Belowground nitrogen dynamics in relation to hurricane damage along a tropical dry forest chronosequence

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Abstract Understanding and predicting the responses of plant communities to multiple overlapping disturbances remains a challenging task. Hurricane Wilma represents a large, yet infrequent type of disturbance that was superimposed on an existing disturbance gradient of time since fire. We examined disturbance and recovery patterns in response to these overlapping disturbances by measuring how canopy structure, fine roots, mycorrhizae, and soil nitrogen dynamics, varied along a fire chronosequence in the 2 years after Hurricane Wilma. Hurricane damage increased canopy openness in all seral stages. In the early-seral stage, canopy openness returned to pre-hurricane conditions within 2 years, whereas canopy openness in the late-seral stage remained significantly higher throughout the study. We observed no significant change in root length density in the early- and mid-seral stages. However, in the late-seral stage, root length density was significantly reduced immediately after the hurricane and remained so 2 years after the hurricane. In the late-seral stage, we also observed a significant reduction in percent soil nitrogen and a significant increase in soil nitrogen isotopic composition (δ^{15}N) values, indicating a loss of soil nitrogen. In contrast, in the early- and mid-seral stages, there were no significant changes in percent nitrogen or soil δ^{15}N values. Results from this study suggest that forest fire disturbance history influences responses to hurricane damage. Moreover, feedbacks between aboveground and belowground processes have the potential to influence forest recovery.

Keywords Large-infrequent disturbance ·
Hurricane Wilma · Nitrogen dynamics ·
Secondary succession · Stable isotopes ·
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Introduction

Understanding and predicting responses to and subsequent recovery of plant communities after large, infrequent disturbances remains a critical and challenging task. Hurricanes are an example of large, infrequent disturbances causing defoliation as well as damaging and killing trees through uprooting and stem breakage (Brokaw and Walker 1991; Tanner et al. 1991; Walker 1991; Whigham et al. 1991; Zimmerman et al. 1996). Hurricane impact on

aboveground forest structure is well documented and varies considerably across the landscape (Weaver 1986; Boucher 1990; Bellingham 1991; Tanner et al. 1991; Yih et al. 1991; Lugo and Scatena 1995). Generally, the importance of large, infrequent disturbances in shaping landscapes and ecosystems has been studied from an aboveground perspective (Turner and Dale 1998). However, changes in belowground processes, such as nutrient cycling, root growth and mycorrhizal colonization can have profound effects on tree growth and forest regeneration (Janos 1980a; Allen 1991; Johnson and Wedin 1997; Kiers et al. 2000; Allen et al. 2003a; Hodge 2004) but have rarely been studied. Understanding the response and recovery of belowground processes after hurricane damage may, in part, help explain the recovery of aboveground forest structure.

Although less evident than aboveground processes, hurricane damage can have pronounced effects on belowground processes, including trace gas fluxes (Steudler et al. 1991; Vargas and Allen 2008), soil nutrients (Scatena et al. 1993), and fine roots (Parrotta and Lodge 1991; Silver and Vogt 1993; Beard et al. 2005). Parrotta and Lodge (1991) showed that more than 1 year may be required for the recovery of fine roots to pre-hurricane levels. In addition to fine roots, mycorrhizal associations between plant roots and fungi may also be adversely affected by hurricane disturbances (Vargas et al. 2009). Because of the loss in stand leaf area, photosynthetic capacity is reduced as a result of the hurricane, simultaneously reducing the carbon supply necessary to support mycorrhizal fungi. However, we know little about the effect of hurricane disturbances on mycorrhizal associations because of the scarcity of studies.

Tropical forests are dominated by trees that form arbuscular mycorrhizal (AM) associations (Read 1991; Allen et al. 1995; Treseder and Cross 2006), and numerous studies have shown the importance of AM fungi for the growth of many tropical trees (Janos 1980a, b; Huante et al. 1993; Fisher et al. 1994; Kiers et al. 2000; Allen et al. 2003a). AM fungal taxa and fungal activity vary among different seral stages (Janos 1980b; Allen et al. 2003a) and with different soil conditions caused by disturbance history (Allen et al. 2005). Nevertheless, numerous studies have shown that fine roots and mycorrhizal fungi are essential for rapid and efficient cycling of nutrients in environments where the potential for

nutrient leaching is high (Went and Stark 1968; Stark 1971; Stark and Spratt 1977; Stark and Jordan 1978; Cuevas and Medina 1988). Changes in root and mycorrhizal dynamics after a hurricane could therefore have pronounced effects on the ability of trees to absorb the pulse of nutrients frequently observed after a hurricane disturbance and mitigate ecosystem nutrient losses.

Hurricane damage also causes a pulse of litterfall (Lodge et al. 1991; Whigham et al. 1991; Allen et al. 2007), which can affect nutrient cycling (Lodge et al. 1991; Lodge and McDowell 1991; Steudler et al. 1991). This litterfall often contains higher than normal concentrations of certain nutrients because there is no opportunity for retranslocation of nutrients to occur before leaf abscission (Blood et al. 1991; Frangi and Lugo 1991; Lodge et al. 1991). For instance, in Puerto Rico the nitrogen content of litterfall after Hurricane Hugo was 1.3–2.2 times the mean annual litterfall (Lodge and McDowell 1991). Such sudden, large additions can lead to increased ammonium availability, net nitrogen mineralization rates, and an increase in nitrate concentrations in the soil, which in turn can lead to nitrogen loss via leaching, volatilization, and denitrification (Steudler et al. 1991).

Natural abundance of ^{15}N in soil and plant pools provides a useful tool for studying nitrogen dynamics in forested ecosystems (Nadelhoffer and Fry 1994; Martinelli et al. 1999; Amundson et al. 2003; Templer et al. 2007). Although isotopic values result from many interacting processes (Handley and Scrimgeour 1997), isotopic data often point to particular mechanisms that are otherwise difficult to measure. In ecosystems that are characterized by high nitrogen availability (e.g., Aber et al. 1989), there are a number of fractionating processes that result in high soil $\delta^{15}N$ values. Microbes discriminate against ^{15}N during decomposition, mineralization (Nadelhoffer and Fry 1994), nitrification (Nadelhoffer and Fry 1994; Högberg 1997; Handley and Raven 1992) and denitrification (Piccolo et al. 1996). As soil nitrogen increases, soil $\delta^{15}N$ values increase because of fractionating pathways of nitrogen loss from the ecosystem such as leaching or gaseous loss (Agren and Bosatta 1988; Aber et al. 1989; Stoddard 1994; Peterjohn et al. 1996; Martinelli et al. 1999). Forested ecosystems with relatively open nitrogen cycles are therefore characterized by enriched soil $\delta^{15}N$ values

due to loss through fractionating pathways compared to systems with relatively closed nitrogen cycles that are depleted in [15]N (Austin and Vitousek 1998; Schuur and Matson 2001).

Seasonally dry tropical forests on the Northern Yucatan Peninsula are subject to anthropogenic disturbances such as land clearing or agriculture conversion (Gómez-Pompa 1992; Gómez-Pompa et al. 2003) as well as natural disturbances such as hurricanes and fire (Boose et al. 2003; Whigham et al. 2003). Consequently, these disturbances create a patchy mosaic of different seral stages undergoing secondary succession. The effect of multiple disturbances in these forests may not be additive, but synergistic in nature, causing non-linear changes in successional trajectories or ecosystem recovery patterns. In this study, we combined soil nitrogen and stable isotope measurements with measurements of root and mycorrhizal dynamics to examine changes in belowground processes after a major hurricane on the Northern Yucatan Peninsula. Our main objective was to examine the immediate and short-term recovery of belowground processes after a hurricane along a chronosequence of secondary succession to better understand how multiple disturbances may influence the recovery of forest structure and belowground processes.

Materials and methods

Study site

The study was carried out at El Eden Ecological Reserve (Gómez-Pompa et al. 2003), located in the northeastern corner of the Yucatan Peninsula, Mexico (21°12.61′N, 87°10.93′W). The Reserve has 2,500-ha of protected landscape in which 800 ha represent mature forest and the remaining area is secondary forest. The landscape is flat, with an elevation 6 m above sea level, and occurs on limestone bedrock. Soils and climate are similar across the Reserve (see Gómez-Pompa et al. 2003). Soils are shallow (depth <20 cm), with mean soil organic matter of 30% and a bulk density of 0.35 g/cm^3. The reserve receives an average of 1,650 mm of annual precipitation with a wet season from June to October. The dry season is from December to May when precipitation is <100 mm per month. The mean annual temperature is 24.2°C, and mean annual soil temperature at 10 cm depth is 23.2°C.

The vegetation of the Reserve is described in Schutlz (2005), and is a mosaic of successional vegetation. Over the past four decades, severe fires have crossed portions of the Reserve (Allen et al. 2003b; Boose et al. 2003; Whigham et al. 2003). During these burns the standing vegetation was consumed and the bedrock was largely exposed due to combustion of the organic soil (Allen et al. 2003a). For this study, we selected forest stands that burned during the dry season of 1999 and 1989. The forest stand that burned during the dry season of 1999 did not burn in 1989. We also selected a late successional forest stand within the protected area of the reserve with no evidence of fire, human or hurricane disturbance for more than 60 years. Thus, we have selected three different forest stands representing a chronosequence of secondary succession ranging in age from an area burned 9 years ago (early-seral stage), an area burned 18 years ago (mid-seral stage) to an area that has not been disturbed for more than 60 years (late-seral stage). All seral stages are greater than 500 ha and are located within a distance of 5 km of each other. Seral stages have a large overlap in tree species with little or no apparent patch structure within the seral units. We assumed that any structural and functional differences among sites (Table 1) are related to time since fire rather than their spatial location because there is no slope or relief difference in the landscape. Unfortunately, we did not determine soil texture among the different seral stages. We know that Mayans cultivated the area that is now the Reserve during the early classic period (1,500 years ago), but land use since has been minimal, with only selective tree harvesting in the late 1800s and early 1900s (Gómez-Pompa et al. 2003). For additional information about the Reserve see Allen et al. (2003a, b) and Vargas et al. (2008).

Hurricane Wilma

On 21 October 2005 Hurricane Wilma made landfall crossing the island of Cozumel and onto the Yucatan Peninsula as a Category IV storm on the Saffir-Simpson scale, and emerged over the Gulf of Mexico on October 23 as a Category II hurricane. While in the Caribbean, Hurricane Wilma was the most intense hurricane recorded in the Atlantic basin with a

Table 1 Stand characteristics of tree species found among the three seral stages undergoing different stages of secondary succession on the Northern Yucatan Peninsula, Mexico

Seral stage	AGB (mg/ha)	Soil organic matter (%)	Percent legumes by species[a] (%)	AM status[b]	EM status[c]	Canopy height (m)
Early	20.1 ± 2.1	28.8 ± 1.6	28	Present	Absent	4
Mid	62.8 ± 2.8	48.12 ± 3.9	17	Present	Few	8
Late	143.9 ± 6.5	59.8 ± 3.0	16	Present	Present	14

Means and standard errors of aboveground biomass (AGB) and soil organic matter are from data collected by Vargas et al. (2008)

[a] Based on the presence/absence or legume trees along line transects within each seral stage

[b] Based on arbuscular mycorrhizal colonization of plant roots

[c] Based on taxonomic affiliation and stable isotope composition of fungal sporocarps

minimum barometric pressure of 882 mbar and maximum winds of 295 km/h. As the eye of the hurricane crossed directly over our study site the barometric pressure dropped from 1,010 to 970 mbar with sustained winds between 190 and 210 km/h (Allen et al. 2007). The Reserve received over 1,500 mm of precipitation during this 3 days period and soils remained saturated for nearly 50 days.

Aboveground hurricane damage

In September 2005, one month before the hurricane, we established three parallel 60 m transects randomly in each of the early-, mid- and late-seral stages. Transects were oriented in a north to south direction and were position far enough into each seral stage to avoid any border effect. The minimum distance between two transects was 150 m. Along each transect we randomly selected two locations where both aboveground and belowground measurements were taken resulting in six locations in each seral stage. At each location, we took hemispherical photographs below the forest canopy at 1 m height and calculated percent canopy openness using Gap Light Analyzer V2.0 (Canham 1988). Hemispherical photographs were taken at the same location during the third week of December 2005 (2 months after) to determine the amount of hurricane damage on canopy openness, and again in September 2007 (2 years after) to determine recovery of the canopy.

Effects of hurricane damage on soil factors

At the same places where hemispherical photographs were taken, soil samples were collected by inserting a 4.5 cm diameter metal soil corer until we encountered the limestone bedrock (usually <10 cm in depth) for a total of six soil samples per seral stage. Soil samples were collected in September 2005 (pre-hurricane), December 2005 (2 months after Hurricane Wilma), September 2006 (1 year after), and again in September 2007 (2 years after). Samples were air dried and transported to the University of California, Riverside where they were stored at −20°C prior to starting laboratory analyses. Fine roots (live roots <2.0 mm in diameter) from individual cores were sorted by hand and rinsed free of organic matter with deionized water. For each sample, fine root length density was determined using the line intersection method (Newman 1966). Fine roots were then divided into two subgroups for various measurements. One sub-sample was used to determine percent AM colonization (see description below), whereas the other sub-sample was dried (70°C, 48 h) and ground to a fine powder for chemical analysis. We choose to examine root $\delta^{15}N$ values, as opposed to foliar $\delta^{15}N$ values, because we expected a stronger relationship between root $\delta^{15}N$ values and soil nitrogen cycling rates since there is a more direct connection between roots and ^{15}N-enrichment processes driven by nitrification, i.e., fewer plant processes occur before the nitrogen is assimilated, and possibly discriminated against in plant tissues (Handley and Raven 1992). Root carbon and nitrogen concentrations and isotopic composition of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were determined with an elemental analyzer (Model ANCA-SL, Europa Scientific, Ltd, Crewe, UK) connected to a continuous flow isotope ratio mass spectrometer (Model 20/20, Europa Scientific) at the Center for Stable Isotope Biogeochemistry of the University of California, Berkeley. Stable isotope abundances are reported as: $\delta^{15}N$ or $\delta^{13}C$ (‰) $= (R_{sample}/R_{standard} - 1) \times 1000,$

where $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$ of the sample and reference standard (atmospheric N_2 and PeeDee beleminite-C, respectively). The standard deviation of isotopic measurements of the internal standards used was typically <0.2‰ for both $\delta^{15}N$ and $\delta^{13}C$.

Mycorrhizal infection

Roughly 10 mg of fine roots from each sample was used to determine AM colonization. We did not distinguish among roots of different plant species because of the large number of species present in these forests. Roots were cleared in 10% KOH (90°C, 1 h) and 3% H_2O_2 (90°C, 20 min), acidified in 1% HCl for 10 min, stained with 0.05% Trypan Blue (90°C, 1 h) and then de-stained in acidified glycerol (Koske and Gemma 1989). Approximately thirty 1 cm root fragments were mounted on glass slides with PVLG (polyvinyl lactoglycerol) medium and microscopically assessed for the presence of mycorrhizal hyphae using the magnified intersection method (McGonigle et al. 1990). At least 100 intersections were scored for each sample.

Statistical analysis

Data sets were tested for normality with a one-sample Kolmogorov–Smirnov test. Percent AM colonization was the only data that was not normally distributed; therefore, it was arcsine transformed to meet the assumptions of analysis of variance. Measurements taken in September 2005 were subjected to a one-way ANOVA to detect significant ($P < 0.05$) differences among seral stages before the hurricane. Within each seral stage, repeated measures ANOVA was used to test for changes in measured variables among sampling dates. All statistical analyses were performed using SPSS statistical software (SPSS Inc., v16.0, 2007).

Results

Aboveground damage

One month before Hurricane Wilma made landfall on the Northern Yucatan Peninsula in October 2005, percent canopy openness was significantly greater in the early-seral forest compared to mid- and late-seral
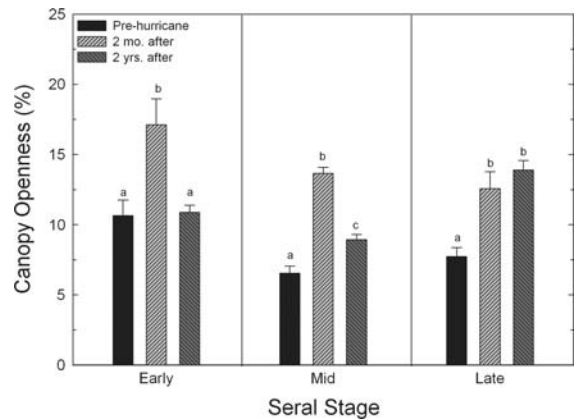
Fig. 1 Mean (±SE) percent canopy openness before and after Hurricane Wilma. As the eye of the hurricane crossed directly over our research site on 22 October 2005 the barometric pressure dropped from 1010 to 970 mbar with sustained winds between 190 and 210 km/h. *Different letters* indicate significant ($P < 0.05$) differences among sampling dates within each seral stage

forests ($F_{2,17} = 7.18$, $P < 0.01$). Immediately following the hurricane there was a significant increase in percent canopy openness in all forest types (Fig. 1; $P < 0.01$). However, aboveground canopy recovery differed among seral stages (Fig. 1). In the early-seral stage, percent canopy openness returned to pre-hurricane levels within 2 years after the hurricane (Fig. 1), whereas canopy openness in the late-seral stage remained significantly higher than pre-hurricane levels 2 years after the hurricane ($F_{2,10} = 16.17$, $P = 0.001$).

Hurricane damage on soil factors

Before the hurricane we detected no differences in fine root length density among the different seral stages ($F_{2,17} = 0.79$, $P = 0.47$). However, the immediate response and short-term recovery of fine roots differed among seral stages (Fig. 2a). In the late-seral stage, fine root length density was significantly reduced 1 year after the hurricane and remained reduced 2 years after the hurricane($F_{3,15} = 5.29$, $P = 0.01$). In contrast, both the early-and mid-seral stages showed no significant difference in fine root length density throughout the study (Fig. 2a).

No significant difference in AM colonization was detected among seral stages before the hurricane ($F_{2,17} = 0.87$, $P = 0.44$). However, when comparing
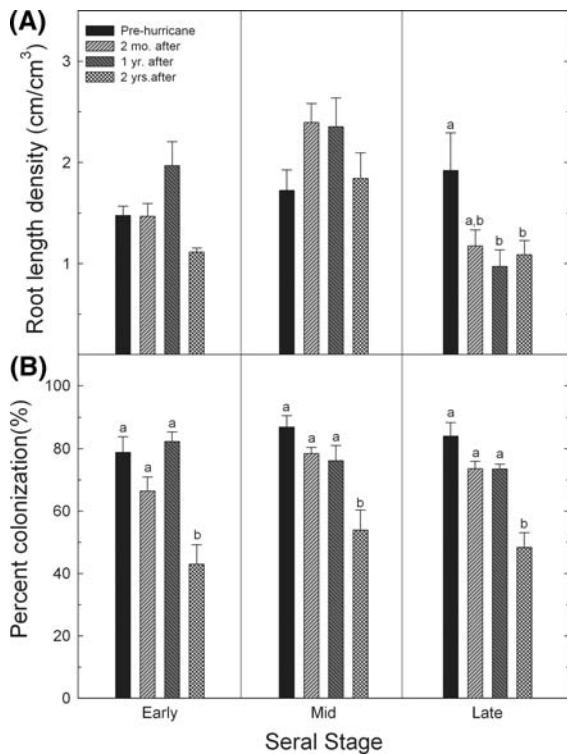
Fig. 2 Immediate impact and short-term recovery of **a** root length density and **b** arbuscular mycorrhizal colonization within different seral stages after Hurricane Wilma. *Different letters* indicate significant ($P < 0.05$) differences among sampling dates within each seral stage (means $\pm$ SE, $N = 6$)

among all seral stages we observed a significant reduction in AM colonization immediately following the hurricane ($F_{3,51} = 38.21$, $P = 0.05$). One year after the hurricane AM colonization return to pre-hurricane levels ($P = 0.18$). Interestingly, AM colonization was severely reduced 2 years after the hurricane compared to pre-hurricane values ($P < 0.001$), with average colonization of $48.42\% \pm 3.38$ (Fig. 2b).

Percent nitrogen in plant roots was not significantly different among seral stages before the hurricane (Fig. 3a, $F_{2,17} = 2.79$, $P = 0.09$). We detected no change in percent root nitrogen among sampling dates (Fig. 3a). Root $\delta^{15}N$ values differed significantly among seral stages before the hurricane ($F_{2,17} = 8.25$, $P < 0.01$). Roots in the early-seral stage had higher $\delta^{15}N$ values compared to roots in both the mid-and late-seral stages. We detected no change in root ^{15}N values among sampling dates (Fig. 3b).

Percent carbon in plant roots was not significantly different among seral stages before the hurricane (Fig. 3c, $F_{2,17} = 2.30$, $P = 0.14$). When comparing among all seral stages, we detected a significant difference among sampling dates ($F_{3,51} = 3.40$, $P = 0.03$). Samples collected 2 years after the hurricane were significantly lower than pre-hurricane samples ($P = 0.04$). Before the hurricane we detected no significant differences in root $\delta^{13}C$ values among seral stages ($F_{2,17} = 1.67$, $P = 0.22$), nor did we find differences among sampling dates (Fig. 3d).

Soil nitrogen differed significantly among all seral stages before the hurricane ($F_{2,17} = 45.08$, $P < 0.001$). Percent soil nitrogen was lowest in the early-seral stage ($1.06\% \pm 0.10$), intermediate in the mid-seral stage ($2.22\% \pm 0.17$), and highest in the late-seral stage ($2.69\% \pm 0.09$). The immediate response and short-term recovery of soil nitrogen differed among seral stages (Fig. 4a). In the late-seral stage, percent soil nitrogen was significantly reduced immediately after the hurricane and remained reduced 2 years after the hurricane ($F_{3,15} = 10.02$, $P < 0.01$). In contrast, in the mid-seral stage the percentage of soil nitrogen was not significantly lower than pre-hurricane values until 2 years after the hurricane ($F_{3,15} = 6.89$, $P < 0.01$). In the early-seral stage we detected no significant change in soil nitrogen ($F_{3,15} = 1.53$, $P = 0.25$). Before the hurricane soil $\delta^{15}N$ values differed significantly among all seral stages ($F_{2,17} = 102.05$, $P < 0.001$). Soil $\delta^{15}N$ values were lowest in the late-seral stage ($1.93\text{‰} \pm 0.10$), intermediate in the mid-seral stage ($2.92\text{‰} \pm 0.24$), and highest in the early-seral stage ($5.75\text{‰} \pm 0.22$). The immediate response and short-term recovery of soil $\delta^{15}N$ values differed among seral stages (Fig. 4b). In the late-seral stage, soil $\delta^{15}N$ values significantly increased after the hurricane and remained higher 2 years after the hurricane ($F_{3,15} = 6.03$, $P < 0.01$). In contrast, in the early-and mid-seral stages we detected no significant change in soil $\delta^{15}N$ values throughout the study (Fig. 4b).

Percent soil carbon before the hurricane differed significantly among all seral stages ($F_{2,17} = 55.42$, $P < 0.001$). Percent soil carbon was lowest in the early seral stage ($9.40\% \pm 1.06$), intermediate in the mid-seral stage ($27.94\% \pm 2.68$), and highest in the late-seral stage ($33.74\% \pm 0.74$). The immediate response and short-term recovery of soil carbon

Fig. 3 Immediate impact and recovery of **a** percent nitrogen, **b** ^{15}N values, **c** percent carbon, and **d** ^{13}C values from plant roots collected in early-, mid-, and late-successional forests. Samples were collected 1 month before (pre-hurricane), 2 months after, 1 year after, and 2 years after the pass of Hurricane Wilma. *Different letters* indicate significant ($P < 0.05$) differences among sampling dates within each seral stage (means ± SE, $N = 6$)
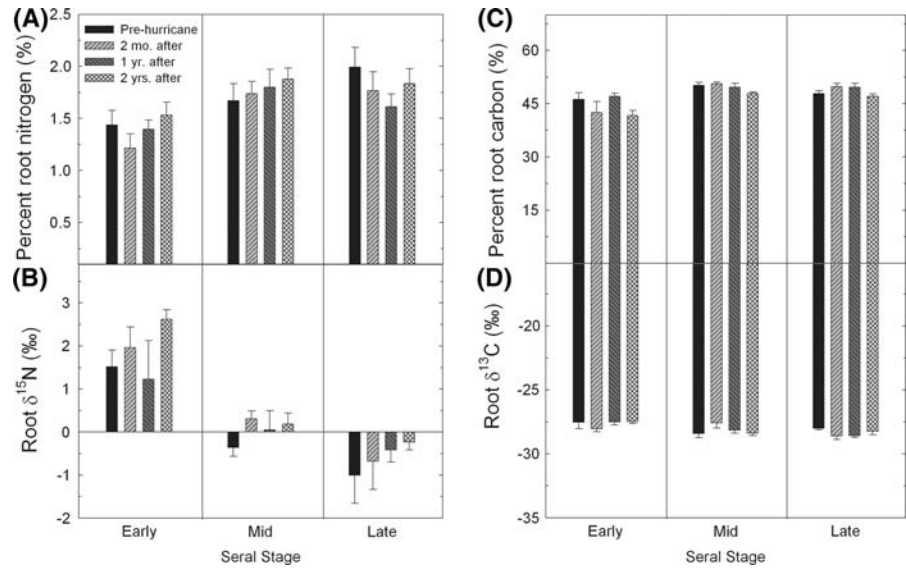
Fig. 4 Immediate impact and recovery **a** percent nitrogen, **b** ^{15}N values, **c** percent carbon, and **d** ^{13}C values (mean ± SE) from soil collected in early-, mid-, and late-successional forests. Samples were collected 1 month before (pre-hurricane), 2 months after, 1 year after, and 2 years after the pass of Hurricane Wilma. *Different letters* indicate significant ($P < 0.05$) differences among sampling dates within each seral stage (means ± SE, $N = 6$)
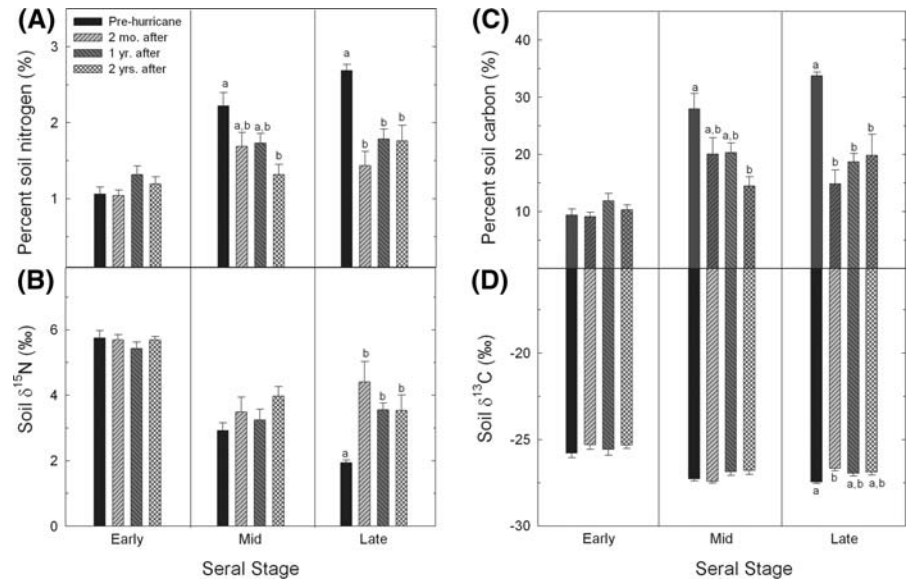
differed among seral stages (Fig. 4c). In the late-seral stage, soil carbon was significantly reduced after the hurricane and remained reduced throughout the study ($F_{3,15} = 11.45$, $P < 0.001$). In the mid-seral stage the percentage of soil carbon 2 years after the hurricane was significantly lower than pre-hurricane ($F_{3,15} = 6.78$, $P < 0.01$). In contrast, in the early-seral stage we detected no significant change in soil carbon ($F_{3,15} = 1.21$, $P = 0.34$). Before the hurricane soil δ^{13}C values in the early-seral stage were significantly higher than mid-and late-seral stages ($F_{2, 17} = 27.10$, $P < 0.001$). In the early- and mid-seral stages we

detected no significant change in soil δ^{13}C values (Fig. 4d). However, in the late-seral stage soil δ^{13}C values significantly increased immediately after the hurricane ($F_{3,15} = 4.96$, $P = 0.01$).

Discussion

Results from this study suggest that large, infrequent disturbances can be an important force in creating the aboveground structure of seasonally dry tropical forests on the Northern Yucatan Peninsula. Moreover,

the recovery of forest canopy after a large, infrequent disturbance is heavily influenced by prior site history (Foster et al. 1999; Uriate et al. 2004; Chazdon 2003; Thompson et al. 2007). We found early-and mid-seral stages to be more resilient to a hurricane disturbance, whereas the taller, late-seral forest (Table 1), with more biomass to lose, appeared more vulnerable. In addition to widespread defoliation, we also observed numerous broken braches in the late-seral stage after the hurricane, whereas the occurrence of broken braches in the early- and mid-seral stages was less common. Similarly, Pascarella et al. (2004) predicted that the effect of hurricanes on forest structure and ecosystem processes would be more pronounced in late-successional forests compared to early-successional forests as a result of increased structural diversity in older forest stands. We also demonstrated that changes in belowground processes are such that they may exert an extensive feedback on the recovery of aboveground forest canopy.

There were important differences in the immediate response and subsequent recovery of fine roots amongst the different seral stages. In both the early- and mid-seral stages, we found no significant change in root length density following the hurricane. In contrast, root length density in the late-seral stage was significantly reduced and remained reduced 2 years after the hurricane. Such a reduction in fine roots can have pronounced affects on the ability of trees to absorb the pulse of nutrients from aboveground hurricane litterfall (Lodge et al. 1991). The loss of nitrogen, in particular, could be extremely important as high leaf nitrogen is critical for high levels of photosynthesis, and nitrogen not absorbed immediately could be lost through leaching and denitrification. Significant and prolonged reduction in fine roots could therefore limit the amount of nitrogen absorbed by plants, which in turn may help explain the arrested regeneration of aboveground canopy in the late-seral stage.

To our knowledge this is the first study to examine the effect of a hurricane disturbance on mycorrhizal associations. Previous studies have examined the response of AM associations to individual treefalls and reported small negative to no effects (Allen et al. 1998; Guadarrama and Alvarez-Sanchez 1999). Other studies have shown that defoliation and herbivory tend to reduce AM root colonization (Eom et al. 2001; Gange et al. 2002; Wearn and Gange 2007),

but these studies are difficult to extrapolate to larger scale damage associated with hurricanes. Here, we observed a reduction in AM colonization immediately following Hurricane Wilma, indicating mycorrhizal associations are adversely affected by hurricane disturbances. Previously, Wearn and Gange (2007) explained the reduction in AM colonization due to herbivory as the result of foliage loss and the corresponding reduction in photosynthesis. Similarly, the observed reduction in AM colonization immediately after Hurricane Wilma may be the result of widespread defoliation and the corresponding reduction in photosynthates available to AM fungi. Reduced photosynthates may also help explain the reduction in AM colonization in September 2007, as this sampling date corresponded to the lowest percent carbon in plant roots.

Immediately following the hurricane, canopy openness increased in all seral stages, indicating widespread defoliation. Nearly 743 g/m^2 of litterfall was deposited on the forest floor and this input was rich in nitrogen because there was no opportunity for retranslocation of nutrients before leaf abscission (Vargas, unpublished data). We observed a rapid reduction in percent soil carbon after the hurricane in the late-seral stage. Because of the high nitrogen in litter, combined with high soil moisture and high soil temperature, rapid decomposition of hurricane litterfall occurred. Evidence for the rapid rate of decomposition comes from the high rates of soil respiration after the hurricane (Vargas and Allen 2008). As a result, evidence points to nitrogen functioning as an excessive nutrient shortly after the hurricane and being lost from the system via leaching of nitrate and gaseous losses (Agren and Bosatta 1988; Aber et al. 1989; Stoddard 1994; Peterjohn et al. 1996), resulting in higher soil $\delta^{15}N$ values (Martinelli et al. 1999). Although we did not directly measure pathways of nitrogen loss in this study, most pathways of nitrogen loss from ecosystems fractionate nitrogen isotopes leaving behind an enriched soil pool of $\delta^{15}N$ (Martinelli et al. 1999; Amundson et al. 2003) and we observed a significant increase in soil $\delta^{15}N$ values after the hurricane, consistent with loss of nitrogen via fractionating pathways.

Before the hurricane, soil $\delta^{15}N$ values in the early-seral stage were significantly enriched in ^{15}N compared to the other two seral stages, suggesting high nitrogen availability and an open nitrogen cycle in the

early-seral stage. However, percent soil nitrogen was significantly lower in the early-seral stage prior to the hurricane compared to the other seral stages, indicating that nitrogen may not be in excess. The discrepancies between $\delta^{15}N$ values and percent soil nitrogen may, in part, be explained by greater proportion of legume species in the early relative to the late-seral stage. Previous examination of these plant roots has revealed the presence of nitrogen-fixing bacteria, suggesting that these species are capable of fixing atmospheric nitrogen (Allen and Rincon 2003). Consequently, high rates of nitrogen fixation in the early-seral stage may be coupled with a high loss of nitrogen through denitrification or leaching of ^{14}N, thereby creating the enriched soil $\delta^{15}N$ values.

Soil $\delta^{15}N$ values varied significantly among the different seral stages after the hurricane. In both the early- and mid-seral stages, we found no significant change in percent nitrogen or soil $\delta^{15}N$ values after the hurricane, indicating minimal loss of nitrogen from these seral stages. In contrast, there was a significant decrease in percent nitrogen and a significant increase in soil $\delta^{15}N$ values in the late-seral stage suggesting a significant loss of nitrogen from this seral stage. This loss of nitrogen may, in turn, help explain the arrested regeneration of aboveground forest canopy in the late-seral stage. Herbert et al. (1999) reported that soil nutrient supply can influence the rate of forest recovery after hurricane disturbance in *Metrosideros polymorpha* forests on Kauai, Hawaii. Two years after Hurricane Iniki, diameter increments of trees in added phosphorus treatments were significantly greater than diameter increments of trees in treatments lacking phosphorus fertilization. Forests on Kauai tend to be phosphorus limited (Treseder and Allen 2002), whereas phosphorus is relatively available at El Eden (Allen et al. 2003b, Allen and Rincon 2003), suggesting potentially greater limitation by nitrogen, but fertilization studies are needed to test the nature of nutrient limitation at El Eden.

In additional to the increased soil $\delta^{15}N$ values, we also observed a gradual, but insignificant, increase in root $\delta^{15}N$ values after the hurricane in the late-seral stage. The increase in root $\delta^{15}N$ values was most likely the result of direct uptake of ^{15}N from enriched soil after the hurricane. However, another plausible explanation for the increase in root $\delta^{15}N$ values may be related to ectomycorrhizal (EM) fungi and their

role in host plant nitrogen acquisition. Although tropical forests are primarily dominated by trees that form AM associations, we recently found evidence of EM fungi at our study site based on stable isotope composition of sporocarps (Hasselquist, unpublished data). The occurrence of EM fungi appears to predominate in the late-seral stage, with few to no observation of EM fungi in mid- and early-seral stages. During nitrogen uptake, EM fungi discriminate against ^{15}N and transfer ^{15}N depleted nitrogen to the host plant while retaining nitrogen that is enriched in ^{15}N (Hobbie et al. 1999; Kohzu et al. 1999). Consequently, plants associated with EM fungi are often depleted in $\delta^{15}N$ as a result of a higher percentage of plant nitrogen being derived from EM fungi. Therefore, the relatively depleted pre-hurricane $\delta^{15}N$ values of plant roots in the late-seral stage may be the result of more nitrogen being derived from EM fungi, compared to early- and mid-seral stages where EM fungi are absent. Using methods of Hobbie and Hobbie (2006) and Macko et al. (1986) we have demonstrated (unpublished data) that EM fungi provide ∼40% of nitrogen in plants before the hurricane and ∼30% after the hurricane, which might explain the gradual increase in root $\delta^{15}N$ values after the hurricane. More research is needed to better understand the importance of EM fungi for host plant nitrogen acquisition in this forest as well as how EM fungi respond to large hurricane disturbances.

In conclusion, we found that the recovery of aboveground forest canopy after a large, infrequent disturbance is, in part, dependent on prior site history. In the early seral-stages, the canopy recovered to pre-hurricane conditions within 2 years after the pass of Hurricane Wilma, whereas aboveground forest canopy in the late-seral stage remained significantly reduced throughout the study. Moreover, this study also shows that constraints in aboveground recovery may be coupled to changes in belowground processes. In the late-seral stage, there appears to be a negative feedback among defoliation, fine roots, and soil nitrogen that, in part, may help explain the arrested regeneration of aboveground forest canopy. Immediately after Hurricane Wilma, we observed a significant increase in canopy openness and a short-term pulse in soil nitrogen availability. We also observed a significant reduction in fine roots, which may have prevented trees from absorbing the pulse of soil nutrients after the hurricane, and as a result soil

nitrogen was lost from the system through leaching and denitrification. Consequently, nitrogen availability may in turn limit aboveground productivity producing a feedback of reduced photosynthates for belowground processes such as fine root production. In contrast, because of the high proportion of legume species in the early- and mid-seral stages, nitrogen does not appear to be limiting aboveground productivity and recovery in these forests.

Across the Northern Yucatan Peninsula natural disturbances, human activities, and environmental gradients continue to interact in a complex and dynamic fashion. Over the past 50 years there has been an increase in the number of category III or greater hurricanes on the Northern Yucatan Peninsula (Boose et al. 2003). Although the recovery of forest structure is commonly thought to be relatively rapid following a hurricane disturbance (Chazdon 2003), future ecological research and management policies in seasonally dry tropical forests must address site history as well as belowground mechanisms influencing the recovery of aboveground forest structure after a large, infrequent disturbance.

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