in Trim, debris not removed, between TRIM 1 and TRIM 2. Together, with less accurately measured but evident increases due to diameter increment, it appears that the trim treatments recovered enough biomass and aboveground carbon to compensate for losses due to trimming. Thus, results from the CTE tend to confirm our hypothesis that during the period after experimental canopy trimming (but no tree felling), regrowth of branches and leaves and stem growth would restore biomass and aboveground carbon loss. Moreover, Hurricane Maria both trimmed and felled trees, and reduced aboveground carbon less than experimental trimming had. Thus, it appears that the amount of regrowth recorded after experimental trimming would also restore aboveground carbon in the forest after a severe hurricane, in the same time span as that of the experiment. Our results also suggest that increased debris and its presumed fertilization effect could add resilience.

However, Hurricane Maria, unlike the trimming treatments, felled trees. Hurricanes affect large trees more than small trees (Brokaw & Everham, 1996), and Caribbean hurricanes are projected to be more intense due to atmospheric warming (Knutson et al., 2010). Over the long term and through a regime of more strong hurricanes, a continued loss of large trees that take years to replace could eventually result in less aboveground carbon stored in this Puerto Rican forest and likewise in other tropical forests affected by cyclonic storms.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Jess K. Zimmerman, Aaron B. Shiels, and Nicholas Brokaw developed the CTE plan. Aaron B. Shiels directed the fieldwork. Samuel C. Matta and John Bithorn worked on the trims and collected routine field data over the 15 years of the project. Hervé Chevalier performed the data analysis. Chevalier, Brokaw, Sheila E. Ward, Aaron B. Shiels, and Zimmerman wrote the manuscript.

DATA AVAILABILITY STATEMENT

The Canopy Trimming Experiment tree dataset (from which sapling abundances and sizes are derived; Zimmerman, 2020) is available from the EDI Portal: https://doi.org/10.6073/pasta/a78ae17d741ace1db304491f7ec5b73f.

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