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Effects of a Hurricane Disturbance on Aboveground Forest Structure, Arbuscular Mycorrhizae and Belowground Carbon in a Restored Tropical Forest

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Abstract

To better understand how management and restoration practices influence the response of terrestrial ecosystems to large-scale disturbances, it is critical to study above- and belowground effects. In this study, we examined the immediate effect of a major hurricane on aboveground forest structure, arbuscular mycorrhizae (AM) and belowground carbon pools in experimentally thinned plots in a tropical forest. The hurricane occurred five years after a thinning treatment, when thinned plots had similar aboveground carbon stocks but different forest structure compared to control plots. Thinned plots had more large diameter (>10 cm) trees compared to the control plots, which were characterized by a higher density of small diameter (<10 cm) trees. Despite pre-hurricane differences in forest structure, there were no significant differences between treatments in changes of canopy openness or number of affected trees following the hurricane. Thinned plots had larger belowground carbon pools than the controls plots before the hurricane, and these differences remained after the hurricane despite rapid decomposition of organic matter rich in nitrogen. There were no pre-hurricane differences in AM fungal spores or total AM root colonization. The hurricane reduced AM sporulation by nearly 50% in both treatments, yet we observed a significant increase in AM root colonization after the hurricane with greater AM colonization in the thinned plots. Hurricanes have well-known visible aboveground effects, but here we showed that less visible belowground effects are influenced by forest management and may play an important role in forest recovery.

Key words: large-infrequent disturbance; restoration; mycorrhizae; forest architecture; rhizosphere; forest thinning; MODIS.

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Introduction

The role of large infrequent disturbances (LIDs) in shaping landscapes and ecosystems has mainly been studied from an aboveground perspective (Turner and Dale 1998). For example, hurricanes affect visible aboveground components of ecosystems by defoliating vegetation and uprooting of trees (Basnet and others 1992; Scatena and others 1993; Ostertag and others 2005). In contrast, little is known about belowground effects because they are less evident than the visible aboveground response (Lugo 2008). Thus, it is crucial to study above- and belowground effects to better understand ecosystem responses and trajectories following hurricanes and other LIDs.

Belowground processes are critical for regulating global climate change (Lal 2004), but how these processes respond to hurricanes has been largely overlooked. Research on belowground responses to hurricanes has focused on changes in soil nutrients (Scatena and others 1993), litter and fine root biomass (Silver and Vogt 1993; Beard and others 2005). For example, there is evidence that litter biomass can recover to pre-hurricane conditions in less than one year (Ostertag and others 2003). In contrast, other studies have shown that fine root biomass is reduced following hurricanes and recovers slower than litter biomass (Silver and Vogt 1993; Beard and others 2005). Less effort has been focused in soil processes such as soil respiration where large emissions of carbon (3821 g C m^{-2} y^{-1}) have been reported following a hurricane event (Vargas and Allen 2008). Hence, it is important to quantify changes in above- and belowground carbon pools to better understand the fate of the net ecosystem carbon response following hurricanes.

Another important but unclear topic is how hurricanes affect mycorrhizae root colonization. Previous studies have shown that arbuscular mycorrhizal (AM) fungi can help plants take up nutrients (Johnson and Wedin 1997; Hodge 2004) and water (Querejeta and others 2003), which in turn may benefit forest development (Huante and others 1993; Kiers and others 2000; Allen and others 2003). Many neotropical forests are dominated by AM fungi (Allen and others 1995; Treseder and Cross 2006; but see Hogberg 1992), thus it is important to identify possible responses of AM root colonization and spore density in soils following hurricanes. Allen and others (1998) have previously shown that an individual treefall may reduce or have no effect on AM colonization in a tropical forest stand, but results from this study are difficult to up-scale to the large-scale effects associated with hurricanes. Other studies have found that defoliation and herbivory reduces AM colonization as a result of a loss in photosynthetic area and a potential reduction of carbon transfer from the plant to the fungi (Eom and others 2001; Gange and others 2002; Wearn and Gange 2007). However, the response of AM colonization may be influenced by the intensity of defoliation and AM fungal species present (Klironomos and others 2004).

Our main objective was to examine the immediate effect on aboveground forest structure, belowground carbon and AM fungi after a major hurricane in a seasonally dry tropical forest. This vegetation type experiences high rates of land-use change (Murphy and Lugo 1986; Janzen 1988; Bullock and others 1995) and restoration or management efforts are needed. Furthermore, previous studies have identified the importance of including ecosystem management in the context of LIDs such as hurricanes (Dale and others 1998; Stanturf and others 2007). Therefore, it is important to understand how managed or restored ecosystems respond to LIDs especially in areas with high rates of land-use change and susceptibility to hurricane effects.

In this study, we compare above- and belowground responses of control and experimental plots that had been thinned five years before Hurricane Wilma hit the northern Yucatan Peninsula on October of 2005. These plots had similar aboveground carbon but differed in structure (that is, basal area, tree density) prior to the hurricane. The goal of the thinning treatment was to restore a dense young stand to reduce the possibility of ground fires extending to the forest canopy and to promote the growth of the remaining trees. Before the hurricane, thinned plots had lower tree density, larger trees, higher fine root biomass, but similar aboveground carbon compared to the control plots (Vargas and others 2009a). We therefore used a replicated experimental design to test how differences in tree density and basal area influenced the immediate response of above- and belowground variables after a hurricane in a tropical forest.

We tested the following hypotheses: (1) thinned plots with greater density of trees larger than 10 cm in diameter at breast height (DBH) may have a greater number of fallen and dead trees than the control plots; (2) defoliation decreases AM root colonization as trees may reduce carbon investment to AM fungi as a response to foliage loss; (3) AM fungal spores in the soil may be reduced after the hurricane; and (4) initial differences in tree density and basal area per tree (that is, forest architecture) will induce a different response in belowground carbon pools and AM fungi following a major hurricane.

Materials and Methods

Site Description

The study was conducted at El Eden Ecological Reserve (latitude 21°12.6′ N, longitude 87°10.93′ W) in the northeast Yucatan Peninsula, Mexico. This site has a mean annual temperature of 24.2°C and annual precipitation of 1650 mm. The climate is typical of seasonally dry tropical forests, with a pronounced dry season (<100 mm/month) from January to April. Recurrent fires during the dry season have created a landscape of forests of different ages (Vargas and others 2008). The soils in the Reserve are shallow (<20 cm depth) with approximately 30% soil organic matter, pH 7.5, bulk density of 0.35 g/cm^3, and overlaying limestone bedrock (Vargas and others 2008).

In July 2000, twenty 20 × 20 m plots were established in a forest that burned during a stand-replacing fire in the summer of 1989. This forest stand had 53 tree species, with the 10 dominants including individuals of *Bursera simaruba* (L.) Sarg., *Dendropanax arboreus* (L.) Decne. & Planch., *Ficus cotinifolia* Kunth., *Guettarda combsii* Urb, *Jatropha gaumeri* Greenm., *Lonchocarpus castilloi* Standl., *Lonchocarpus rugosus* Benth., *Nectandra salicifolia* Kunth, *Piscidia piscipula* (L.) Sarg., and *Vitex gaumeri* Greenm. A vegetation thinning treatment was applied to ten of these plots in a blocked replicated design by cutting all trees with a DBH less than 2 cm (Vargas and others 2009a). The remaining ten plots were left uncut and used as control plots. Five years after the thinning there were no significant differences in tree height (mean 6 m) and above ground carbon (~38 Mg C/ha) between the control and thinned plots (Vargas and others 2009a). However, the control plots had significantly higher tree density mainly composed of trees with DBH less than 2 cm, whereas the thinned plots had higher density and basal area of trees with DBH greater than 10 cm (Figure 1).

Hurricane Wilma

Hurricane Wilma was the most intense hurricane on record in the Atlantic basin with winds over 295 km h^{-1} and a record low barometric pressure of 882 mbar (www.nhc.noaa.gov). On October 21, 2005, it made landfall over the island of Cozumel, Mexico, as a Category 4 storm on the Saffir-Simpson scale, and emerged over the Gulf of Mexico on October 23 as a Category 2. During the passage of the hurricane, barometric pressure decreased from nearly 1010 mbar to 975 mbar as the eye of the hurricane crossed over the study site (Figure 2A). The immediate effect of the hurricane was an increase in soil water content for nearly 50 days (Figure 2B), and the defoliation of vegetation as recorded by a sharp increase in photosynthetic active radiation (PAR) in the understory of the study plots (Figure 2C). Soil temperature was only affected during the first 50 days following the hurricane and thereafter decreased as expected by seasonally lower temperatures in December (Figure 2D). More details on environmental measurements during the hurricane can be found in previous studies (Allen and others 2007; Vargas and Allen 2008).

Aboveground Hurricane Effects

During September 2005, one month before the hurricane, we selected ten thinned and ten control plots to calculate canopy openness. We took hemispherical photographs below the forest canopy at the center of each plot and calculated percent canopy openness and effective leaf area index using a Gap Light Analyzer V2.0 with the 60° ring (Frazer and others 1999). Hemispherical pictures were taken again during the third week of December 2005 to test for hurricane effects on canopy openness.

During September 2005 we set one litter basket (1 × 1 m) at the center of each plot where the hemispherical pictures were taken to capture litterfall. We could not gain immediate access to the litterfall baskets due to hurricane damage on roads. Hence, litter from the baskets was collected in December of 2005 but is likely an under estimation of total litterfall due to decomposition over two months.

In December of 2005, at each one of the plots where hemispherical pictures were taken, we counted and identified affected trees. We identified trees that had fallen, had tip-up mounds with torn roots (usually those leaning at least 45°), or were snapped at any level. We recorded the following categories for affected trees: (1) *dead trees* as fallen dead, leaning dead, snapped dead and these trees were not producing new leaves; or (2) *living trees* that may be snapped alive, fallen alive, and leaning alive and these trees were producing new leaves as most of the standing trees.

We were not able to measure photosynthesis at the study plots. Therefore, we used MODIS Land Product (MOD17A2) Subsets to estimate changes in gross primary production (GPP) at the landscape scale (Running and others 2004). We used a 3 × 3 km grid using the average of all nine cells centered at the location of the plots to get a landscape estimate of the response of GPP following the

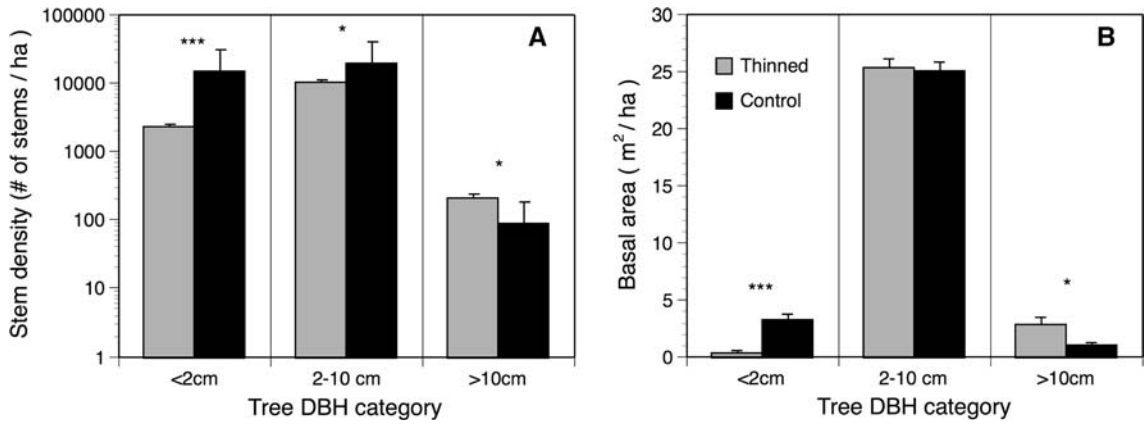

Figure 1. Pre-hurricane forest structure in terms of (**A**) stem density and (**B**) basal area in the thinned and control plots. Differences in forest architecture were a result of a thinning treatment applied in 2000 in which all trees smaller than 2 cm in DHB were cut (after Vargas and others 2009a). DBH means diameter at breast height. * $P < 0.05$, *** $P < 0.001$.

hurricane. These values were derived from the product MOD17A2 generated with Collection 4 from the ORNL DAAC (2006), and previous studies have discussed in detail the validation of this product (Turner and others 2005; Heinsch and others 2006). Details about preparation of subsets including data MODIS reprocessing, methods and formats can be found at ORNL DAAC (http://www.daac.ornl.gov/MODIS/modis.html). Temporal interpolation was used to replace pixels that have quality control flags indicating poor quality. The 8-Day MODIS-GPP values were extrapolated to daily GPP values (gC m^{-2} d^{-1}) using a Savitzky-Golay smoothing filter. We do not mean that these values represent the photosynthesis activity at the study plots, but we present them as evidence of potential effects on photosynthesis activity following the hurricane. We will refer to the values

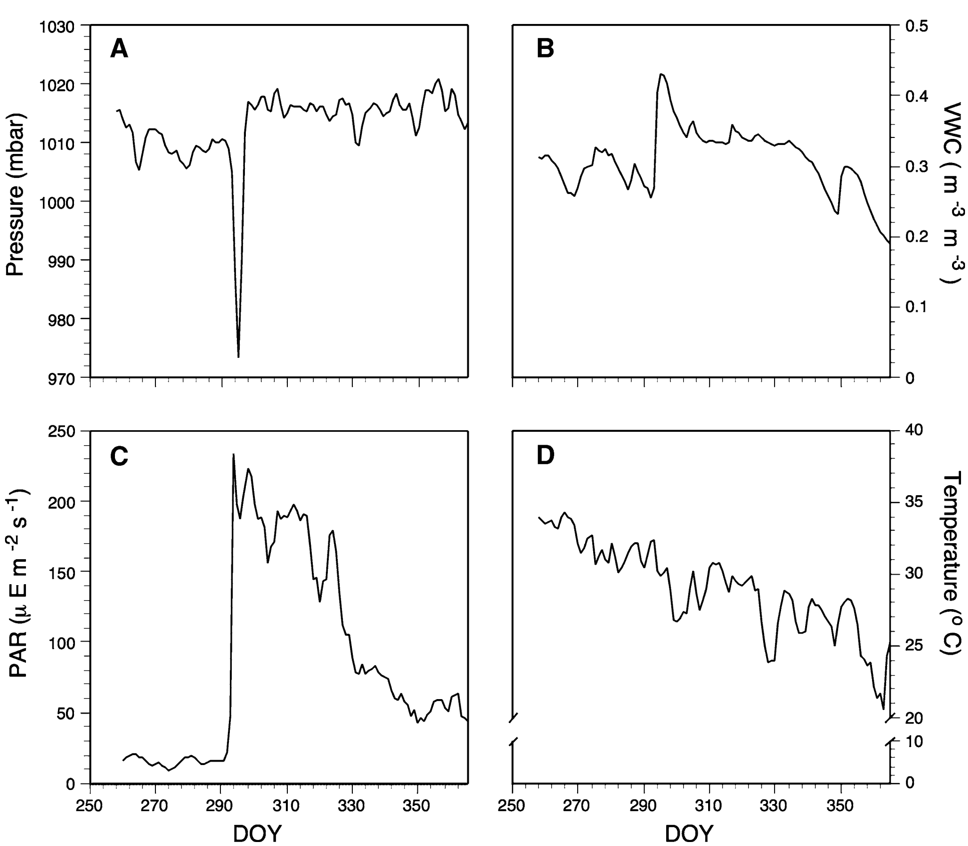

Figure 2. Mean daily values of climatic variables including (**A**) barometric pressure, (**B**) soil volumetric water content (VWC), (**C**) photosynthetically active radiation (PAR) under the canopy, and (**D**) soil temperature in control plots between day of the year (DOY) 250 and 365 of 2005. Hurricane Wilma made landfall over our study site on October 22 as a Category 4 storm on the Saffir-Simpson scale, and emerged over the Gulf of Mexico on October 23 as a Category 2.

generated by the product MOD17A2 as GPP throughout the text.

Belowground Hurricane Effects

During September 2005, we selected six thinned and six control plots, and within each plot we established two 0.5 × 0.5 micro-plots set 5 m apart to study belowground carbon (BGC) pools. These pools were defined as the Oi-horizon (litter layer or slightly decomposed litter with debris <5 cm in diameter), Oe-horizon (decomposed litter layer) and fine roots (<2.0 mm in diameter). The material found in the Oe-horizon was subdivided into Oe > 2 mm (material larger than 2 mm; partially decomposed litter) and Oe < 2 mm (material smaller than 2 mm; highly decomposed litter) as reported in previous studies at the research site (Vargas and others 2008, 2009a). At the center of each 0.5 × 0.5 m plot we collected two samples of the Oa-horizon (including fine roots) by inserting a 4.5 cm diameter metal soil corer until we encountered limestone bedrock (up to 10 cm in depth). All samples (O horizons and fine roots) taken within the same 20 × 20 m plot were pooled. Soil samples were air dried and transported to the University of California, Riverside and stored at −20°C. Fine roots from cores were sorted by hand and rinsed free of organic matter with deionized water. All soil and fine root samples were dried at 65°C for 72 h to determine dry weight and then ground (250 µm sieve) for carbon and nitrogen analysis. Total nitrogen and carbon percentage was determined by dry combustion using a Thermo Finnigan Flash EA1112N/C analyzer (Milan, Italy). A similar protocol was followed during December of 2005 to sample BGC pools following the hurricane event.

Mycorrhizal Colonization and Spore Count

During September and December of 2005, two additional soil cores of the Oa-horizon (including fine roots) were collected at the center of each 0.5 × 0.5 m plot. Importantly, here we sampled all the soil profile to bedrock because of the shallow nature of the soils (<20 cm depth). In all cases, soil cores were sieved through a 2 mm mesh and fine roots were sorted by hand to determine AM colonization. The 2 mm fraction of soil that passed through the sieve was used to study the presence of AM spores in the soil.

The collected fine roots were washed in deionized water to determine mycorrhizal colonization (1 m of fine roots analyzed per treatment). We did not distinguish among roots of different plant species because of the large number of species present in these forests (Schultz 2005). Roots were prepared according to McGonigle and others (1990) for analysis of percentage colonization of AM structures (hyphae, arbuscules and vesicles) using the intersection method (McGonigle and others 1990). At least 100 intersections were scored for each sample.

Spores were extracted by sucrose floatation from 5 g of the sieved soil (Ianson and Allen 1986), and identified based on spore morphology (Perez and Schenck 1987). Only entire, living spores were counted and AM spore density was expressed per gram of dry soil. We divided the spores based on size; (1) small spores less than 100 µm and (2) large spores greater than 100 µm. These categories were selected based on previous analyses at the study site, where we observed that most of the spores less than 100 µm were primarily in the genus *Glomus*, and spores larger than 100 µm were from the genus *Acaulospora*, *Gigaspora*, *Scutellospora*, and *Sclerocystis* (Allen and others 2003).

Statistical Analysis

Datasets were tested for normality (one-sample Kolmogorov–Smirnov test), arcsine transformed when needed. To test for overall (control and thinning plots combined) differences between pre-hurricane and post-hurricane effects we used paired samples *t*-tests. To test pre-hurricane or post-hurricane differences between control and thinning plots, we used independent sample *t*-tests. Values are reported as means ± standard errors. All statistical analyses were performed using SPSS statistical software (SPSS Inc., v13.0, 2006).

Results

Aboveground Hurricane Effects

Mean canopy openness did not differ significantly between thinned and control plots before (mean 6.5 ± 0.3%) or after the hurricane (mean 13.8 ± 0.8%) showing that the response of canopies was similar regardless of treatment. The overall (control and thinned plots combined) effect was a significant ($t = 7.646$, $P < 0.001$) increase in canopy openness of nearly 115% following the hurricane. The increase in canopy openness corresponded to a sharp increase in PAR on the forest floor immediately after the hurricane (Figure 2C). Increased canopy openness was coupled with a significant ($t = 12.147$, $P < 0.001$) reduction in leaf area index (LAI) from 3.4 ± 0.08 to 2.2 ± 0.06.

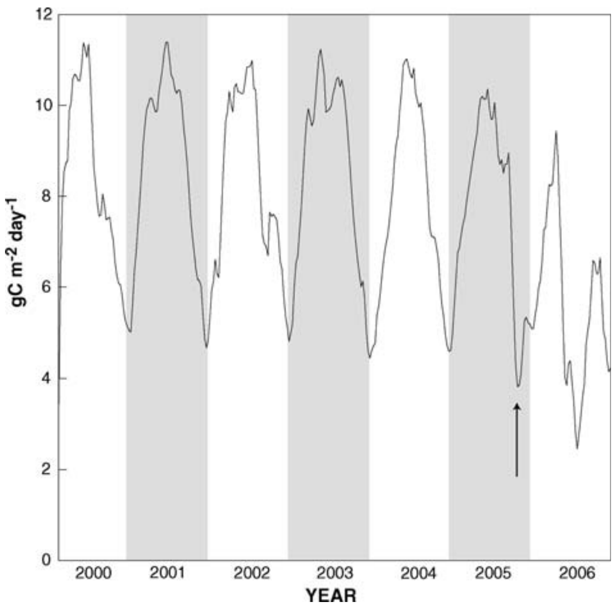

Figure 3. MODIS/Terra gross primary production (GPP, gC m^{-2} d^{-1}) 8-Day L4 from year 2000 to 2008 at the study site. The *arrow* in the figure represents the approximate time when Hurricane Wilma hit the study site.

We were not able to measure photosynthesis at the plot level but the reduction in LAI was consistent at the landscape scale at El Eden Ecological Reserve (see Vargas 2009). Using the MODIS product MOD17A2, we found that the reduction in LAI was associated with a reduction of GPP at the landscape scale from nearly 9 to 4 gC m^{-2} d^{-1} (Figure 3).

Two months after the hurricane we found 590 g m^{-2} of remaining litter in the litter baskets and there were no significant differences between thinned and control plots. Using the mean carbon percentage of the Oi-horizon of 49.2% after the hurricane (data not shown), we determined that this input is equivalent to 2.9 MgC ha^{-1}.

We did not find significant differences in the number of dead trees (mean = 590 ± 13 trees/ha) between thinned and control plots, but dead trees in thinned plots had significantly ($t = -2.86$, $P = 0.043$) larger DBH (5.9 ± 0.02 cm) than affected dead trees in the controls (4.7 ± 0.04 cm). Importantly, there were no differences in the DBH (4.9 ± 0.03 cm) or number of affected living trees (mean = 530 ± 7 trees/ha) between thinned and control plots. Overall, the control plots lost a higher proportion of trees larger than 10 cm DBH in comparison to the thinned plots because there were less of these trees before the hurricane (Table 1).

Belowground Hurricane Effects

Over 90% of the AM spores in the small category were *Glomus* spp., whereas the spores from the large category represented *Acaulospora* spp. (~70%), *Scutellospora* spp. (~15%), and *Gigaspora* spp (~15%). Overall (control and thinned plots combined), we found a significant reduction of nearly 50% of small ($t = 4.803$ $P = 0.001$) and large ($t = 3.705$ $P = 0.003$) AM spore density after the hurricane (Figure 4). However, we did not detect significant differences in AM spore density between plots before or after the hurricane (Figure 4).

Overall (control and thinned plots combined), total AM colonization (sum of hyphal, vesicle and arbuscules) significantly ($t = -4.419$, $P = 0.001$) increased after the hurricane, from nearly 58% ± 7.7 to 76% ± 3.5 (Figure 5). This increment was significantly ($t = -4.029$, $P = 0.002$) driven by an increase in hyphal colonization from nearly 56% ± 8.3 to 74% ± 3.3, and to a minor extent by a marginal increase in arbuscules colonization ($t = -2.089$, $P = 0.061$) from 0.6% ± 0.6 to 1.7% ± 0.3. No significant differences were found before and after the hurricane in vesicle colonization with a mean of 0.9% ± 0.4.

Before the hurricane there were no significant differences in total AM colonization or in any of the AM structures (hyphae, vesicles and arbuscules) between the thinned and control plots (Figure 5). After the hurricane, total AM colonization was significantly higher ($t = -3.043$, $P = 0.012$) in the thinned plots (84%) compared to control plots (69%), mainly driven by an increase in AM colonization of hyphae ($t = -2.798$, $P = 0.019$; Figure 5).

Overall (control and thinned plots combined), we found significant reduction in (a) total BGC ($t = 3.865$, $P = 0.003$) from 9.1 to 7.9 MgC ha^{-1}; (b) Oi-horizon ($t = 2.242$, $P = 0.47$) from 4.5 to 4.0 MgC ha^{-1}; and (c) fine root carbon ($t = 6.689$, $P < 0.001$) from 2.4 to 1.2 MgC ha^{-1} after the hurricane. In contrast, we found a significant ($t = -3.08$, $P = 0.01$) increase in the Oe > 2 mm fraction from 1.3 to 2.0 MgC ha^{-1} after the hurricane.

Before the hurricane there was significantly more carbon stored in total BGC ($t = -7.177$, $P < 0.001$), fine roots ($t = -2.780$, $P = 0.019$), the Oe > 2 mm fraction ($t = -2.494$, $P = 0.032$), and the Oi-horizon ($t = -3.43$, $P = 0.006$) in thinned plots compared to control plots (Figure 6). In contrast, after the hurricane there was significantly more carbon only in total BGC ($t = -3.335$, $P = 0.008$), fine roots ($t = -2.678$, $P = 0.023$), and the Oi-horizon ($t = -3.526$, $P = 0.005$) in thinned plots compared to the control plots (Figure 6).

Table 1. Mean Percent Nitrogen in Different Belowground Pools in Control and Thinned Plots Before and After Hurricane Wilma

Belowground pool	Treatment	Pre-hurricane		Post-hurricane	
		Mean (%)	SE	Mean (%)	SE
Fine roots	Control	2.4	0.06	2	0.11
	Thinned	2.4	0.11	2.3	0.17
Oi-horizon	Control	2.2	0.03	**2.9**	**0.04**
	Thinned	2.1	0.09	**2.7**	**0.02**
Oe > 2 mm	Control	2.1	0.2	2.7	0.05
	Thinned	2.3	0.12	2.6	0.13
Oe < 2 mm	Control	**2.2**	**0.17**	2.2	0.35
	Thinned	**2.8**	**0.1**	2.7	0.1

Numbers in bold indicate significant differences ($P < 0.05$) between treatments. SE indicates standard error. Oi-horizon indicates litter layer or slightly decomposed litter; Oe > 2 mm indicates decomposed litter layer with material larger than 2 mm; Oe < 2 mm indicates decomposed litter layer with material smaller than 2 mm.

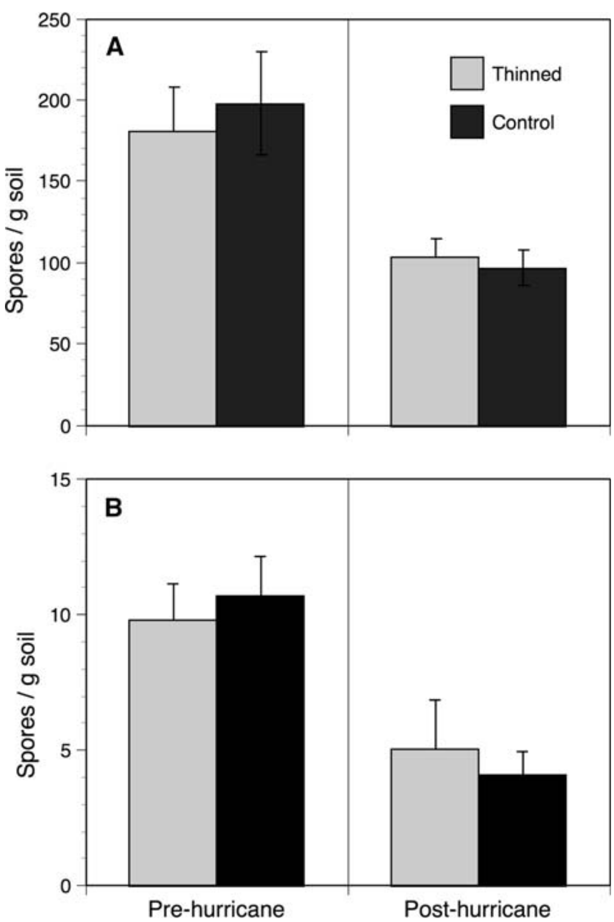

Figure 4. Mean (±SE) number of (**A**) small- and (**B**) large-arbuscular mycorrhizal (AM) fungal spores per gram of soil in thinned and control plots before and after Hurricane Wilma. Over 90% of the AM spores in the small category were *Glomus* spp., whereas the spores from the large category represented *Acaulospora* spp. (~70%), *Scutellospora* spp. (~15%), and *Gigaspora* spp. (~15%). Pre-hurricane data were collected in late September and post-hurricane data were collected in early December 2005.

Overall (control and thinned plots combined), percent nitrogen in the Oi-horizon significantly increased ($t = 4.52$, $P < 0.001$) from 2.1 to 2.8% after the hurricane, but percent nitrogen in fine roots and Oe-fractions remained similar following the event (Table 1). Before the hurricane the thinned plots had significantly higher ($t = 3.609$, $P = 0.0159$) percent nitrogen in the Oe < 2 mm fraction than the control plots, but no significant differences in any other belowground pool (Table 1). Following the event there was significantly higher ($t = 4.19$, $P = 0.008$) percent nitrogen in the Oi-horizon at the control plots but no other differences in nitrogen percentage between control and thinned plots were found (Table 1).

Discussion

Experimental plots were established in 2000 to restore a dense fire-prone stand in a seasonally dry tropical forest on the northern Yucatan Peninsula. The removal of smaller diameter trees in the thinned plots resulted in larger, but fewer trees compared to control plots that had a higher density of small diameter trees (Vargas and others 2009a). Despite initial aboveground structural differences among treatments (Figure 1), we found similar aboveground responses after the hurricane. In contrast, belowground processes responded differently between control and thinned plots after the hurricane.

Our results do not support the hypothesis that the high density of larger trees in thinned plots would suffer greater tree fall than trees in the control plots. Previous studies have described the aboveground effects in trees at several tropical forests (Basnet and others 1992; Scatena and others 1993) where evident damage was seen in thick

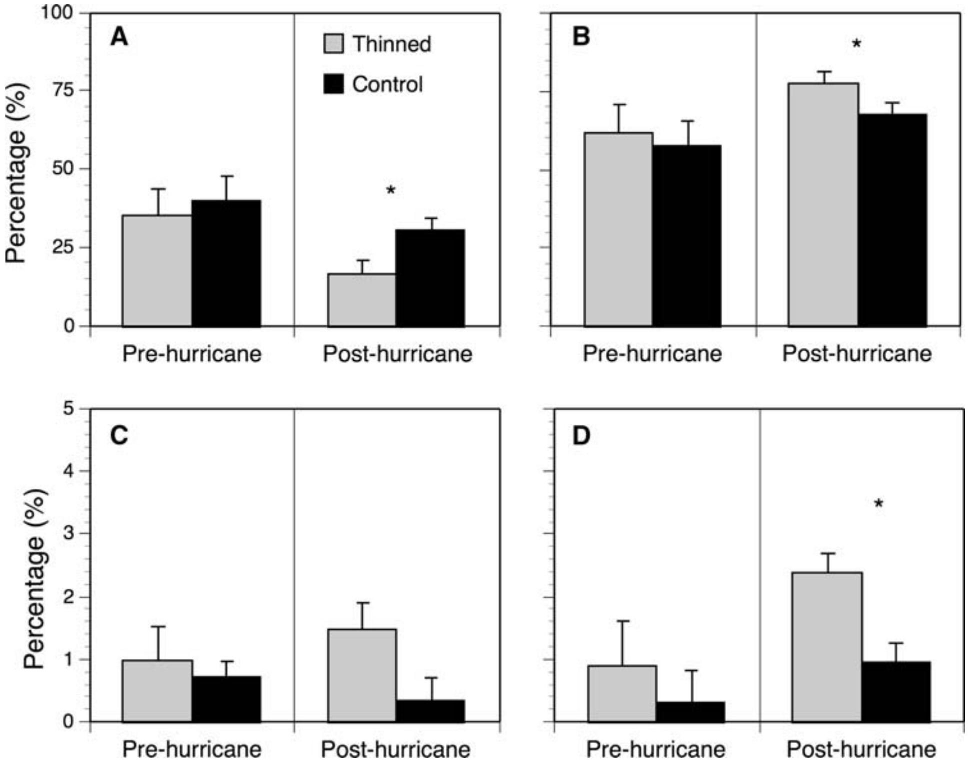

Figure 5. Arbuscular mycorrhizae (AM) root colonization: (**A**) non-infected, (**B**) hyphae, (**C**) vesicles, and (**D**) arbuscles in control and thinned plots before and after Hurricane Wilma. Pre-hurricane data were collected in late September and post-hurricane data were collected in early December 2005. *Bars* represent means ± SE. * $P < 0.05$.

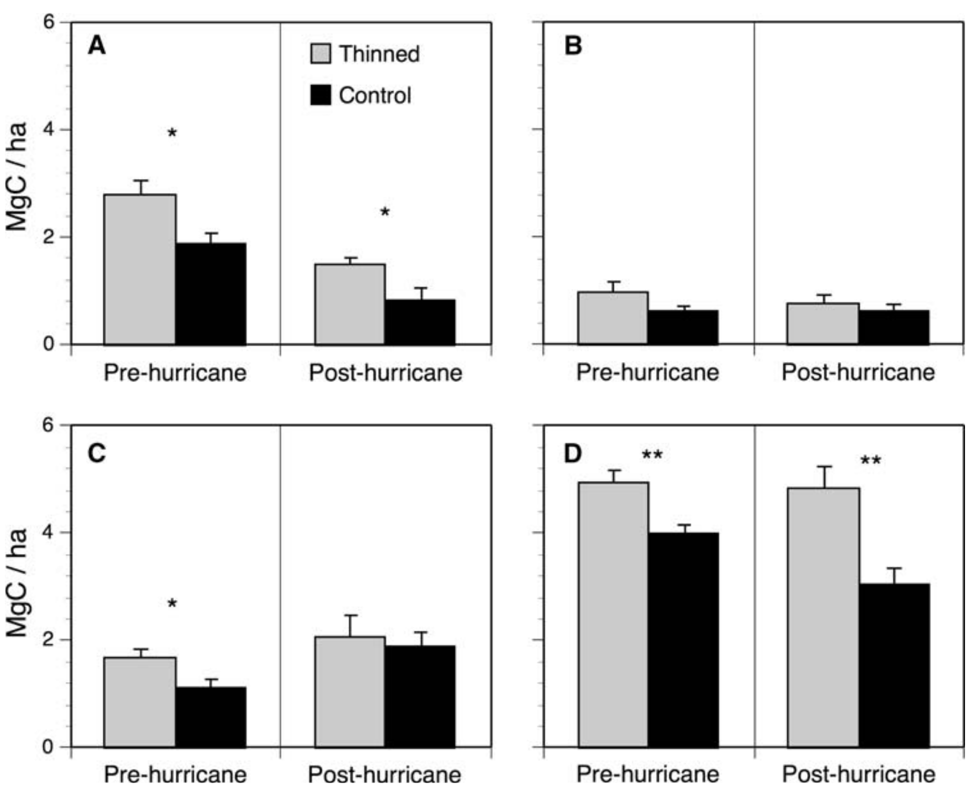

Figure 6. Belowground carbon stored in (**A**) fine roots, (**B**) Oe < 2 mm fraction, (**C**) Oe > 2 mm fraction, and (**D**) Oi-horizon before and after Hurricane Wilma in control and thinned plots. Pre-hurricane data were collected in late September and post-hurricane data were collected in early December 2005. *Bars* represent means ± SE. * $P < 0.05$, ** $P < 0.01$.

branches of large trees (DBH > 20 cm). Our restored forest had a mean height of 6 m and the trees have not developed thick branches, thus this young stand is more flexible to wind forces than a mature stand. However, the control plots lost a greater proportion of trees larger than 10 cm than the thinned plots because there was a lower density of these trees before the hurricane (Figure 1).

Despite initial differences in canopy structure, we observed similar increments in canopy openness and a reduction in effective leaf area index LAI at control and thinned plots following the hurricane. Thus, independently of the number of fallen trees and the basal area distribution within the plots, canopy defoliation was consistent among treatments. The original goal of the thinning treatment was to reduce the possibility of ground fires extending to the forest canopy, but this treatment did not influence the response of aboveground variables (for example, number of tree fall and changes in LAI) to a hurricane disturbance in comparison to the control plots.

Total belowground carbon remained higher in the thinned plots following the hurricane. However, the initial differences in carbon stored in the Oe > 2 mm fraction disappeared after the hurricane. A possible explanation is that the Oi layer in the control plots was more rapidly decomposed in the Oe > 2 mm fraction because the Oi-horizon had more nitrogen in the control plots that may help the decomposers process the litterfall pulse faster. Our results support previous findings that fine roots decrease immediately following a hurricane (Silver and Vogt 1993; Beard and others 2005), and that recently deposited litter could decompose in less than three months in tropical forests (Ostertag and others 2003). In this study, we did not take into account coarse woody debris (for example, branches >5 cm in diameter) other than fallen trees. However, this pool is critical to estimate the total carbon deposited in the soil following a hurricane (Whigham and others 1991). Whether the effect of LIDs on decomposition processes or soil CO_2 efflux could be differentially influenced by a forest management practice remains unclear, but further studies are needed to properly manage ecosystems in the context of LIDs (Dale and others 1998).

Our results support the hypothesis of a reduction in AM fungal spores after the hurricane. However, we found no differences in the number of AM spores before or after the hurricane between the thinned and control plots. Seasonal changes in AM spore density have been reported in tropical forests (Lovelock and others 2003), but to our knowledge no seasonal study has reported a decrease of approximately 50% in less than three months. Possible explanations for reduced AM spores after the hurricane include (a) the hurricane reduced leaf area and plant photosynthesis, which in turn might have contributed to lower carbon allocation to fungal sporulation; (b) sporulation may have been inhibited by high soil water content; and (c) spores were decomposed or washed away from the soil by the high water contents following the event. Reduction in AM spores can lead to a decrease in the inoculum potential as well as changes in AM fungal community. Previous studies have shown that different AM fungal communities can affect seedling recruitment and growth in tropical forests (Allen and others 2003), but further long-term studies are needed to better understand how changes in AM fungal communities and inoculum may influence the resilience of these ecosystems.

Our results do not support the hypothesis that defoliation decreases AM root colonization. After the hurricane canopy openness increased approximately 115%, and GPP was likely to be reduced as seen in other ecosystems (Li and others 2007). With limited photosynthate available to AM fungi, as a response to foliage loss, we would expect to see a decrease in AM colonization. Contrary to our expectations, we observed an increase in AM colonization following the hurricane. One possible explanation for the increase in AM colonization may be related to the pulse in nutrient availability. Our results show that litterfall input (Oi-horizon after the hurricane) is rich in nitrogen because nutrients could not be mobilized from the leaves back into the plant before defoliation. We postulate that this increase in soil nitrogen in combination with high values of soil moisture and high soil temperatures increased decomposition, thereby changing the proportion of carbon and available nitrogen present in the soil. To take advantage of this pulse in nutrient availability, plants appeared to preferentially invest more carbon to AM fungi rather than production of fine roots after the hurricane.

A possible explanation is that the carbon invested to maintain and to increase the percent of root length colonized by AM fungi may have come from non-structural carbon pools (Vargas 2009). There is evidence that plants can allocate stored carbon pools for root and mycorrhizae following fire disturbances (Langley and others 2002) and that this carbon may come from non-structural carbon pools stored in plants (Wurth and others 2005; Poorter and Kitajima 2007; Keel and others 2007). A recent study has shown evidence that plants in these tropical forests can allocate old stored carbon for production of fine roots following the hurricane (Vargas and others 2009b). We propose that differences in colonization between control and thinned plots may be explained by difference in density of large diameter trees because most carbon is stored in the stem volume (Wurth and others 2005). Thus, one possibility is that a higher proportion of remaining large diameter trees in the thinned plots may have greater carbon reserves (per volume of tree) that could be used to maintain higher AM colonization compared to trees in the control plots with less volume. It has been hypothesized that carbon allocation to AM fungi instead of the roots is promoted under stressful conditions because the production of AM hyphae is more economical in terms of carbon than the production of an equivalent length of fine roots (Jakobsen and others 2002). Thus, it is important to understand how plants allocate non-structural carbon reserves following LIDs to better understand the effects and recovery trajectories of terrestrial ecosystems.

Conclusion

The novelty of this study is that it provides an estimate of evident aboveground hurricane effects and less evident belowground effects under restored plots in a seasonally dry tropical forest. Land-use change in these forests is increasing (Bullock and others 1995) and more restoration or management efforts will be needed, but management plans may need to consider the concept of LIDs (Dale and others 1998). The main findings of this study are (a) initial forest structural differences resulted in similar aboveground responses but different belowground responses; (b) AM fungal spores were substantially reduced following the hurricane; and (c) contrary to expectations, we found that following plant defoliation and a decrease in GPP and fine root biomass, AM root colonization increased after the hurricane. Ecosystem restoration and management plans should not be conceived without considering the potential influence of LIDs and the synergistic effects of belowground and aboveground ecosystem components.

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