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The Impacts of a Large Hurricane on Understory Sapling Dynamics and Diversity in North Carolina Piedmont Forests, USA

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ABSTRACT

We analyzed population dynamics and changes in species diversity and composition of saplings (tree or shrub stems >50 cm in height and < 1 cm diameter at breast height) during an interval lasting from 5 years before the 1996 Hurricane Fran to 5 years post-hurricane through use of permanent transects where individual sapling stems were censused annually. The study site was the Duke Forest, located in the Piedmont plateau, North Carolina, USA. We hypothesized that understory sapling dynamics are significantly influenced by canopy tree damage caused by the large, infrequent hurricanes, through enhanced recruitment of light-demanding species and increased growth rates of established saplings. Our results showed that sapling damage by Hurricane Fran was largely secondary (i.e. 44-70% of damaged saplings were pinned to the ground by falling parts of large neighbor trees). All survey transects experienced decreased sapling density as a result of increased mortality. The average mortality rate of saplings nearly doubled, increasing from 7.04 ± 3.98% to 13.22 ± 5.71%. Although the changes in sapling density were dramatic, species diversity of saplings remained relatively stable or decreased slightly due to the hurricane-induced damage. Large gaps created by the hurricane resulted in the release of established, shade-intolerant or mid-tolerant saplings. We conclude that large, infrequent windstorms appear to be responsible for temporal and spatial variation in understory regeneration.

Keywords: advanced growth, canopy disturbance, forest dynamics, Piedmont forests, understory heterogeneity

INTRODUCTION

The importance of windthrow for temperate forest regeneration has been emphasized in several previous studies (e.g., Finzi and Canham 2000; Xi *et al*. 2008; Xi and Peet 2008), and intensive windstorms have been hypothesized to influence species composition and diversity through enhanced understory recruitment, establishment, and growth (Peet and Christensen 1980a; see review by Webb 1999, Xi and Peet 2011). Nonetheless, to date few studies have explicitly investigated understory response to major wind-induced canopy disturbance as ecologists and foresters have rarely had available the combination of long-term pre- and post-wind disturbance data on plant establishment, growth, and mortality necessary for definitive assessment of change in populations. In 1996, Hurricane Fran, a large, category-3 hurricane, significantly damaged the forest canopy above many long-term census plots in the Duke Forest of Piedmont, North Carolina, USA. The occurrence of Hurricane Fran provided a rare opportunity to examine the impacts of a major wind event on a series of forest sites for which pre- and post-disturbance data on tree dynamics were available.

We analyzed changes in the composition and diversity of saplings over an interval lasting from 5 years prior through 5 years post Hurricane Fran. A sapling in this study was defined as any tree or shrub stem > 50 cm in height and < 1 cm diameter at breast height (dbh). The first goal of this study was to examine whether large canopy disturbances increase understory sapling diversity and alter their population structure and dynamics. Our general hypothesis was that major canopy disturbances enhance understory recruitment of the more light-demanding species due to increased resource availability. The second goal was to examine the impacts of large-scale hurricanes on sapling growth patterns. We hypothesized that large gaps created by Hurricane Fran would result in the release of established, shade-intolerant or mid-tolerant saplings in the damaged forests. By taking advantage of the fortuitous availability of detailed, long-term pre- and post-hurricane sapling demographic data, we were able to examine the extent of increased growth and the degree of difference among species in response to large, hurricane-induced canopy openings.

In previous papers we have examined the changes in forest structure, species diversity and spatial pattern of trees (dbh >1 cm) following hurricane disturbance (Xi and Peet 2008; Xi *et al*. 2008). In this paper, we focus on the understory saplings and address the following questions: (1) How did understory sapling stem density, mortality, and recruitment change after a major canopy disturbance event? (2) Did this event enhance sapling species diversity? (3) Did growth rates of saplings increase after the event? (4) Which saplings have increased in understory density, and how were the rates of establishment modified? (5) Did the understory saplings assemblage become less consistent in species composition after the large hurricane disturbance?

MATERIALS AND METHODS

Study site

This study was conducted in the Duke Forest (35°53'-36°12' N, 78°54'-79°03'), located near the southeastern edge of the Piedmont Plateau in Orange and Durham Counties, North Carolina, USA. Elevation ranges from 85 to 250 m above sea level. The annual

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average temperature is around 15°C. Precipitation averages about 1120 mm annually and is well distributed across the year. The natural vegetation in this region belongs to the oak-pine forest group of Braun (see Martin *et al*. 1993; Peet and Christensen 1980b). Varied topography, moderate climate and the complex disturbance history support vegetation composed of a diversity of plant species and forest types. Over 100 species of trees have been identified (Palmer 1990) in the 3500 ha Duke Forest. The major current forest cover types are successional pine forest and uneven-aged oak-hickory forest. Most of the current pine stands are the result of reversion from past farmland abandonment, and loblolly pine (*Pinus taeda*) is the dominant pine species in forests of this type. The hardwood forests are mostly uneven-aged, secondary stands with composition that reflects soil type, topographic position and past disturbance. The dominant hardwood species include red oak (*Quercus rubra*), white oak (*Q. alba*), mockernut hickory (*Carya alba*), pignut hickory (*C. glabra*), shagbark hickory (*C. ovata*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*), sweetgum (*Liquidambar styraciflua*), tuliptree (*Liriodendron tulipifera*), and hophornbeam (*Ostrya virginiana*). More detailed descriptions of site conditions, community types, and forest succession can be found in previous research papers for this area (e.g., Peet and Christensen 1980b; McDonald *et al*. 2002; Xi and Peet 2008; Xi *et al*. 2008).

Field work and data

A set of long-term sapling transects (50 × 4 m), with individual sapling stems mapped and censused annually, were established throughout the Duke Forest in the late 1980s as part of a long-term forest dynamics project. Those transects cross the normal range of spatial variation in forest composition in the Duke Forest, and are within four large, mapped forest stands that represent mature, mixed-aged hardwood forests (both dry-mesic upland hardwood forest and moist, semi-alluvial lowland hardwood forest) and transition-phase loblolly pine stands. Specifically, the Graveyard plot and the Land's end plot represent the transition phase of older (*ca*. 80-100 years) but even-aged pine forest stands with a hardwood understory (**Fig. 1**), whereas the Bormann and Rocky plots represent the 'steady-state' phase of mixed-aged, upland deciduous hardwood forest. The four mapped forest stands were substantially damaged by Hurricane Fran in 1996 and are representative of damaged areas in the Duke Forest (Xi and Peet 2008; Xi *et al*. 2008).

The sapling census was generally conducted between the middle of May and the end of July of each year. For each sapling in each survey, a condition code from 1 to 5 was assigned to each sapling individual: 1 = alive and reasonable normal, 2 = dead, 3 = missing, 4 = significant loss in height, 5 = severely damaged. Natural sapling height (the distance between the terminal bud and the ground directly below it) and stem diameter at breast height (dbh) were recorded. The census contents also included sprouts, ingrowths and sapling loss (stems of dead, missing, or growing out of the size range, i.e., a living stem > 1 cm in dbh which by definition had thus grown out of the sapling category). Sprouts were not mapped unless they were actually rooted in the soil. Where multiple sprouts had grown from the same genetic individual (i.e. clones) but were not rooted separately, only the tallest was mapped and the others were considered as branches. If a clump of clones had the largest stem > 1 cm in dbh, then new individuals from this clump were not recorded for ingrowth. In the summer of 1997, the first growing season following Hurricane Fran, hurricane damage status for each sapling individual stem in the transects was quantified with four ordinal stem damage codes representing uprooting, breakage, leaning, and leaned on (i.e., bent or leaning or pinned by large tree neighbors or their parts). Botanical nomenclature follows USDA Plants v 4.0 (USDA 2009).

From the complete dataset, we extracted a total of 13 intensively-mapped transects within four mapped forest stands in the Duke Forest (**Table 1**). These transects include annually records of saplings for 5 years pre-Fran (1990-1994) and 5 years post-Fran (1997-2001). In 2001, there were in total 1785 saplings in the selected sapling transects (**Table 2**).

These times-series data of saplings spanning the 1996 Hurricane Fran event and representing a diversity of sites and stand

Fig. 1 Large windstorm disturbances appear to be responsible for temporal and spatial variation in understory regeneration, which contributes to a diverse but temporally relatively stable canopy layer. Large canopy disturbances can, to a certain extent, promote local tree species diversity in the understory of temperate Piedmont forests as a result of colonization by new, light-demanding species. This 2000 photograph shows the diverse understory habitat and the sapling regeneration in the Graveyard plot of the Duke Forest four years after Hurricane Fran (Photo by Weimin Xi).

Fig. 2 The 1996 Hurricane Fran created various sizes of forest canopy gaps that greatly increased understory light. This hemispherical (fish-eye) photograph shows a hurricane-induced forest gap in the Graveyard plot of the Duke Forest. The hemispherical photograph was taken using an 8 mm f2.6 fish-eye Nikon (FC-E8) lens (183° of angle of view) with a Nikon digital camera (Coolpix 995) at height of 1.8 m at predawn in the summer of 2001 (Photo by Weimin Xi).

Table 1 The characteristics of the 13 selected sapling transects in the Duke Forest, North Carolina, USA.

Forest type	Stand name	Number of transects	Transect size	Survey period
Loblolly pine stands	Graveyard	4	50 × 4 m	1989-2001
	Land's end	3	50 × 4 m	1989-2001
Mixed-aged hardwoods	Bormann	3	50 × 4 m	1989-2001
	Rocky	3	50 × 4 m	1989-2001
Total		13	2600 m^2	

Table 2 Sapling sampling size for 13 selected major taxa in two loblolly pine plots (Graveyard and Land's end) and two mixed-aged hardwood stands (Bormann and Rocky) in the Duke Forest, North Carolina, USA.

			Number of sapling in 2001			
Species	**Code**	**Family**	**Graveyard**[a]	**Land's end**[b]	**Bormann**[b]	**Rocky**[b]
Acer rubrum	ACRU	Aceraceae	97	41	101	24
Carpinus caroliniana	CACR	Betulaceae	42	0	0	0
Carya spp.	CARY	Juglandaceae	1	40	26	68
Cercis canadensis	CECA	Fabaceae	1	27	0	13
Fraxinus spp.	FRAX	Oleaceae	2	21	1	46
Liquidambar styriciflua	LIST	Hamamelidaceae	5	2	1	0
Liriodendron tulipifera	LITU	Magnoliaceae	0	0	7	0
Nyssa sylvatica	NYSY	Nyssaceae	0	2	3	1
Ostrya virginiana	OSVI	Betulaceae	132	67	0	1
Pinus spp.	PINU	Pinaceae	1	0	0	0
Prunus serotina	PRSE	Rosaceae	19	12	4	14
Quercus alba	QUAL	Fagaceae	6	10	0	7
Quercus red group	QURG	Fagaceae	3	0	4	6
Ulmus spp.	ULMU	Ulmaceae	1	4	1	1
Others			266	375	123	140
Total			592	601	271	321

[a] The total sample area in the Graveyard plot is 800 m^2 for saplings.
[b] The total sample area in other three plots (Land's end, Bormann, and Rocky) is 600 m^2 for saplings, respectively.

ages allows examination of both immediate and longer-term changes in sapling dynamics in stands that vary in site conditions and stage of successional development.

Quantifying forest canopy disturbance

The degree of canopy openness (percentage of open sky seen beneath the canopy) was determined for each transect by using a series of hemispherical photographs taken along transect at 4-m intervals. The hemispherical photographs were taken using an 8 mm f2.6 fish-eye Nikon (FC-E8) lens (183° of angle of view) with a Nikon digital camera (Coolpix 995) at a height of 1.8 m for saplings in the summer of 2001 (**Fig. 2**). All the photographs were taken at predawn or post sunset, when no direct sunlight was visible, or on days with evenly overcast sky. In total 507 hemispherical photographs were taken along these transects. The photographs were then analyzed by using the Gap Light Analyzer (GLA, version 2.0), a computer program that computes forest canopy structure attributes including canopy openness (CO), effective leaf area index (LAI), sunfleck frequency distribution and daily duration, and the amount of above- and below-canopy transmitted direct, diffuse, and total solar radiation incident on a horizontal or arbitrarily inclined receiving surface. These data were then used with available sapling population data to examine the effect of forest canopy disturbance intensities on sapling diversity and growth.

Statistical analyses

The sapling census data were used to calculate species richness, species diversity, annual rates of mortality and recruitment. The sapling species richness was defined as the number of woody species present per transect (i.e., per 200 m^2). The Shannon-Wiener index (*H'*) was used to assess species diversity ($H' = - \Sigma p_i \log_e p_i$ where p_i = the proportion of the individuals in the i^{th} species; Peet 1974).

Two common parameters of annual growth rates in height were calculated for saplings. Annual growth increment (*GI*) was calculated as the change in height between two consecutive years (year *i* and year *i+1*) following the formula $GI = (H_{ti+1}-H_{ti})$, whereas relative growth rate (*RGR*) was calculated as the height increment between two consecutive years (year *i* and year *i+1*) rescaled by initial height following the formula $RGR = (H_{ti+1}-H_{ti}) / H_{ti}$ (Xi and Peet 2008). While *GI* represents absolute annual growth increment of a sapling, *RGR* for this analysis is used for removing the effect of plant size and thereby exposing the effects of other major factors on stem growth (e.g., light).

Nonparametric statistical procedures were employed to examine the disturbance effects of the hurricane on tree seedling population dynamics and analyze the changes in sapling composition and diversity. The Wilcoxson ranked test was used to examine whether the changes in relative growth increase, stem density, and tree diversity were significant.

We also examined the effects on sapling recruitment and growth of canopy disturbance intensity (CO, which ranges from 0 for complete obstruction to 100% for open sky). The value of CO of each sub-block (4 × 4 m in size) was used to represent the canopy disturbance intensities. The measured variables (Diversity versus CO or RGR versus CO) were first presented as means, and then were examined using linear regression (PROC REG, SAS 9.1, SAS Inc. 2003).

Compositional patterns and trends were assessed with Non-metric Multidimensional Scaling (NMDS) using PC-ORD 4 (McCune *et al*. 2002). All 13 sapling transects with data from 1990-2001 were used to assess the change in composition and relationships between different forest stands at the transect-level. Ordinations of the multiple transect measurements over time allowed examination of plot trajectories in ordination space and patterns of community change (McCune *et al*. 2002).

RESULTS

Hurricane-induced understory sapling damage and mortality

The impact of canopy damage by Hurricane Fran resulted in a significant amount of secondary mechanical damage to the understory saplings. The damage of sapling stems appeared mainly to be caused by their large, upper-canopy-layer neighbors. As **Fig. 3** shows, 44-70% of damaged sapling stems were pinned by their large neighbor trees, suggesting that hurricane damage on understory was largely secondary damage.

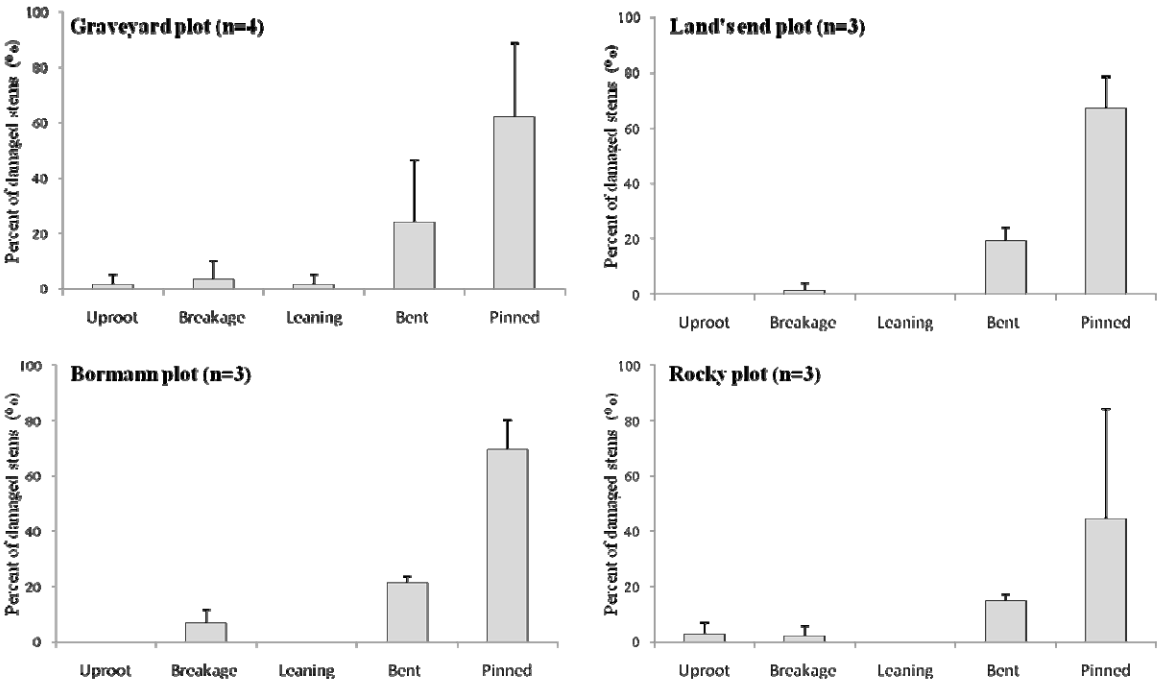

Fig. 3 Damage type frequency observed in the saplings in the four forest stands in the Duke Forest, North Carolina, USA. (**A**) Graveyard plot (n=4), (**B**) Land's end plot (n=3), (**C**) Bormann plot (n=3), and (**D**) Rocky plot (n=3). The error bars are standard errors, and 'n' is the number of transects in a forest stand. Damage percentage refers the proportion of a damage type in all damaged stems.

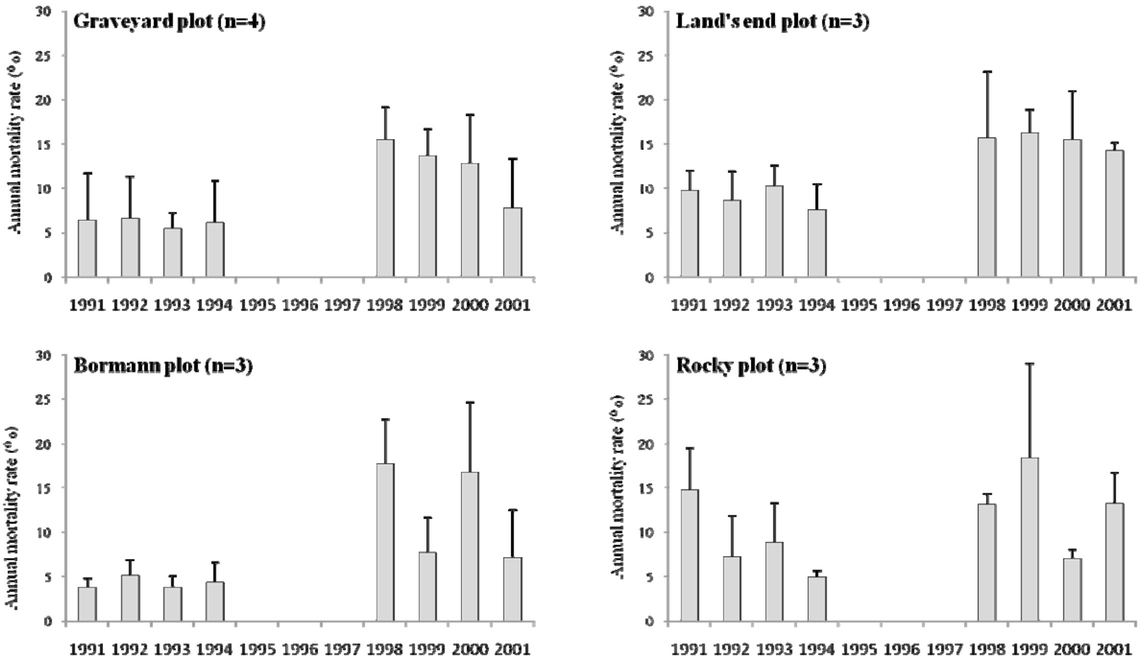

Fig. 4 Annual sapling mortality rates (%) for four stands in the 4 forest stands in the Duke Forest, North Carolina. (**A**) Graveyard plot (n=4), (**B**) Land's end plot (n=3), (**C**) Bormann plot (n=3), and (**D**) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. 'n' is the number of transects in a forest stand.

Understory saplings experienced significantly higher mortality rates following the hurricane as compared to their pre-hurricane background mortality (**Fig. 4**). The average mortality rate of saplings (5-year average for all sapling transects) nearly doubled, increasing from (mean ± Standard Deviation, SD) 7.04 ± 3.98% to 13.22 ± 5.71%. The increase in mortality rate varied among the four forest stands, increasing from (mean ± SD) 7.39 ± 3.64% to 13.70 ± 4.86% for the pine stands and from 6.63 ± 4.39% to 12.66 ± 6.62% for the mixed hardwood stands.

Increased sapling mortality was not a one-time event, but rather was sustained for several years following Hurricane Fran. In all four forest stands we surveyed, sapling mortality was elevated over background not just immediately following the hurricane, but also for the five-year monitoring period following the windstorm event. The year-to-year change of hurricane-induced sapling morality was also different between forest types. In the pine forests, sapling mortality peaked in 1998 or 1999 (**Fig. 4**), whereas in mixed hardwood forest, there was relative high sapling mortality in 1998 or 1999, but less consistency in the decline in mortality.

Change in understory sapling richness and diversity

Although Hurricane Fran greatly reduced understory stem density, it had only a modest impact on species richness and

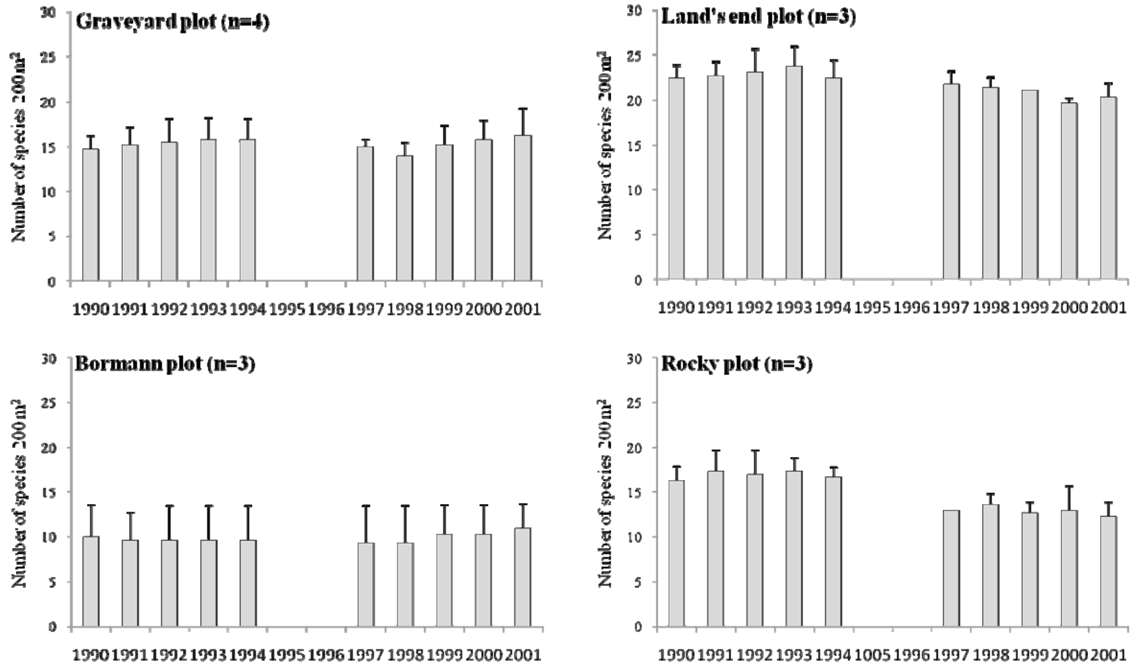

Fig. 5 The species richness of saplings in the 4 forest stands in the Duke Forest, North Carolina, USA. (**A**) Graveyard plot (n=4), (**B**) Land's end plot (n=3), (**C**) Bormann plot (n=3), and (**D**) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. 'n' is the number of transects in a forest stand.

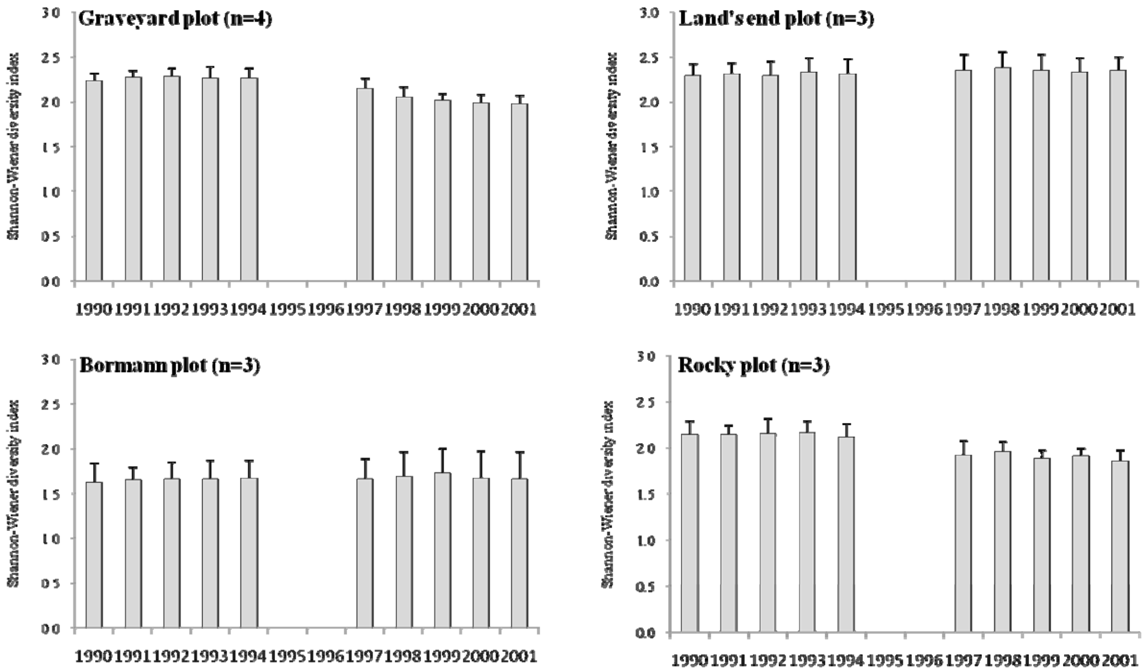

Fig. 6 The species diversity of saplings in the 4 forest stands in the Duke Forest, North Carolina, USA. (**A**) Graveyard plot (n=4), (**B**) Land's end plot (n=3), (**C**) Bormann plot (n=3), and (**D**) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. 'n' is the number of transects in a forest stand.

diversity. Sapling richness (**Fig. 5**) and diversity (**Fig. 6**) were relatively stable over the course of the study. Two of the plots (Graveyard and Rocky plots) slightly decreased in diversity compared to their pre-disturbance level ($p<0.05$).

Effects of the hurricane on sapling recruitment

Post-hurricane sapling recruitment was general higher than pre-hurricane (**Fig. 7**), in large part due to enhanced growth of the larger saplings, as well as increased sprouting from damaged tree stems. Compared to pre-hurricane recruitment, Hurricane Fran resulted in increased rates of sapling recruitment. In the Duke Forest, sapling ingrowth was largely from advanced growth and sprouting played a relatively minor role in forming the new sapling cohorts. In the Graveyard pine plot, sapling recruitment rates were about the same as pre-hurricane level in the first and second years, but significantly higher in 1999-2001 reaching levels 2-3 fold those of pre-hurricane. In the other pine stand, the ingrowth rate was higher than pre-hurricane 1994, although appeared lower than other pre-hurricane years such as 1990 and 1991 when there was a surprisingly high level of sapling recruitment. In the two hardwood plots, increases in sapling recruitment were significant with high year-to-year variance. However, we found that sprouting was more common for some light-demanding tree species such as the tuliptree and sweet gum. The net results from these combined responses were that one pine forest stand had sig-

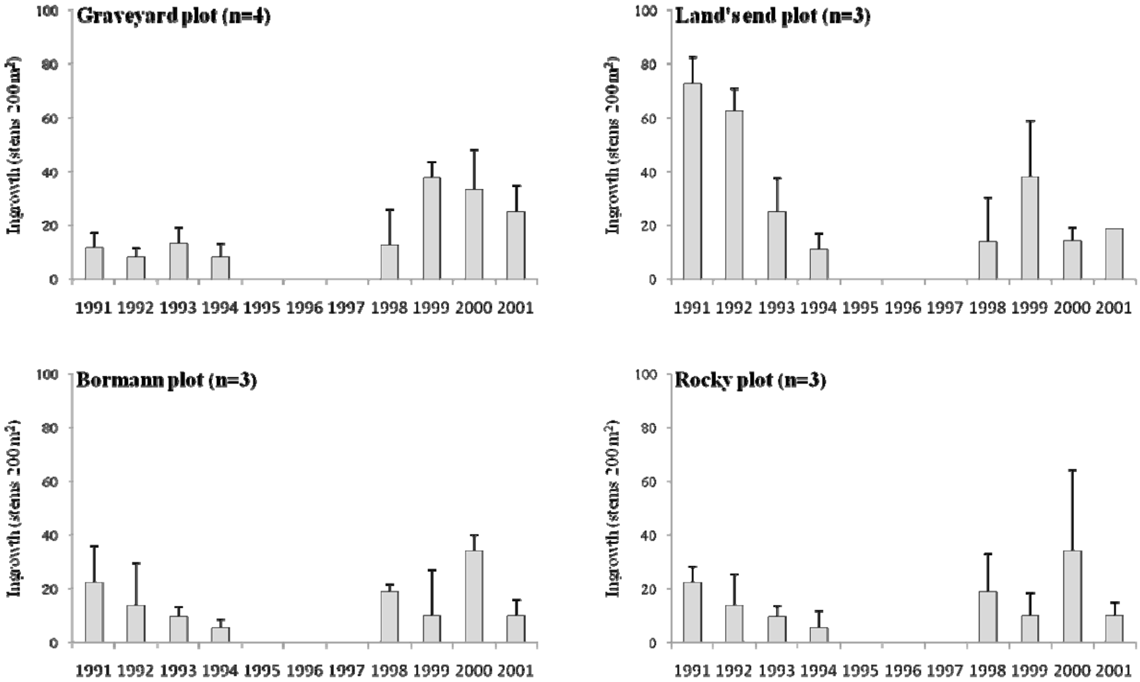

Fig. 7 Sapling ingrowths in the 4 forest stands in the Duke Forest, North Carolina, USA. (**A**) Graveyard plot (n=4), (**B**) Land's end plot (n=3), (**C**) Bormann plot (n=3), and (**D**) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. 'n' is the number of transects in a forest stand.

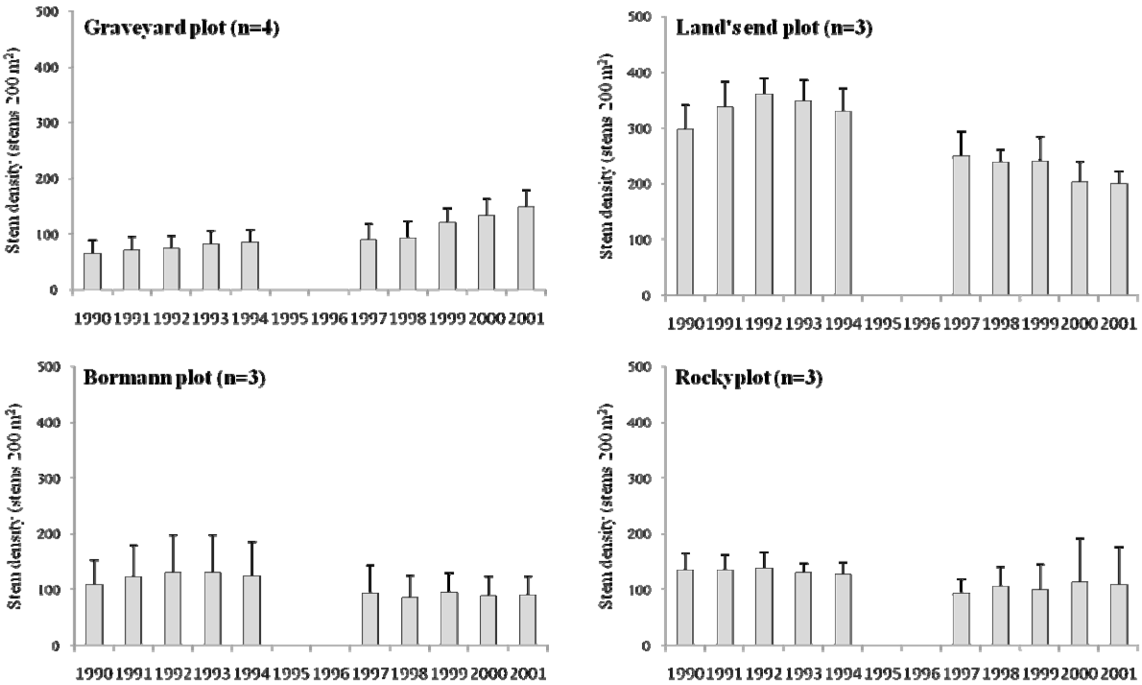

Fig. 8 The stem density of saplings in the 4 forest stands in the Duke Forest, North Carolina, USA. (**A**) Graveyard plot (n=4), (**B**) Land's end plot (n=3), (**C**) Bormann plot (n=3), and (**D**) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. 'n' is the number of transects in a forest stand.

nificantly increased sapling stem density after the hurricane, whereas the sapling stem density in the other three stands decreased (**Fig. 8**).

Effects of the hurricane on understory sapling growth

We found significant but varied sapling releases across the damaged understories after the hurricane. Prior to Hurricane Fran, saplings grew at very slow rates due to the canopy tree suppression and light limitation. Post-hurricane relative growth rates of saplings increased significantly (**Fig. 9**). The higher growth rates were generally maintained for one to two years before gradually decreasing. In one loblolly pine stand, sapling growth was higher in the fourth year than in the first year, suggesting small-scale multiple release.

We found a mixed relationship between light intensity and growth rates after Hurricane Fran at the sub-transect scale (i.e., 4 × 4 m sub-plot, the data and figs were not shown due to space limitation). The growth rates were weakly correlated with light intensity, but the relationship was not significant. The relationship between growth and canopy openness was negative in the two loblolly pine stands, whereas it was positive in one of the hardwood stands.

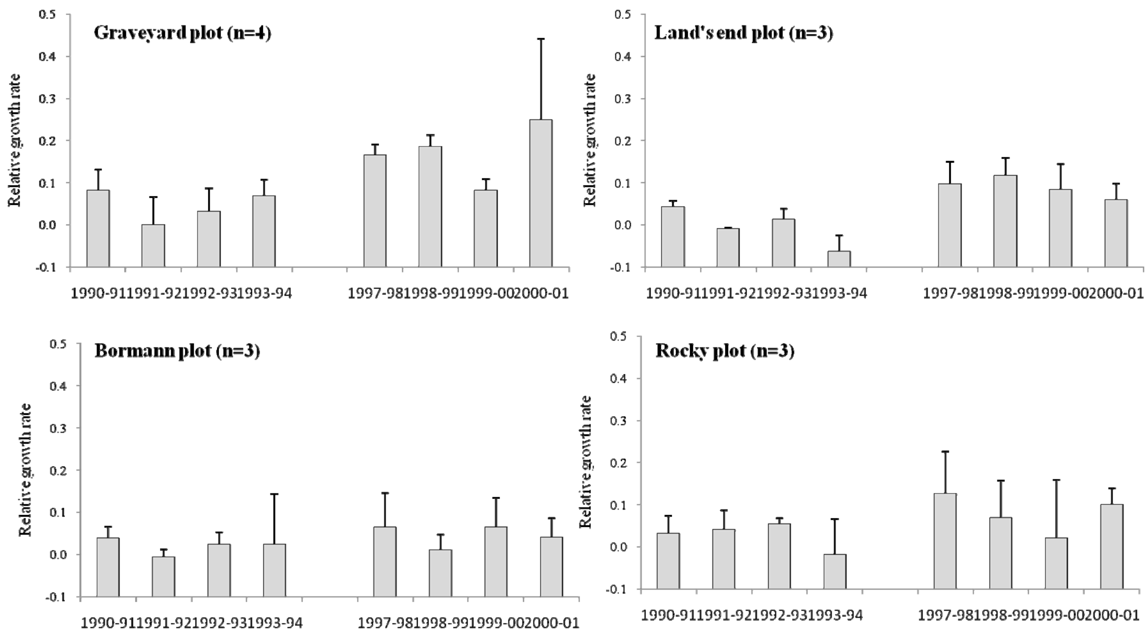

Fig. 9 Sapling relative growth rates in the 4 forest stand in the Duke Forest, North Carolina, USA. (**A**) Graveyard plot (n=4), (**B**) Land's end plot (n=3), (**C**) Bormann plot (n=3), and (**D**) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. 'n' is the number of transects in a forest stand.

Hurricane influence on understory tree species composition

The successional trajectory in composition of saplings over the 11-year observation period in ordination space (i.e., 5 years prior to Hurricane Fran and 5 years after) is shown in **Fig. 10** using the intervals 1990-94, 1994-97, and 1997-2000. NMDS indicated that the composition of saplings in the transects changed substantially for each of the three intervals. Transects within a forest plot were generally consistent in trajectory for a given interval, but the direction of change was significantly altered with stand recovery from the Hurricane (1997-2000). Some light-demanding tree species (e.g., tuliptree, sweetgum) showed increased ingrowth. But overall Hurricane Fran led to an increase in shade-intolerant species. The shade intolerant species, in most cases, are only represented by a few individuals, and may soon be lost through competition. For example, in several transects tuliptree was quite abundant soon after canopy disturbance, but they had vanished 5 years after the hurricane. This reconfirms the importance of examining long-term pre- and post-disturbance data when assessing the impacts of major disturbance events.

DISCUSSION

The effects of canopy disturbance on damage and mortality of saplings

The data we present here show that understory damage and mortality were variable among forest types and species, and post-damage growth responses of saplings varies in time and space as well. In the heavily-disturbed forests, understory sapling regeneration is complex due to uneven availability of light and the differences among tree species in response to the heterogeneous canopy openings.

Nonetheless, some patterns are evident. Consistent with a few studies of the roles of canopy damage by large hurricanes on sapling mortality in disturbed forests, canopy damage by winds increased mortality of saplings in the first two years after the hurricane (e.g., Finzi and Canham 2000; Walker 2000).

In the Duke Forest, mortality of saplings of many species remained high 5 years after the canopy disturbance, but so did relative growth rate, perhaps more than compensating and leading to an overall increase in potential contribution to future canopy composition. We expect that the increased spatial heterogeneity in the upper canopy has strong influences on tree species diversity, survivorship, abundance, growth, and spatial arrangement within the understory layers, and is likely to affect the future structure and dynamics of the damaged forests.

Change in understory diversity induced by canopy damage

Results from this study only partially support observations from other hurricane damage studies showing that major canopy damage could increase tree diversity (e.g. Vandermeer *et al.* 2000). The census sapling plots in our study experienced an immediate drop in density and species richness due to high mortality in established saplings and limited recruitment in the first post-disturbance growing season.

Effects of hurricane damage on sapling growth rates

It has long been recognized that growth rates of understory tree species may increase after canopy gap creation due to increased light resource availability (Brown 1996; Brown *et al*. 1999). However, subtle year-to-year variation in growth has received little attention. In this study, we found large gaps created by Hurricane Fran resulted in release of established saplings with higher growth of plant saplings. Canopy damage increased the overall understory growth rate by a factor of 2 (**Fig. 9**), and the increased rates tended to consistently decrease toward baseline levels over time.

The regenerative capacity of Piedmont forests as represented by the Duke Forest was limited. This study of the damaged sites confirms that regeneration after hurricanes results from a reproductive and growth response to the temporary increase in resource availability. Together, these lead to rapid regrowth of damaged vegetation. The major biological effects of hurricane damage are to promote and synchronize regeneration and growth mechanisms.

Importance of understory dynamics in Piedmont forests

The understory plays a major part in Piedmont forest response to canopy disturbance by windstorms. The success of hurricane-induced establishment and growth into the sap-

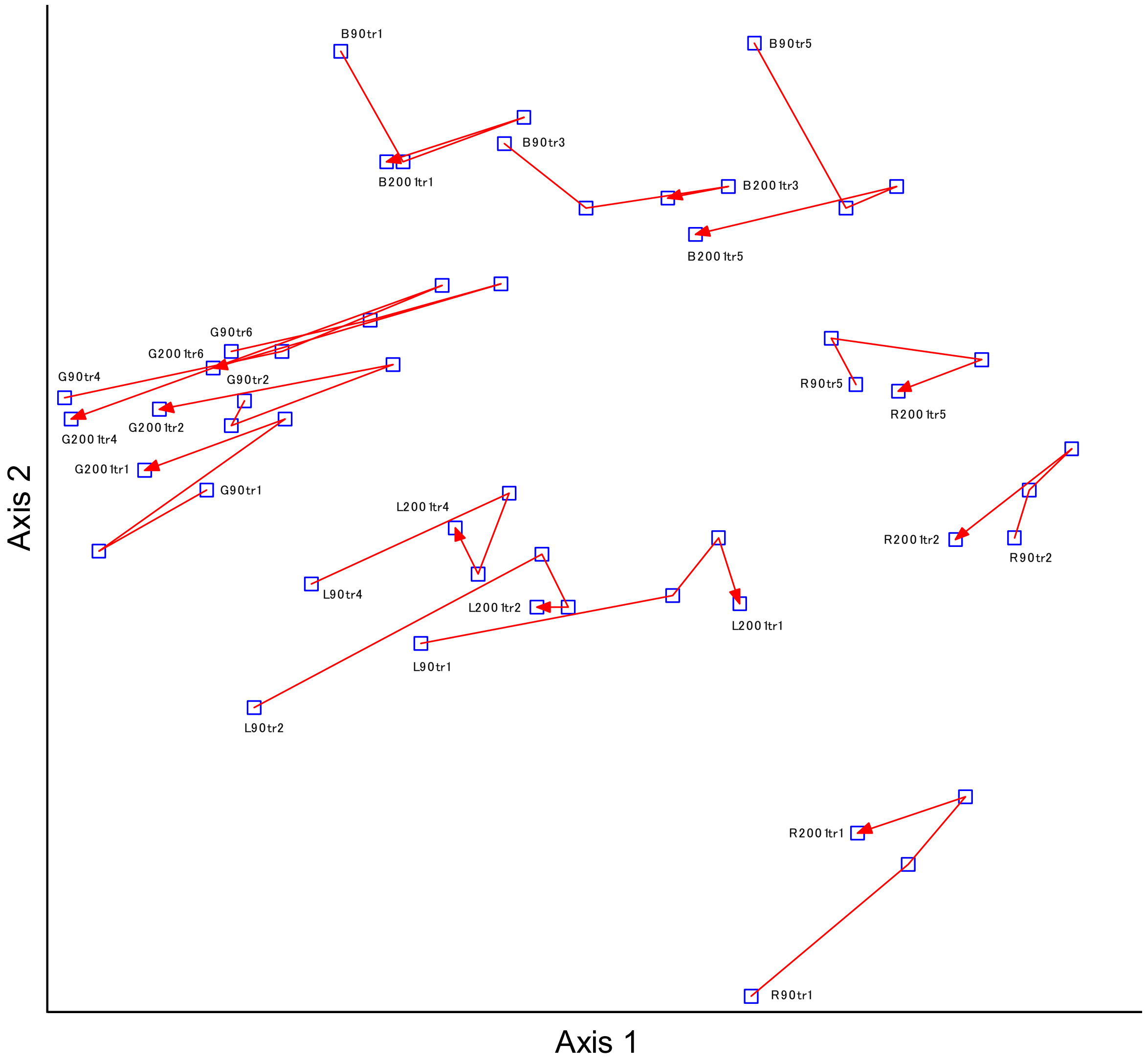

Fig. 10 Non-metric Multidimensional Scaling (NMDS) ordination of 7 even-aged pine sapling transects and 6 mixed-aged sapling transects in Duke Forest measured pre-Hurricane Fran (1990 and 1994) and post-Hurricane Fran (1997 and 2001). Empty squares are the transect locations on first and second axes of NMDS ordination. 'n' is the number of transects in a forest stand. G, L, B and R refer to the Graveyard, Land's end, Bormann and Rocky plots respectively. The sequences start at 1990 ('90'), progress through 1994 and 1997, and end with 2000 ('200').

ling layer, and then growth from the sapling layer into the midstory layer following major canopy disturbances, is crucial for forest regeneration, especially when natural regeneration is otherwise limited for important canopy species. In some cases the shade-intolerant saplings likely to benefit from death of canopy trees continue to shade the forest floor and limit establishment of the light-demanding species with the consequence that in tree gaps there may be an absence of pioneer species.

Several studies in the tropical forests have supported the hypothesis that wind damage could contribute significantly to tree species diversity (e.g., Vandermeer *et al*. 2000). The theory suggests that removal of canopy trees releases shade-intolerant species that benefit from increased resource availability and causes relaxation of competition among species. Under this theory, forest composition and dynamics are strongly dependent on intensity, size and frequency of disturbances. Species richness is greatest in a community experiencing some intermediate level of disturbance, which is consistent with the widely-accepted hypothesis that disturbances promote the coexistence of species having different resource use strategies and dispersal and competitive abilities (e.g., Pacala *et al*. 1994).

We did not find significant evidence to support Connell's intermediate disturbance hypothesis in that we failed to find a consistent relation across the entire sapling transect dataset. The intermediate disturbance hypothesis states that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent (Connell 1978; Roxburgh *et al*. 2004). Given the slow rate of establishment and growth of seedling in these Piedmont forests, we expect that if support is to be found for Connell's hypothesis, another 5-10 years will be required for it to be evident in the sapling layer. Sapling regeneration following large canopy disturbance does provide an indication as to the direction that forest succession will take and the potential importance of wind disturbance for the regeneration of canopy species.

CONCLUSIONS

Our previous research on hurricane damage and forest dynamics in Piedmont forests suggests a trend toward accelerated loss (characterized by high mortality and low recruitment) of pines in the region, even in those significantly damaged stands with increased light (Xi *et al*. 2008). This study shows that understory sapling populations are highly dynamic and in a continuous state of flux and regeneration, even without major canopy disturbance. Overall, the effects of the hurricane disturbance on the understory are variable among forest types, sites, species, stem sizes, and depend upon both hurricane damage intensity and pre-hurricane understory characteristics. Clearly, hurricanes have distinct effects on the understory through alteration of the light regimes and other micro-site conditions, but the effects of a hurricane are mostly secondary. The most distinctive impacts of intensive canopy disturbance were that the hurricane immediately reduced understory density, at least over 5 years, and resulted in an increase of understory growth rates. The intensity of canopy disturbance is weakly related to the degree of change in density and diversity. Consequently, the mortality of understory saplings after the storm was generally higher. This information is particularly important for predicting changes in species composition, community structure, and tree diversity of the Piedmont forests, where the regeneration of the dominant canopy species is often limited.

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REFERENCES

Brown ND (1996) A gradient of seedling growth from the center of a tropical rain forest canopy gap. *Forest Ecology and Management* **82**, 239-244

Brown N, Press M, Bebber D (1999) Growth and survivorship of dipterocarp seedlings: Differences in shade persistence create a special case of dispersal limitation. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences* **354**, 1847-1855

Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302-1310

Finzi AC, Canham CD (2000) Sapling growth in response to light and nitrogen availability in a southern New England forest. *Forest Ecology and Management* **131**, 153-165

Guariguata MR (1998) Response of forest tree saplings to experimental mechanical damage in lowland Panama. *Forest Ecology and Management* **102**, 103-111

McCune B, Grace JB, Urban DL (2002) *Analysis of Ecological Communities*, Mjm Software Design, Gleneden Beach, OR, USA, 304 pp

McDonald RI, Peet RK, Urban DL (2002) Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea* **67**, 84-95

Pacala SW, Canham CD, Silander JA, Kobe RK (1994) Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* **24**, 2172-2183

Peet RK (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics* **5**, 285-307

Peet RK, Christensen NL (1980a) Succession: A population process. *Vegetatio* **43**, 131-140

Peet RK, Christensen NL (1980b) Hardwood forest vegetation of the North Carolina piedmont. *Veröff. Geobot. Inst. ETH Stiftung Rübel* **69**, 14-39

Roxburgh SH, Shea K, Wilson JB (2004) The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology* **85**, 351-371

Runkle JR, Stewart GH, Veblen TT (1995) Sapling diameter growth in gaps for two *Nothofagus* species in New Zealand. *Ecology* **76**, 2107-2117

SAS Institute Inc (2003) SAS/STAT Software, Version 9.1. Cary, NC. URL http://www.sas.com/

USDA NRCS (2011) The PLANTS Database (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA 70874-4490 USA

Vandermeer J, Cerda IGDL, Boucher D, Perfecto I, Ruiz J (2000) Hurricane disturbance and tropical tree species diversity. *Science* **290**,788-791

Walker LR (2000) Seedling and sapling dynamics of treefall pits in Puerto Rico. *Biotropica* **32**, 262-275

Webb SL (1999) Wind disturbances in temperate forests. In: Walker LR (Ed) *Ecosystems of Disturbed Ground*, Elsevier, New York, NY, pp 245-289

Welden CW, Hewett SW, Hubbell SP, Foster RB (1991) Sapling survival, growth, and recruitment - relationship to canopy height in a neotropical forest. *Ecology* **72**, 35-50

Xi W, Peet RK, Urban DL (2008) Changes in forest structure, species diversity, and spatial pattern following hurricane disturbance in a Piedmont North Carolina forest, USA. *Journal of Plant Ecology* **1**, 43-57

Xi W, Peet RK (2008) Hurricane effects on the Piedmont forests: Patterns and implications. *Ecological Restoration* **26**, 295-298

Xi W, Peet RK (2011) The complexity of catastrophic wind impacts on temperate forests. In: Lupo A (Ed) *Recent Hurricane Research - Climate, Dynamics, and Societal Impacts*, pp 503-534