

FOREST RESPONSE TO NATURAL DISTURBANCE: CHANGES IN STRUCTURE
AND DIVERSITY ON A NORTH CAROLINA PIEDMONT FOREST
IN RESPONSE TO CATASTROPHIC WIND EVENTS

Weimin Xi

A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology.

Chapel Hill
2005

Approved by:

Advisor: Professor Robert K. Peet

Reader: Professor Peter S. White

Reader: Professor Seth R. Reice

Reader: Professor Dean L. Urban

Reader: Professor Aaron Moody

© 2005
Weimin Xi
ALL RIGHTS RESERVED

ABSTRACT

WEIMIN XI: Forest response to natural disturbance: Change in structure and diversity on a North Carolina Piedmont forest in response to catastrophic wind events
(Under the direction of Dr. Robert K. Peet)

Large hurricanes have profound impacts on temperate forests, but owing to their infrequent nature these effects rarely have been examined in detail. In 1996 Hurricane Fran significantly damaged many long-term census plots in Duke Forest in Piedmont North Carolina, thereby providing a unique research opportunity. I combined over 20 years of pre-hurricane and five years of post-hurricane data on individual trees, seedlings and saplings to determine how hurricanes affect forest structure, diversity, and succession. Several plots severely damaged in 1954 by Hurricane Hazel allowed comparison of recovery patterns and evaluation of long-term effects.

I first assessed hurricane-induced structural and compositional changes and evaluated mortality risk factors. Fran caused widespread uprooting of large canopy trees. Stand-level damage severity varied substantially across the distributed network of permanent plots. Hurricane-induced mortality of large-size hardwoods was often delayed. Although tree damage was primarily caused by winds and rainfall, damage was also found to be correlated with site exposure, topographical position, tree size, and species susceptibility to wind.

Next, to test the hypothesis that hurricanes maintain local tree diversity through increased heterogeneity and resource availability I examined changes in understory survivorship, recruitment, and growth. The understory experienced highly variable

population impacts as well as subtle changes in tree diversity. Following Fran both seedlings and saplings exhibited an immediate drop in stem density followed by a rebound. In addition, the hurricane resulted in release of established, shade-intolerant or mid-tolerant seedlings and saplings, thereby potentially increasing future canopy tree diversity.

Finally, I assessed whether hurricanes have long-term effects on tree diversity and succession. Past hurricanes appear to have accelerating succession in even-aged pine stands toward a later, hardwood-dominated successional stage, and to have shifted the hardwood forests toward more diverse composition, although with increasing dominance of red maple. I concluded that large, infrequent hurricanes play an important role in shaping forest structure and maintaining tree diversity in the Piedmont region. However, the effects on tree composition and diversity vary greatly and depend on local damage severity, pre-hurricane stand characteristics, and the temporal and spatial scales at which the changes are observed.

ACKNOWLEDGEMENTS

Many people have helped me during my long journey to become an ecologist. I am truly grateful to all of them. I first must thank Bob Peet, my graduate advisor and mentor, who gave me the opportunity to work with him and provided support throughout various stages of my graduate career. Bob introduced me to the Duke Forest, helped me to shape research ideas and laboriously edited all my writing. He taught me to think big, but always reminded me to start from clear objectives, and taught me how. I feel greatly privileged to have developed as an ecologist under his guidance. I have benefited tremendously from communicating with other ecologists, including Drs. Herbert Bormann, Norman Christensen, William Schlesinger, Charles Canham, Dennis Whigham, Thomas Wentworth, Paul Harcombe, Robert Ricklefs, Alan Weakley, and Jingyun Fang. Drs. Peter White, Seth Reice, Dean Urban, and Aaron Moody deserve special thanks for guiding my dissertation work as members of my graduate advisor committee. I am deeply indebted to them for all their suggestions, guidance, and encouragement throughout the course of my graduate study.

My colleagues in the UNC Plant Ecology Lab were a constant source of inspiration, encouragement, friendship and enjoyment. I have benefited from my connection and interaction with all of them, particularly Becky Brown, Jason Fridley, Patricia Corry, David Vandermast, Andy Gerschutz, Joel Gramling, Andrea Jones Gramling, Todd Jobe, Dane Kuppinger, Meghan McKnight, Jeffrey Ott, Lee Anne Jacobs, Amanda Senft, and Brooke Wheeler who provided me constant feedback on many aspects of my research. Rickie White,

Rob MacDonald and Michael Lee provided field assistance, did an excellent job of maintaining the Duke Forest database, and served as a source of inspiration for my research. Several former lab members including Drs. James DeCoster, Thomas Philippi and Philip Townsend provided me detailed help in methodological approaches and data analyses. In addition, I am very grateful to Carol Ann McCormick, our “lab mother”, for her friendship, helpful advice, and direct assistance during my stay in Chapel Hill.

My research work depended upon the long-term data in Duke Forest collected by many previous researchers and field assistants over a nearly 70-year period. Their vision, dedication, and hard work made my research possible. Staff in the Duke Forest office, in particular Judson Edeburn and Richard Broadwell, provided me great help with Duke Forest data and other logistical assistance. Meteorologists Joel Cline at the National Weather Service and Ryan Boyles at the State Climate Office of North Carolina kindly provided critical climate data. Professor George Hess and Ms. Kathleen Summitt at North Carolina State University provided me their project design information and GIS data for the Hill Experimental Forest. Drs. Coleman Doggett and Donald Rogers in the Forest Division of North Carolina Natural Resource Department provided me their hurricane damage survey data, reports, maps, and many insights on windstorm damage issues.

I deeply appreciate many people for their kindness and friendly assistance during my graduate study and academic training. I wish to thank Dr. Phyllis Howren, my English professor, for her great patience reading my writing, Dr. Jack Weiss in Curriculum in Ecology for providing me very helpful statistical advice, Ms. Julia Nichols for her great help when I really needed it, and librarians Jeffery Beam and Bill Burke, for their unfailing support whenever I needed literature. In addition, I wish to extend my deep thankfulness to

Professors Shupeng Chen, and Weiming Bi, and to Drs. Hua Fu, Tiaojiang Xiao and Xianhua Liu for their advice, friendship and help. Furthermore, a portion of detailed revisions of my dissertation was completed in the Knowledge Engineering Laboratory at Texas A&M University, Department of Entomology, where I have worked as a post-doctoral research associate with Dr. Robert Coulson. I greatly appreciate Dr. Robert Coulson, Ms. Audrey Bunting, and other members of the Knowledge Engineering Laboratory for their great support and friendly assistance.

My dissertation work would have been impossible without various forms of financial support. The major financial support for my research came from a National Science Foundation grant awarded to Drs. Robert Peet, Peter White, Dean Urban and Patrick Halpin (DEB97-07551), a Dissertation Completion Fellowship from the Graduate School of the University of North Carolina (UNC) at Chapel Hill, and two William Chambers Coker Fellowships from the UNC Department of Biology. Numerous Alma Holland Beers Scholarships and Mrs. W. C. Coker Summer Fellowships from the UNC Department of Biology also supported fieldwork and data analyses. I am truly grateful for all this support as it has all been critical to my success.

Most of all, I would like to thank cordially my family, who have provided me unconditional support in achieving my career goals. I must first thank my wife, Jie Zhao, for her love, support and incredible patience over the years, and for her considerable direct help in refining many figures and formatting my whole dissertation. She has sacrificed her time to our family and to my educational pursuits. Although she is more talented and brighter than I, she is always more giving, so instead of her it is I finishing a Ph.D.. I am also deeply indebted to my parents and parents-in-law, for their love, understanding, encouragement, and

countless forms of direct and indirect support during my voluntary exile to pursue higher education abroad. And - last but by no means least! - I thank my loving daughter Ziwei (Vivien) for a constant reminder of the importance of family. She has been a terrific kid who always makes me proud. The forest I studied might not have changed much during my five-year survey, but this invaluable learning experience at UNC-Chapel Hill has undoubtedly changed many aspects of my life.

PREFACE

In this dissertation I focus on the effects of large, infrequent hurricane disturbances on temperate forests and their impacts on forest dynamics and successional development. This work is driven by my belief that a better understanding of disturbance effects and subsequent forest response is required for effective forest management and biodiversity conservation. This information is particularly important as ongoing climate change is likely to sustain the recent increased incidence of major hurricanes for the foreseeable decades (Goldenberg et al. 2001, Emanuel 2005).

The work reported here is based on a 5-year study of post-hurricane change in tree, seedling and sapling populations in and around the Duke Forest. The Duke Forest, located in the Piedmont region of North Carolina, provides an especially valuable venue for such work in that it has long served as a model system for study of forest succession (Oosting 1942, Peet and Christensen 1980, 1987, 1988, Christensen and Peet 1981, 1984, see review by Peet 1992). The opportunity to document forest response to a major disturbance following a long period of baseline observation provides a unique opportunity to separate disturbance effects from the effects of background forest dynamics.

Studies of disturbance have long been a central focus of ecological research and have increased dramatically in recent decades (e.g., White 1979, Bormann and Likens 1979, Mooney and Godron, 1983, Pickett and White 1985, Walker 1999, White and Jentsch 2004). This work has greatly increased our understanding of the importance of disturbance for

community composition and ecosystem function, and has led to the wide acceptance among researchers of a nonequilibrium perspective (Reice 1994, 2001). In particular, the distinct and dramatic impacts of large and infrequent catastrophic events such as volcanic eruptions, large wildfires, and large hurricanes have attracted the attention of ecologists (e.g., Turner et al. 1998). While large, infrequent disturbances are easily seen to have profound impacts on forest structure, the longer-term effects on less conspicuous ecosystem attributes such as species diversity and composition are more complex. These subtle and highly variable effects often can be understood only in the context of specific forest sites and histories, and with detailed, but rarely available time-series data spanning the disturbance events. This dissertation is largely a detailed work on these subtle and variable effects of large, infrequent hurricane disturbances on forest structure, tree diversity, and successional development in the Piedmont region.

Hurricanes are the most destructive force of nature and affect a particular Piedmont forest on average about once every 50 years. Hurricane Fran crossed central North Carolina in 1996 and caused substantial tree mortality in Piedmont forests. The storm passed directly over the Duke Forest, an ecological research area for which there are available many years of baseline data on tree, seedling, and herb dynamics, in some cases dating to the early 1930s. The occurrence of Hurricane Fran has provided an exceptional opportunity to examine the immediate impacts of a major wind event on a series of forest sites of differing composition and disturbance histories with pre-disturbance records spanning over 60 years. Moreover, the fact that several plots in the Duke Forest were severely damaged in 1954 by Hurricane Hazel allows comparison of the recovery patterns following Hurricanes Hazel and Fran and evaluation of their long-term effects on the current forest structure and species diversity.

The introductory first chapter provides a general framework for understanding the complexity of windstorm effects on temperate forests and subsequent forest response. There is a large, widely distributed literature on windstorm impacts on forests, but a conceptual synthesis has been lacking. In this chapter, I combine illustrative examples to present a conceptual framework and then link them to several important themes that have emerged in recent years. The extensive literature cited in this chapter shows two, relatively separated lines of investigation, one focused on the complexity of forest damage patterns and their risk factors, and the other focused on the high degree of variation among forests in their structural and compositional responses to windstorm disturbances. This chapter provides an organizational framework that guides the rest of the dissertation.

Hurricane Fran caused substantial tree damage and created a complex of heterogeneous patches across the landscape. The altered forest structure and uneven resource availability (e.g., lights and soil nutrients) created by the hurricane was a strong force driving subsequent changes in understory species composition, diversity, and succession. In the second chapter, I assess the immediate impacts of Fran on the major community structural attributes and the short-term compositional responses of the damaged stands to the windstorm. Categorical damage records on individual trees allow quantification of immediate tree damage patterns as well as delayed effects spanning five years of post hurricane recovery. I examine size-specific stem damage and subsequent changes in tree mortality and basal area. As spatial heterogeneity in damage rarely has been examined, I quantify variation in damage among small plots. Spatial point pattern analysis reveals a clumped distribution of stand-scale tree mortality during the hurricane and indicates that Hurricane Fran significantly altered the structure of the damaged forest stands. The documentation of hurricane-induced variation in

stand structure presented in this chapter provides the essential foundation for my subsequent efforts to examine the dynamics of recovery.

In the third chapter I focus on biotic and abiotic influences on damage and on consistency between storms in mortality risk factors. At the stand scale I focus on the relationship between tree damage and tree size. The large range of tree sizes (≥ 1 cm) monitored in the Duke Forest allows detailed examination of the tree size-damage relationship. The long-term character of the Duke Forest data allows me to provide a detailed assessment of the relationship between competitive history, hurricane-induced tree mortality, and subsequent tree growth. At the landscape scale I examine the influence of topography and pre-disturbance species composition. At the regional scale I examine the relationships among forest damage, wind speed, amount of rainfall, and proximity to the hurricane path. In addition, I compare risk factors identified or associated with mortality during Hurricane Fran with factors previously found to be important for predicting wind-induced tree mortality. I address the importance of scale in observations of forest damage patterns and demonstrate the value of the pre-hurricane tree data in predicting the damage possibility. This multiple-windstorm comparison demonstrates how the risk factors interact to influence forest damage patterns at various scales.

In the fourth chapter I focus on understory responses to hurricane-induced changes in diversity and growth. Large hurricanes have been found to influence tree species coexistence in some forests systems (e.g., Glitzenstein et al. 1986) and have been hypothesized to have this function in Piedmont forests through enhanced establishment and survival of tree seedlings during periods of reduced competition and associated increased resource availability (Peet and Christensen 1987, Beckage et al. 2000). I observe changes in seedling

establishment and survival as well as growth and survival of established individuals. Previous seedling demographic work in the Duke Forest revealed a negative correlation between growth in sequential years (Philippi et al. 1993). I hypothesized that large gaps created by Hurricane Fran would result in release of established, shade-intolerant or mid-tolerant seedlings and saplings and thereby reverse the negative correlation observed between relative growth in successive years. I test this hypothesis by comparing the increase in growth rates among different shade-tolerance species and the release responses among different size and age groups. I also examine the effect of canopy characteristics (light regime) on individual plants. Data from seedling and sapling stems censused annually across the 15 years prior to Fran and 5 years post-Fran provide new insights into species dynamics. Understanding of changes in understory seedlings and saplings following disturbance is important for understanding patterns of forest recovery and improving forest simulation models. This chapter also provides an example of the complexity of understory response to wind damage and the mechanisms that influence long-term forest dynamics.

In the last chapter, I assess the impacts of Hurricane Fran on successional trajectories and assess the potential long-term effects on forest structure and species composition. Previous demographic work in the Duke Forest has shown that although oaks and hickories have long remained the dominant canopy species of mature stands, there has been a steady decline in their dominance over the past 70 years, along with a simultaneous increase in abundance of red maple (McDonald et al. 2002). The mechanisms for this phenomenon are little understood, though various hypotheses have been proposed. One popular hypothesis is that the oaks and hickories are well adapted to the chronic, low-intensity fires that ceased during the late 1800s (see Abrams 1992). However, an alternative hypothesis is that these

relatively shade-intolerant species are adapted to rapid growth following major canopy disturbances such as those associated with hurricanes and tornados (see Glitzenstein et al. 1986). Hurricane Fran provides a way to at least partially discriminate among these possibilities. To clarify long-term effects of hurricanes on relative abundance of trees, I further compare post-Fran recovery patterns with those following the 1954 Hurricane Hazel and conclude by suggesting that historically hurricanes have played an important though variable role in forest development.

In summary, this dissertation offers comprehensive descriptions and detailed analyses of how large hurricanes influenced forest composition, structure, diversity, and dynamics. This work should help us to better understand the role of windstorm disturbance, increase our ability to predict future forest dynamics, and to a certain extent help improve forest management practices in a period of increasing hurricane risks.

LITERATURE CITED

- Abrams, M. D. 1992. Fire and the development of oak forests in eastern North America, oak distribution reflects a variety of ecological paths and disturbance conditions. *Bioscience* 42:346-353.
- Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research* 30:1617-1631.
- Bormann, F. H. and G. E. Likens. 1979. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag New York Inc. New York, New York, USA.
- Carpino, E. 1998. Ecological determinants of hurricane damage in a southeastern piedmont forest. Master thesis. Duke University, Durham, North Carolina, USA.
- Christensen, N. L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in piedmont, North Carolina. *American Midland Naturalist* 97:178-188.
- Christensen, N. L. and R. K. Peet. 1981. Secondary forest succession on the North Carolina piedmont. Pages 230-245 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest Succession: concepts and application*. Springer-Verlag, New York, New York, USA.
- Christensen, N. L. and R. K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* 72:25-36.
- DeCoster, J. K. 1996. Impacts of tornados and hurricanes on the community structure and dynamics of north and South Carolina forests. Ph.D. Dissertation. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.
- Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, southwestern New Hampshire, USA. *Journal of Ecology* 76:105-134.
- Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology* 76:135-151.
- Foster, D. R. and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology* 80:79-98.
- Glitzenstein, J. S., P. A. Harcombe, and D. R. Streng. 1986. Disturbance, succession, and maintenance of species-diversity in an east Texas forest. *Ecological Monographs* 56:243-258.
- Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nunez, and W. M. Gray. 2001. The recent increase in Atlantic hurricane activity: causes and implications. *Science* 293:474-479.

- Emanuel, K. A., 2005: Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* **486**:686-688.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina piedmont. *Castanea* **67**:84-95.
- Mooney, H.A. and M. Godron, editors. 1983. Disturbance and ecosystems. Components of response. Springer-Verlag, New York, New York, USA.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of piedmont, North Carolina. *American Midland Naturalist* **28**:1-126.
- Peet, R. K. 1992. Community structure and ecosystem properties. Pages 102-151 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession: theory and prediction*. Chapman and Hall, London, UK.
- Peet, R. K. and N. L. Christensen. 1980. Succession - a population process. *Vegetatio* **43**:131-140.
- Peet, R. K. and N. L. Christensen. 1987. Competition and tree death. *Bioscience* **37**:586-595.
- Peet, R. K. and N. L. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina piedmont. Pages 233-245 in H. J. Doring, M. J. A. Werger, and J. Willems, editors. *Diversity and pattern in plant communities*. SPB Publishers. The Hague. The Netherlands.
- Philippi, T. E., R. K. Peet, and N. L. Christensen. 1993. Tree seedling demography in old-field *Pinus taeda* and mature mixed hardwoods stands in a piedmont forest. *Bulletin of the Ecological Society of America* **74(Suppl.)**:393.
- Pickett, S. T. A. and P. S. White. 1985. Editors. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida, USA.
- Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* **82**: 424-435.
- Reice, S. R. 2001. *The silver lining: the benefits of natural disasters*. Princeton University Press, Princeton, New Jersey, USA.
- Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* **1**:511-523.
- Walker, L.R. 1999. Editor. *Ecosystems of Disturbed Ground*. *Ecosystems of the World* 16. Elsevier, Amsterdam, The Netherlands.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229-299.

White, P. S. and A. Jentsch. 2004. Disturbance, succession, and community assembly in terrestrial plant communities. Pages 342-366 *in* V. Temperton, R. Hobbs, and S. Halle, editors. *Assembly Rules and Restoration Ecology*. Island Press, Washington, DC, USA.

White, R. D. 1999. The impacts of hurricane Fran on a North Carolina piedmont woodland. Master thesis. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.

TABLE OF CONTENTS

LIST OF TABLESxxi

LIST OF FIGURESxxv

Chapter

1.	THE COMPLEXITY OF CATASTROPHIC WIND IMPACT ON TEMPERATE FORESTS	1
	Abstract	1
	Why study catastrophic wind disturbance?	2
	Understanding catastrophic wind disturbance	4
	Complexity of forest damage resulting from catastrophic wind disturbances	11
	Factors influencing mortality and their interactions	19
	Forest responses	25
	Long-term effects of catastrophic wind disturbance	28
	The role of the predictive models for evaluating wind impacts	32
	Synthesis and future directions	34
	Literature cited	36
2.	THE IMMEDIATE IMPACT OF HURRICANE FRAN ON THE STRUCTURE AND TREE SPECIES COMPOSITION OF NORTH CAROLINA PIEDMONT FORESTS	54
	Abstract	54
	Introduction	55

	Methods	58
	Results	66
	Discussion	78
	Conclusions	83
	Literature cited	85
3.	A COMPARISON OF MORTALITY RISK FACTORS ASSOCIATED WITH LARGE, INFREQUENT WIND DISTURBANCES OF CAROLINA PIEDMONT FORESTS.....	129
	Abstract	129
	Introduction	130
	Methods	134
	Results	144
	Discussion	149
	Conclusions	155
	Literature cited	157
4.	THE IMPACT OF HURRICANE FRAN ON WOODY SEEDLING AND SAPLING DYNAMICS AND DIVERSITY IN NORTH CAROLINA PIEDMONT FORESTS	182
	Abstract	182
	Introduction	183
	Methods	187
	Results	193
	Discussion	200
	Conclusions	204
	Literature cited	206

5	HURRICANE DISTURBANCES, TREE DIVERSITY, AND SUCCESSION IN NORTH CAROLINA PIEDMONT FORESTS	235
	Abstract	235
	Introduction	236
	Methods	239
	Results	248
	Discussion	255
	Literature cited	261
6	GENERAL CONCLUSIONS	292
	APPENDICES	299
	Appendix I	299
	Appendix II	303
	Appendix III	305
	Appendix IV	306
	Appendix V	312

LIST OF TABLES

Table

1.1.	List of studies of catastrophic windstorms in temperate forests since 1998 by geographic locality, forest type, and windstorm type	48
1.2.	Comparison of temperate forests and tropical forests, early succession forests and late succession forests in their responses to catastrophic wind disturbance events	49
2.1.	Characteristics of the seven mapped plots in the Duke Forest, North Carolina, USA	99
2.2.	Stem damage (%) by 1996 Hurricane Fran in the seven MPPs in the Duke Forest, North Carolina, USA	100
2.3.	With-stand damage variation in two mapped pine and five mapped hardwood plots, and among-stand damage variation in 34 permanent sampling plots in the Duke Forest, North Carolina, USA. The damage severity was examined by using stand damage index.	101
2.4.	Mean annually mortality (%/yr) in the Graveyard and the Bormann plot in the Duke Forest, North Carolina, USA	102
2.5.	Annual mean mortality rates (<i>m</i>) of tree species in the Graveyard and the Bormann plot in three periods in the Duke Forest, North Carolina, USA	103
2.6.	Mean diameter growth rate (cm/yr.) of major tree species in the Graveyard and the Bormann plot in three periods (pre-h., h., and post-h; *h = hurricane) in Duke Forest, North Carolina, USA	104
2.7.	Comparison of gap formation rate for seven mapped plots in the Duke Forest before and after Hurricane Fran	106
3.1.	Characteristics of the eight mapped tree census plots in the Duke Forest of Piedmont region, North Carolina, USA	167
3.2.	Characteristics of the 22 pine permanent sampling plots (PSPs) in the Duke Forest, North Carolina, USA	168
3.3.	Comparison of stand level damage of the eight mapped plots and three groups of PSPs according to their locations i.e. (1) PSP 12-23,	

49,50,51; (2) PSP 4,5,6,7,24,25,26 and (3) Hill Forest 23, 24 25 vs. their distances to hurricane path	169
3.4. Mean damage and standard deviation for mapped plots in the Duke Forest	170
3.5. Logistic regression models of hurricane damage during Hurricane Fran at a regional scale. Heavily damaged trees are examined as a function of wind speed, the amount of rainfall, tree size (d.b.h.), tree species composition ratio and the distance to the hurricane path. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$	171
3.6. Logistic regression models of hurricane damage during Hurricane Fran for 22 pine stands in the Duke Forest. Plot-level damage severity was examined as a function of stand density, height, topographic position, aspect, slope, site exposure. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$	172
3.7. Logistic regression models of hurricane mortality during Hurricane Fran in a pine stand and hardwood stand in the Duke Forest. Tree mortality was examined as a function of pre-hurricane d.b.h. and tree growth rates. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$	173
3.8. Factors that were significantly related to wind damage at three relevant scales (i.e. regional, landscape and stand). *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$	174
3.9. Wind speed variation largely explains the variation in tree damage during 1989 Hurricane Hugo. Note that species characters play an important role in damage risk	175
4.1. The characteristics of the 13 selected seedling and 13 sapling transects in the Duke Forest, North Carolina, USA. The number in the first column is for seedlings, and the second column (parenthesis) is for the sapling's information	212
4.2. Seedling and sapling sampling size for 13 selected major taxa in the two loblolly pine plots (Graveyard and Land' send) and the two mixed-aged hardwood stands (Bormann and Rocky) in the Duke Forest, North Carolina, USA. The number in the first column is for seedlings, and the second column (parenthesis) is for the sapling's information. The total sample area in the Graveyard plot is 200 m ² for seedlings and 800 m ² for saplings. And total sample area in other three plots (Land' end, Bormann, and Rocky) is 150 m ² for seedlings and 600 m ² for saplings	213

4.3.	Changes in seedling population of major species over 11 years in a loblolly pine stand (Graveyard plot) in the Duke Forest, North Carolina, USA. The density values used are the means of four seedling transects of the forest stand. Note no data available for 1995 and 1996	214
4.4.	Changes in seedling population of major species over 11 years in a loblolly pine plot (Land's end plot) in the Duke Forest, North Carolina, USA. The density values used are the means of three seedling transects of the forest stand. Note no data available for 1995 and 1996	215
4.5.	Changes in seedling population of major species over 11 years in a white oak plot (Bormann plot) in the Duke Forest, North Carolina, USA. The density values used are the mean of three seedling transects of the forest stand. Note no data available for 1995 and 1996	216
4.6.	Seedling composition and population change of major species over 11 years in hardwood stand (Rocky plot) in the Duke Forest, North Carolina, USA. The density values used are the mean of three seedling transects of the forest stand. Note no data available for 1995 and 1996	217
5.1a.	Characteristics of 20 selected permanent sample plots (PSPs) in the Duke Forest, North Carolina, USA. The percentage of basal area change before and after the hurricanes was as a measurement of plot-level damage severity. The time period during which this basal area change occurred for Hurricane Hazel was 1950 to 1954, and for Fran was from 1993-1997	274
5.1b.	Characteristics of the seven mapped plots (MPPs) in the Duke Forest, North Carolina, USA	275
5.2.	Changes in species richness (S) and diversity ($\exp H'$) of 14 selected permanent sampling controls in the Duke Forest, North Carolina, USA. The first number in each column is tree species richness; the second number in each column (parentheses) is the Shannon-Weiner's index of diversity ($\exp H'$)	276
5.3.	Changes in species richness (S) and diversity ($\exp H'$) of 6 selected Permanent Sample Plots in the Duke Forest, North Carolina, USA. These plots were damaged by Hurricane Hazel in 1954, and some had a thinning manipulation prior to Hazel. The first number in each column is tree species richness; the second number in each column (parentheses) is the Shannon-Weiner's index of diversity ($\exp H'$)	277

5.4a.	Effect of Hurricane Hazel on tree establishment and tree diversity in a moderately damaged upland hardwood forests (PSP 36) in the Duke Forest, North Carolina, USA	278
5.4b.	Effect of Hurricane Hazel on tree establishment and tree diversity in a significantly damaged upland hardwood forests (PSP 37) in the Duke Forest, North Carolina, USA	279
5.5a.	Community composition and population change over 12-year period in a 1.3 ha loblolly pine permanent plot (Graveyard plot) in the Duke Forest, North Carolina, USA	280
5.5b.	Community composition and population change over 11-year period on a 1.96 ha white oak permanent plot (Bormann plot) in the Duke Forest, North Carolina, USA	281
5.6.	Annual mean mortality rates (<i>m</i>) of tree species in two major forest stands in three periods in the Duke Forest, North Carolina, USA	282
5.7.	Change in relative abundance by shade-tolerance class in a 1.3 ha mapped loblolly pine stand and a 1.9 ha oak forest in the Duke Forest after Hurricane Fran	283

LIST OF FIGURES

Figure

- 1.1. Conceptual model of temperate forests in response to varied wind regime (as a function of wind intensity, frequency and size). Forest structure, species composition, and diversity are more predicable when wind frequency is high but wind intensity is low (light portions). Community structure and diversity of the damaged forests become less predictable when intensity increases and frequency decreases, as in the case of large, infrequent hurricanes in temperate forests (dark portions). The importance of pre-disturbance community attributes and site conditions decreases when wind intensity increases50

- 1.2. Damage severity and importance of site factors vary with wind intensity. Hurricane force is a function of wind speed, duration of storm and rainfall. Vegetation damage is a function of combined progression from defoliation to treefall, and from localized to widespread destruction51

- 1.3. Conceptual model of temperate forest regeneration following hurricane disturbance. Two major recovery pathways are represented by large arrows. The microsite environment influences each stage of the pathway of regeneration from seed but exerts less influence on the pathway of regeneration from surviving vegetation52

- 1.4. Old-field succession on Piedmont and four-stage forest succession model and hypothesized tree species diversity curve (as showed in solid line) over time. The effect of a hurricane on tree species diversity is low during the establishment and thinning phases, impacts are potentially high at the transition and steady-state phases. Changes in species richness impacted by extreme and modest hurricanes are showed as dash-lines. When wind intensity is low, tree richness changes minor. Modest wind intensity may increase tree diversity over time. When extreme winds occur, tree species diversity may decrease53

- 2.1. The location of the Duke Forest and the path of 1996 Hurricane Fran in North Carolina, USA107

- 2.2. The locations of the seven mapped permanent plots (MPPs) and the 34 long-term permanent sample plots (PSPs) used in this study in Durham Division and Korstian Division of the Duke Forest, North Carolina, USA. The sub-areas within the two divisions are the forest cover types. Note the legends of forest cover types are not shown in this figure (Data source: the Duke Forest office, Duke University

2001)	108
2.3. The probability of a tree uprooting increased with an increase in tree size in (a) the Graveyard plot and (b) the Bormann plot. Empirical log odds and the probability of uprooting as a function of pre-hurricane tree size are shown. The observed response is plotted as stacked points at the top (i.e., uprooting) and bottom of the figure (i.e. no such type damage). The squares show the empirical sample logits and the analogous adjusted sample probability. The curves on these plots show predicted probabilities and 95% confidence bands	109
2.4. Change in IV (importance value) of major tree species in three mapped plots in three periods (pre-hurricane, hurricane period and post hurricane) over 10 yr. Data are shown for all species with IV ≥ 1 over the three periods. The total value of IV is 100. The survey year for each plot pre-hurricane varies from 1989 – 1993, and post-hurricane varies from 2000 – 2001	110
2.5a. Pattern of tree mortality (Stem d.b.h. ≥ 5 cm) in a loblolly pine stand (Graveyard plot) in the Duke Forest after the 1996 Hurricane Fran, North Carolina, USA	112
2.5b. The mortality stem (dbh ≥ 5 cm) maps of Bormann plot in the Duke Forest after the 1996 Hurricane Fran, North Carolina, USA	113
2.6a. Transformed Ripley's K(d) for tree mortality over time in Graveyard and Bormann plot for the middle and upper layer trees (i.e., d.b.h. > 10 cm) in the Duke Forest, North Carolina, USA. The sample statistic L(t) is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness	114
2.6b. Transformed Ripley's K(d) for alive-trees over time in Graveyard plot in the Duke Forest, North Carolina, USA. The sample statistic L(t) is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness	115
2.6c. Transformed Ripley's K(d) for alive-trees over time in Bormann plot for the major species in the Duke Forest, North Carolina, USA. The sample statistic L(t) is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness	117
2.7. Percentage of azimuths of uprooting trees in six mapped plots in the Duke Forest, North Carolina, USA	119
2.8a. Changes in tree size distribution for major species in the Graveyard plot in the Duke Forest, North Carolina, USA	121

2.8b.	Changes in tree size distribution for 8 manor species in the Bormann plots in the Duke Forest, North Carolina, USA	123
2.9.	Nonmetric Multidimensional Scaling (NMS) ordination of 32 permanent sampling plots in the Duke Forest measured in 1984 through 2000. Squares are plot locations on first axe one and axe two of NMS ordination over time. Crosses show NMS ordination of primary species on same axes. Note labeled PSP10, PSP35, PSP36, PSP37, PSP43, PSP44 are six hardwood PSPs	125
2.10.	Nonmetric Multidimensional Scaling (NMS) ordination of seven mapped plots measured in mostly from 1978 through 2000. Squares are plot locations on first axe one and axe two of NMS ordination over time. Crosses show NMS ordination of primary species on same axes	126
3.1.	location of the Duke Forest and the path of 1996 Hurricane Fran in North Carolina, USA	176
3.2.	Map of estimated maximum sustained wind speeds across North Carolina during the 1996 Hurricane Fran. Wind speed data are from Joel Cline in National Weather Service (1996). Isobars indicated wind speeds intervals of mile/hour. The estimated maximum sustained wind speeds do not take into account fine-scale variation in wind speeds due to gusts, downburst and tornados which can greatly exceed the values presented here	177
3.3.	Map of precipitation across North Carolina during the 1996 Hurricane Fran. Precipitation data are from Joel Cline in the National Weather Service (1996). Isobars indicated precipitation intervals of inches	178
3.4.	The possibility of a tree uprooting increased with increases in tree size in (a) the Graveyard plot and (b) the Bormann plot. Empirical log odds and the probability plot for uprooting as a function of pre-hurricane tree size. The observed response are plotted as stacked points at the top (i.e., uprooting) and bottom of the figure (i.e. no such type damage). The squares show the empirical sample logits and the analogous adjusted sample probability. The curves on these plots show predicted probabilities and 95% confidence bands	179
3.5.	The probability of uprooting during the 1996 Hurricane Fran in Gravetayd plot of the Duke Forest increased with increases in tree size (d.b.h.). Interactions between diameter and species showed that rate of increase with diameter varies among	

species	180
3.6. The possibility of uprooting tree during the 1996 Hurricane Fran increased with increases in tree size (d.b.h.) for four major species in Bormann plot, Duke Forest, North Carolina, USA	181
4.1. Damage types of 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. <i>n</i> is the number of transects in a forest stand. Damage percentage refers the proportion of damage type in all damaged stems	218
4.2. The stem density of seedlings 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	219
4.3. The species richness of seedlings 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	220
4.4. The species diversity of seedlings 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	221
4.5. Seedling mortality rates (%) for four stands 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	222
4.6. Seedling ingrowths for four stands 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. Note no data on 1995 and 1996. <i>n</i> is the	

	number of transects in a forest stand	223
4.7.	Seedling relative growth rates for four stands 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	224
4.8.	Relationship between seedling growth and canopy openness in the four forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard, (b) Land's end. The X axis is the canopy openness (%) and the Y axis is the Relative Growth Rate (RGR) of seedlings. The upper and lower lines are 95% prediction intervals. R-squared is 0.0216 for (a) and 0.0357 for (b)	225
4.9.	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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	227
4.10.	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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	228
4.11.	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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	229
4.12.	Sapling mortality rates (%) for four stands 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	230
4.13.	Sapling ingrowths for four stands 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	231
4.14. Sapling relative growth rates for four stands 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. Note no data on 1995 and 1996. <i>n</i> is the number of transects in a forest stand	232
4.15. Non-metric Multidimensional Scaling (NMDS) ordination of 7 even-aged pine sapling transects and 6 mixed-aged sapling transects in the 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. <i>n</i> is the number of transects in a forest stand	233
4.16. Non-metric Multidimensional Scaling (NMDS) ordination of 7 even-aged pine seedling transects and 6 mixed-aged seedling transects in the 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. <i>n</i> is the number of transects in a forest stand	234
5.1. Survivorship of <i>Pinus taeda</i> (d.b.h.>1.25 cm) in eleven even-aged loblolly pine stands in the Duke Forest. The plot sizes are 404 m ² for (a) group and 808 - 1011 m ² for (b) group. Despite extreme variation in initial densities, differential mortality has led to convergence in density during 66-year period. Four of the permanent plots (PSP14, 19, 49 and 50) were greatly damaged by 1996 Hurricane Fran, resulted in substantially high mortality and low tree density	284
5.2. Depletion curves illustrating differences in mortality rates of trees from two upland, mixed-aged, mixed-species stands. Species abbreviations: CARY- <i>Carya spp</i> ; CACA- <i>Carya caroliniae-septentrionalis</i> ; CATO- <i>Carya tomentosa</i> ; CAGL- <i>Carya glabra</i> ; COFL- <i>Cornus florida</i> ; JUVI- <i>Juniperus virginiana</i> ; QUSP- <i>Quercus spp.</i> . Note that <i>Quercus spp.</i> in PSP 10 and <i>Cornus florida</i> in PSP 36 greatly decreased in or shortly after Hurricane Fran	285
5.3. Change in understory (stem 1 cm =<d.b.h. <5 cm) species richness (number of species per ca.1000 m ²) and tree diversity (exp H' per ca. 1000m ²) in two mapped permanent plots over 18 years in the Duke Forest, North Carolina, USA. (a) tree richness in the Graveyard	

	plot; (b) tree diversity in the Graveyard plot; (c) tree richness in the Bormann plot and (d) tree diversity in the Bormann plot. The error bars on the columns are standard errors	286
5.4.	The relationship between canopy damage intensity and change in species diversity in Graveyard plot and (a) and Bormann plot (b) in the Duke Forest. X-axis is the damage index (by definition, from 0-3, 0 means no damage stems and 3 is maximum, means that all the stems are severely damage). Y-axis is the difference of tree diversity (as exp H') between 2001 (5 years after Hurricane Fran) and 1992 (4 years before Hurricane Fran). The mapped plots were divided into about 1000 m ² . This result supports "Intermediate Disturbance Hypothesis" proposed by Connell (1978)	287
5.5.	Change in IV (importance value) of major tree species in three mapped plots in three periods (pre-hurricane, hurricane period and post hurricane) over 10 yr. Data are shown for all species that IV >=1 over the three periods. The total value of IV is 100. The survey years for each plot pre-hurricane vary from 1989 – 1993, and post hurricane vary from 2000 – 2001. (a) Graveyard plot and (b) Bormann plot. Increases in some species such as <i>Acer rubrum</i> reflect their disproportionate abundance in the understory of forests that experienced significant mortality of the larger trees	288
5.6.	Nonmetric Multidimensional Scaling (NMS) ordination of 13 control permanent sampling plots in the Duke Forest Vectors indicate sequences of observations of a single plot over the interval 1933 to 2000	290
5.7.	Nonmetric Multidimensional Scaling (NMS) ordination of seven mapped plots measured in mostly from 1978 through 2000. Squares are plot locations in two-dimensional NMS ordination space over time. Observations are label with specific plot and year (G = Graveyard, L = Land's end, R = Rocky, W = Wooden Bridge, Bm = Bormann, By = Bryan Center, and O = Oosting plot). Hardwood plots on the left and bottom, whereas successional pine plots are in the upper right	291

CHAPTER 1

THE COMPLEXITY OF CATASTROPHIC WIND IMPACT ON TEMPERATE FORESTS

Abstract. Catastrophic wind disturbance events (hurricanes, tornados, downbursts, gales and severe windstorms) occur in nearly all forest ecosystems and have profound impacts on forest structure, species diversity and ecosystem functions. Such ecological effects are often complex, subtle, and at smaller scale relatively unpredictable. Many factors (meteorological, topographical, and biological), simultaneously interact to influence the patterns of damage and dynamics of recovery. I present a brief synthesis of the complexity of forest responses to catastrophic wind disturbances, with particular attention on forest responses to large, infrequent hurricanes in temperate forests.

Four major aspects of wind damage provide an organizational framework for syntheses and future research: 1) consistent patterns in the damage exhibited by forest communities, 2) factors that influence damage patterns and predict damage risks, 3) forest responses to and recovery from the catastrophic wind damage, and 4) the long-term effects of wind disturbances on species diversity and succession. This review reveals highly variable and complex effects of catastrophic windstorms on community structure, composition, diversity, and succession. A deep understanding of the consequences of catastrophic wind disturbances is essential for effective long-term forest management and biodiversity conservation planning. More long-term studies and multiple-scale analyses are needed to fully understand the associated scale-dependent processes and to more accurately predict their consequences.

Key words: Catastrophic winds, hurricanes, forest damage, stand recovery and dynamics, intermediate disturbance, complex effects, long-term impacts, within-stand heterogeneity, temperate forest.

WHY STUDY CATASTROPHIC WIND DISTURBANCE?

Catastrophic wind disturbance events are nearly ubiquitous in forest ecosystems and have profound impacts on forests in many parts of the world. As an ecological factor (primarily as a destructive force), catastrophic wind not only causes extensive damage to trees, but also affects many aspects of the disturbed forests including community structure, individual tree growth, tree regeneration, species diversity, and ecosystem function (Coutts and Grace 1993, Ennos 1997). While catastrophic windstorms are easily seen to have major impacts on forest structure, the longer-term effects on less conspicuous ecosystem attributes such as species composition and diversity are more complex, subtle, and at smaller scale relatively unpredictable. Many factors, meteorological, topographical and biological, simultaneously interact to influence the complexity of patterns of damage and dynamics of recovery. A deep understanding of wind disturbance effects is essential for effective forest management and biodiversity conservation. This information is particularly important as ongoing climate change is likely to sustain the recent increased incidence of major windstorms for the foreseeable decades (Goldenberg et al. 2001, Emanuel 2005).

The effects of wind damage have long been recognized and observed by foresters and ecologists (e.g., Baker 1915, Bromely 1939, Curtis 1943, Spurr 1956, and Webb 1958). Extensive research has been conducted on the ecological impacts of catastrophic windstorms in recent decades (e.g., Canham and Loucks 1984, Foster 1988, Webb 1988, 1989, Boucher et al. 1990, Brokaw and Grear 1991, Walker 1991, Peterson and Pickett 1991, Merrens and

Pearl 1992, Bellingham et al. 1992, 1994, 1995, Boose et al. 1994, Vandermeer et al. 1995, Imbert et al. 1996, Turner et al. 1997, Herbert et al. 1999, Sinton et al. 2000, Burslem et al. 2000, Boose et al. 2001, Platt et al. 2002, Woods 2000, Peterson 2004, Uriarte et al. 2004). Much progress has been made in elucidating wind regimes and forest recovery in some specific wind-damaged forest communities. This work has greatly increased our understanding of the importance of wind disturbance for community composition and ecosystem function, and has led to the wide acceptance among researchers of a nonequilibrium perspective (Reice 1994, 2001). As a consequence of this and related work, the traditional view of wind as a simple damage force has evolved into the contemporary view of wind as a spatially heterogeneous, multi-scale disturbance agent that affects forest structure, diversity, dynamics, and some ecosystem processes.

Several reviews of windstorm impacts have provided a general framework for viewing how various windstorm disturbances might influence forest patterns and processes and some useful generalizations have emerged from those reviews (Brokaw and Walker 1991, Tanner et al. 1991, Foster and Boose 1995, Everham and Brokaw 1996, Whigham et al. 1999, Webb 1999, and Peterson 2000). Important reviews by Webb (1999) and Peterson (2000) have shown highly variable forest responses to windstorm disturbances in temperate forests, but there has been a continuous increase in knowledge about the complexity of the impacts (Table 1.1). A new review focusing on the complex effects of large, infrequent windstorm disturbances in temperate forests is necessary to incorporate new knowledge and changing perceptions. In addition, this review, combined with others, may provide useful information for improving forest management that helps to minimize the timber loss under the increasing risk of catastrophic damage in temperate forest regions.

The purpose of this review is to present a brief synthesis of the complexity of forest responses to catastrophic windstorm disturbances and a framework for its interpretation and future study. I particularly focus on large, infrequent hurricane disturbances in temperate forests. The extensive literature cited in this review documents complex patterns of forest response to highly variable windstorm disturbance regimes in temperate forests. I attempt to combine in one common conceptual framework several important concepts and theories pertaining to wind disturbance effects that have emerged in recent years. This synthesis is structured around four questions: 1) Are there consistent patterns in the damage exhibited by forest communities? 2) What factors influence damage patterns and predict damage risk? 3) How do forests respond to and recover from the catastrophic wind damage? 4) What are the long-term effects of wind disturbances on species diversity and succession?

UNDERSTANDING CATASTROPHIC WIND DISTURBANCE

Concepts

Despite extensive previous work on catastrophic wind disturbance and subsequent ecological effects, there has been no specific definition. Defining catastrophic wind disturbance is difficult because wind varies within/between events in intensity, size and frequency. In this review, I refer to catastrophic wind disturbance as including high wind events, mainly hurricanes, tornados, downburst, gales and severe windstorms that may potentially result in substantial tree damage. In most cases, the catastrophic wind disturbances I focus on in this synthesis are a form of large, infrequent disturbance (LID) proposed by Turner and others (1998) as natural catastrophic events that are ‘large in spatial extent and infrequent in occurrence’.

Catastrophic wind disturbances can be identified from their high wind intensity and extreme maximum gusts (Foster and Boose 1995, Everham and Brokaw 1996, Peterson 2000). The strongest winds (maximum wind speed about 125 m/s and average speed about 100 m/s) characterize tornadoes. A hurricane is a tropical windstorm when its wind speed is higher than 35 m/s and a typical hurricane has an average wind speed of 70 m/s (Baldwin 1995). Gales (average wind speed about 50 m/s) and severe windstorms (average wind speed about 30-50 m/s) more often produce winds of only moderate intensity, but in some cases, they can also generate winds as destructive as tornadoes. A downburst is a straight-direction catastrophic surface wind in excess of 17 m/s caused by a small-scale, strong downdraft from the base of convective thundershowers and thunderstorms (Fujita 1985), and can exceed 50 m/s (or even 75m/s) and cause tornado-like damage.

Occurrences of catastrophic wind events vary greatly in frequency and return times among windstorm types and localities. Hurricanes are tropical, high-wind events and can be common in near-coast tropical regions, but are less frequent in inland tropics. Catastrophic hurricanes (defined as Saffir-Simpson category 4 or 5) reoccur for a particular area of the coastal tropics on average every 20-60 years (Brokaw 1991). The frequency of hurricanes decreases from tropical coasts to inland temperate regions. Major hurricanes only occasionally achieve landfall in temperate areas, and rarely reach the inland temperate areas (Webb 1999).

The reoccurrence intervals of major hurricanes in temperate forests vary greatly from less than 20 years in the Southeastern coastal regions (Gresham et al. 1991, Doyle 1997, Platt et al. 2000), to about 50 years in the temperate Piedmont of the Southeastern United States (Xi Chapter 5), to about 70-100 years in the Northeastern United States (Foster and Boose

1986, 1995). Storms like the 1938 hurricane (Category 5) that caused disastrous forest damage in the last century in the Northeastern United States typically occur in the region only once a century. The reoccurrence rates of major hurricanes on a geological time scale for a specific location in a temperate region might be even longer. A sediment core study used to quantify hurricane activity in the Lake Shelby region of coastal Alabama showed a recurrence interval of about 300 years for catastrophic hurricanes during the last 5,000 years, and about 600 years during the last 10,000 years (Liu and Fearn 1993).

Compared to hurricanes, the frequencies of other types of catastrophic wind events (e.g., tornado, gales, downburst and severe storms) are highly variable in the temperate zone. Tornadoes have been reported widely in temperate North America, especially in the central Great Plains of the United States, where they can be particularly violent. In the Tornado Alley region (Oklahoma-Kansas, USA), the number of tornadoes can reach 40 per 105 km² per year (Fujita 1985). Downbursts are more frequent than tornadoes, but due to their isolated and sudden nature (lasting several minutes to half an hour), their recurrence rates are rarely reported in the literature. To date, few studies have reported the occurrences of gales, although Gallagher (1974) and Fraser (1971) reported 34 years and 75 years for return times in forest regions of Ireland and Scotland respectively. For windthrow, Zhang and others (1999) reported the average rotation period over the Upper Peninsula of Michigan to be 541 years. In the northern temperate forests of Wisconsin, severe windstorm return periods vary greatly, ranging between 450 to 1200 years (Canham and Loucks 1984, Schulte and Mladeoff 2005).

The spatial extent or magnitude of catastrophic wind disturbances, which can be expressed as mean affected area per disturbance event, varies significantly among windstorm

types. Sizes of hurricanes are generally large. A hurricane normally has a 300-340 km diameter and severe wind damage could extend 50-100 km in width along its path (Baldwin 1995). One example to illustrate the potential large size of a hurricane was the 1938 hurricane, one of the most catastrophic windstorms in United States history, which blew down more than 2,400 km² of forestland in central New England (Spurr 1956). In contrast, a tornado usually causes substantial damage only along its long and narrow path. A typical tornado path is normally several dozen to several hundred meters wide, and 15-20 km long (Ruffner and Bair 1984). The actual surface damaged by a tornado may be much less than its path owing to the way tornadoes skips across the landscape (Peterson 2000). Similar to tornados, gales, downbursts, and severe storms are more localized wind events, and their sizes are often limited varying from several km² to less than a 100 km².

Scales

Both spatial and temporal scale are particularly important in understanding effects of catastrophic winds; catastrophic wind damage and subsequent forest recovery are scale-dependent phenomena. As Levin (1992) pointed out, “no single mechanism explains pattern on all scales.” Consequently, it is essential to clarify both the spatial and temporal scale over which wind damage and recovery patterns are examined.

Windstorms are often distributed over a broad range of spatial scales, and certain damage effects and recovery patterns can only be observed at a specific spatial scale in the context of specific processes. In their series of papers on hurricane impacts in Northeastern temperate forests of the United States, Foster and Boose (1992, 1994, 1995, and 2000) demonstrated that certain processes are dominant only for a specific spatial scale. For example, the geographic and meteorological factors that control the formation and movement

of hurricanes can be only be understood on a continental scale (~5000 km), whereas wind velocity, local topography (variation in site exposure), and individual stand attributes are the controlling factors of hurricane damage at the landscape scale (~10 km). At small scales biotic factors become more significant. For example, Peterson (2004) found that within-stand damage variation can be largely explained in the context of tree size and species. My study in the Piedmont forests of the southeastern United States also showed that at the stand scale, tree size (i.e., its vertical stratum) and resistance to wind are the most important indicators of mortality probability and damage type during a major hurricane (Chapter 3).

Recovery time from catastrophic windstorms varies tremendously between forests from a few years to a predicted period of >100 years, depending on wind intensity and the regeneration capability of the damaged forest. Moreover, forest recovery processes also vary with time. For example, during and immediately after a hurricane, mortality processes dominate, whereas the recruitment process becomes important in the years immediately after the wind damage. Consequently, the timing of surveys of wind-disturbed forests is critical for understanding the damage, mortality and recovery. Ecologists often divide windstorm impacts and post-disturbance forest responses into three temporal categories: immediate (a few months to one year, e.g., Walker et al. 1992), short-term (few months to several years, e.g., Vandermeer et al. 2000, Pascarella et al. 2004) and long-term (few decades to centuries, e.g., Hibbs 1983, Foster 1988, Burslem et al. 2000). Thus, it is important to clarify the temporal scale across which the research is conducted and ecological patterns are compared.

The predictability of forest damage and recovery pattern from catastrophic winds generally is scale-dependant. Although wind conditions are highly variable in all aspects during a windstorm, wind gusts are more random at smaller scales. The predictability of

forest damage at the stand scale (~1 km) is, therefore, relatively low due to the random effects of wind gusts and the complex interactions among their neighbor individuals. The larger-scale forest damage patterns and recovery processes (e.g., at landscape and regional scale) can be predicted reasonably well (Figure 1.1). For example, forest damage patterns across post-hurricane landscapes are predictable based on wind speeds, topography (site exposure), stand structure, disturbance, and land-use history (e.g., Foster 1998, Foster and Boose 1992, DeCoster 1996).

A framework for understanding large, infrequent catastrophic winds

Catastrophic winds play an important role in shaping the forest structure, composition and diversity of temperate forests. However, the effects are often complex and variable. Before reviewing past work, I briefly provide a theoretical framework for viewing how natural disturbance and patch dynamics apply to empirical observations of windstorm-driven forest dynamics events, and how catastrophic windstorms might affect forest community attributes and processes in temperate forests.

Temperate forests vary greatly in their disturbance regimes. Wind event intensity, size, and frequency vary among storm types (Foster and Boose 1995). In fact, wind intensities of any catastrophic wind events can be highly complex and variable in space and time during their courses due the interactions between the unstable turbulences and the complex ground surface features over which the air moves (Barnes et al. 1998). Overall, damage severity of a specific forest at a given site depends on three interrelated aspects of the wind disturbance event: magnitude, intensity, and frequency. Naturally, windstorms that are exceptionally large and/or intense cause particularly high levels of damage and mortality.

Both abiotic (e.g., winds, topography, soil) and biotic factors (e.g., individual tree characteristics, tree species, stand attributes) have long been recognized to interact to generate complex damage and mortality patterns. The features of a storm, forest location relative to the windstorm, pre-disturbance community attributes, disturbance history, and species susceptibility to wind all play a role in generating the complex and subtle patterns of damage.

Wind speeds undoubtedly are the primary determinant of damage severity. Rainfall is also a critical factor influencing both damage severity and tree damage type. At the landscape scale, the predictability of tree mortality risk is often correlated with site exposure and tree size. In most cases, much of the damage is concentrated at the topographic extremes, particularly near stream bottom as where the wettest soils are located (e.g., Carpino 1998, Chapter 3) and on ridges where the exposure to wind is greatest. Tree mortality risks at the stand scale are related to tree size and resistance to wind (which is determined largely by wood strength and fungal infections). Moreover, the occurrence of windstorms may also interact with other disturbance forces such as subsequent wildfires, insect outbreaks, and fungal infections in complex ways to increase the degree and unpredictability of damage in temperate forest (Pickett and White 1985, Webb 1999, Platt et al. 2003).

In temperate-zone forests, the most conspicuous changes caused by catastrophic winds are structural changes, and the degree of the structural change varies greatly. Relative to tropical forests, large but varied changes in species composition are reported in temperate forests following catastrophic winds (Table 1.2). The effects of high winds on tree composition and diversity vary greatly and depend on many contributing factors such as specific windstorm characteristics, site conditions, pre-disturbance community attributes,

forest disturbance history, and the temporal and spatial scales at which the changes are observed. With respect to tree diversity, previous studies in temperate forests have shown three possible outcomes: diversity enrichment, compositional maintenance, and loss of species diversity. Clearly, forests exhibit a wide range of responses to windstorms.

Consequently, the effects must to be examined at relevant spatial and temporal scales and in the context of specific site conditions and stand history.

Catastrophic windstorms have various effects on forest dynamics and successional development. Those effects vary greatly from setting back forest succession to speeding up succession. For example, in the Piedmont region I found that historical windstorms appear to have reduced the predictability of stand composition and to have accelerated the existing trend of late successional oak and hickory replacement by more light-demanding red maple. In addition, windstorms in these forests appear to be responsible for increased variance in regeneration, which contributes to a diverse but temporally relatively stable canopy layer. The long-term effects of catastrophic windstorms on forest composition, diversity, and succession are less known, but available evidence indicates that hurricane-induced changes in tree species composition and diversity can be long lasting. The occurrence of past hurricanes has served to further document and clarify the variable and non-equilibrium nature of late-successional, mixed-aged temperate hardwood forests (Chapter 5 and 6).

COMPLEXITY OF FOREST DAMAGE RESULTING FROM CATASTROPHIC WIND DISTURBANCES

Impacts on community structure

The most conspicuous forest changes caused by catastrophic winds are structural changes, which are often measured in terms of the changes in tree size or age distributions,

basal area or biomass, stem density, or canopy heterogeneity. Three relatively consistent patterns in structural change that have been reported in both wind-damaged tropical and temperate forests are 1) immediate increase in canopy heterogeneity, 2) short-term decrease in biomass, and 3) immediate decrease in density of all tree sizes followed by a dramatic increase in understory density a few years after wind damage. In temperate forests, degrees of the structural change vary greatly depending on many abiotic and biotic factors including wind intensities, rainfall associated with the storm, community attributes, site conditions, and susceptibility to windstorm damage.

Studies of forest damage have reported loss of stand biomass following catastrophic wind disturbances to be highly variable and to depend on wind intensity, forest type, site exposure to wind, pre-disturbance species composition, and interactions of these major factors with subsequent risk factors such as fires and insect infestations. Reported losses of stand biomass vary greatly from 2% to 94% among forests and wind events. In most reported cases, temperate forests have experienced extreme biomass loss due to the extreme intensities of windstorms and the high vulnerability of temperate forests to windstorm disturbances. The largest basal area loss reported thus far was in the northeastern temperate forests of the United States during the 1938 hurricane which resulted in about 94% basal area loss in a 2000-ha survey area (Spurr 1956, Foster 1988).

Catastrophic windstorms can substantially alter forest structure by simultaneously decreasing overall canopy height, increasing canopy patchiness, and increasing understory light heterogeneity. For example, hurricanes often result in a substantially increased gap size and a dramatic rise in understory light. Among studies of forest structural changes, canopy damage varies greatly from slight defoliation to about 90% increases in understory light

(Turton 1992, Veblen et al. 1989, Bellingham et al. 1996). In addition, catastrophic winds can increase within-stand spatial heterogeneity through clumped distribution of hurricane-induced tree mortality and aggregation patterns of surviving trees within the wind-damaged forest stands as a result of the uneven uprooting and stem snapping among different species and tree size classes (McDonald et al. 2003, Chapter 2).

Catastrophic winds have profound impacts on the size distribution of trees and can induce substantially increases in the relative abundance of small size-class trees in the damaged forests during the subsequent years. Although catastrophic windstorms usually cause immediate reduction in tree densities of all sizes, especially for large canopy trees, they often result in a dramatic increase in the density of understory seedlings and saplings several years after the windstorms due to subsequent release of suppressed understory stems and widespread sprouting. Sprouting is undoubtedly an important mechanism of tree recovery following windstorms in temperate forests. Studies have shown sprouting rates in the 20-80% percent range to be typical for temperate forests (Harcombe and Mark 1983, Peterson and Pickett 1991, DeCoster 1996).

My study on the effects of the 1996 Hurricane Fran on the Duke Forest in North Carolina has shown that hurricanes significantly diversify the live-tree size distribution in damaged forest stands. Overall, the predominant tree species of the upper canopy layer in both pine and hardwood forests decreased substantially due to the higher mortality of large-size trees. In the damaged pine stands, the mean size of the most dominant tree species (*Pinus taeda*) was increased and the density of pines decreased in all size classes. The hurricane also greatly affected pine stands by decreasing the relative abundance of small sized oaks (*Quercus spp.*) and hickories (*Carya spp.*). Several light-demanding and shade-

intolerant hardwood species, such as tuliptree (*Liriodendron tulipifera*) and sweetgum (*Liquidambar styraciflua*) increased dramatically in density in the smallest size class (1-3 cm) during the 5 years following the hurricane, whereas dogwood (*Cornus florida*), the most damaged tree in the pine stands, decreased in stem density in all tree sizes (Chapter 2). These general patterns should be broadly applicable to Piedmont forests and more generally to adjacent areas of the southeastern United States.

Complex patterns of tree mortality

The most obvious effect of catastrophic wind is tree mortality. Tree mortality in general appears to be positively related to wind intensity and inversely related to frequency. However, wind-induced mortality can be subtle, complex, and delayed, depending on several contributing factors such as the wind intensity, species of interest, individual size, and life form. In the literature, wind-induced tree mortality rates in temperate forests vary greatly among forest types and wind events ranging up to around 80%. Nonetheless, we lack a clear relationship between forest type and damage or tree mortality (Everham and Brokaw 1996).

In the tropics, tree mortality rates after a severe hurricane tend to be low. Walker (1991), for example, only recorded 7% mortality one year following Hurricane Hugo (a category 3 hurricane) in Puerto Rico. Bellingham (1991) found 8% tree mortality 23 months after Hurricane Gilbert in Jamaica. Whigham and others reported 11.2 % in a Mexican forest 17 months after Hurricane Gilbert. These forests experience high hurricane return rates and the tree species that occupy them appear well adapted to these frequent disturbances.

Wind-induced tree mortality in temperate forests varies from low to extremely high. For example, Batista and Platt (2003) reported 7% mortality for the overstory trees after the relatively modest 1985 Hurricane Kate in an old-growth forest. However, high tree mortality

by catastrophic winds has been reported for a number of temperate forests. Foster (1988) reported about 30% tree mortality for the 1938 hurricane in central New England, USA. Similarly, Hook and others (1991) found that Hurricane Hugo caused over 80% tree mortality in the Santee Experimental forest, South Carolina. In Piedmont forests, I found tree mortality of large-size trees to be doubled in the period that spanned the hurricane event, in comparison to the pre-hurricane, although this increased mortality was not uniformly distributed across species. In addition, there was widespread delayed mortality of hardwood tree species following the hurricane. These significant structural and dynamic changes appear likely to have a great and continuing influence on stand regeneration and forest development.

Tree mortality may vary among species. Several studies have assessed species-specific mortality caused by hurricanes in temperate forests (Foster 1988, 1992, Bellingham et al. 1995, 1996, Batista and Platt 2003). In a comprehensive study of response of trees to the 1938 hurricane in central New England, Foster (1988, 1992) found large differences among tree species in their susceptibility to windstorm damage. However, species-specific mortality may not always be clearly distinguished since other mortality risk factors may interact to contribute to the complex patterns of tree mortality. For example, in a study of the impact of a typhoon on Japanese warm temperate forests, Bellingham and others (1996) found that there was no consistent mortality pattern for most common species, but they found a few species, such as *Symplocos prunifolia*, sustained a high level of basal area loss, while others, such as *Podocarpus nagi*, had low mortality.

Understory mortality patterns are less documented than those of the overstory, both in tropical and temperate forests. In some cases understory mortality may be low due to the shielding effects from high canopy trees (Imbert 1996), but these effects vary among forests.

Other factors such as leaf litter, woody debris, and light may also contribute to the mortality patterns of seedlings and saplings. In temperate Piedmont forests, the most rapid changes following catastrophic winds were seen in the understory seedling layer (Chapter 4).

Seedling density and species richness experienced an immediate drop. This was followed by a rapid rebound in seedling density and more gradual recovery and enhancement in richness and diversity. Seedling recruitment did not increase continuously over time and overall seedling density was relatively low compared to pre-hurricane level. These disturbance-induced changes in the understory must be viewed in the context of variation in pre-disturbance tree species composition resulting from differences in habitat and stand history.

Cross-site comparisons of tree mortality between forests are needed for a number of reasons. One is the need to correct for variable background mortality rates among tree species, forest types, and successional phases. Another one is that mortality following large catastrophic windstorms is often delayed (Walker 1991, 1995, Sharitz et al. 1992). Temperate forest researchers have noticed that most damaged deciduous hardwood trees can remain alive for many years while still suffering enhanced mortality, plus a certain portion of the damaged trees might grow back through sprouting (e.g. Peterson and Pickett 1991, DeCoster 1996, Paciorek et al. 2000). Consequently, tree mortality must be examined over a long time period and in the context of background mortality of the specific species and successional phases. An immediately survey after a catastrophic wind event could significantly underestimate wind-induced tree death rates. I concur with the suggestion of Everham and Brokaw (1996) that “Mortality should be tracked for several years after catastrophic wind events to determine the extent of elevated mortality.” I further suggest that the 5-10 years of

observation of the damaged plots is critical for a better understanding of long-term recovery process, particularly the underlying mechanisms of forest recovery from large disturbances.

Change in species composition and diversity

Changes in species composition and diversity following wind damage in temperate forests are often gradual and complex. Such subtle compositional changes can only be understood through longer-term observation, and in the context of baseline data at specific spatial and temporal scales. To a large extent, these changes are difficult to detect without baseline data, which are rarely available.

A variety of patterns of change in species composition and diversity following large wind events have been reported in the literature. Relatively large changes in species composition and diversity are often, though not always, reported in temperate forests following catastrophic winds. With respect to tree species diversity, studies in temperate zone to date have shown three alternative outcomes: diversity enrichment, compositional maintenance, and loss of diversity. Species diversity enrichment may occur during long periods of recovery in places where a canopy species has been heavily damaged, thereby releasing species present in the understory and perhaps allowing establish of new species in the less competitive environment (Spurr 1956, Abrams and Scott 1989). Severe wind intensities are needed to create large patches and to reconfigure the limited resources such as light and soil nutrients. In these cases species diversity is enriched at the scales of the multiple-patch mosaic, and succession is set back (Webb 1999).

Changes in species composition in temperate forests following wind disturbance can be modest if the same species that regenerate in disturbed patches are most heavily damaged. For example, after examining changes in two Minnesota forests during 14 years following a

catastrophic windthrow, Palmer and others (2000) concluded that the windstorm affected understory species composition; and that the forests increased in understory species richness, but the magnitude of the changes was modest. There is also the case for positive neighborhood effects suggested by Frelich and Reich (1995). This model links the fate of a disturbed forest patch to the nature and strength of the overstory and understory relationship. Where the positive neighborhood effect is strong, little compositional change will occur because wind-thrown trees are often replaced by the same species (Webb 1999).

The third possible outcome of wind disturbance commonly seen in temperate forests is loss of species diversity following large wind disturbance. This outcome results when shade-intolerant species sustain heavy mortality and are unable to colonize disturbed patches because of a pre-established understory of shade-tolerant species. Sharitz and others (1992), for example, found that Hurricane Hugo reduced the tree diversity in the slough forest communities in a South Carolina riparian area by having disproportionately larger negative effects on shade-intolerant and transition species of the canopy than on the shade-tolerant species that dominated the subcanopy.

In the Piedmont temperate forests, changes in sapling diversity following the 1996 Hurricane Fran were varied. Mostly, sapling diversity increased slightly following the hurricane. However, a decrease of sapling diversity was also observed where canopy damage was extreme high, though this may ultimately prove to be compensated for by increased establishment of new seedlings of shade-intolerant species. The density of saplings initially decreased in most damaged plots, but sapling recruitment subsequently increased due to release of previously established seedlings. This observation is consistent not only with the

hypothesized relaxation of competition, but also the hypothesis that windthrow contributes greatly to tree diversity in the Piedmont temperate forests (Chapter 4).

FACTORS INFLUENCING MORTALITY AND THEIR INTERACTIONS

Severity of tree damage and mortality is related to both abiotic factors (e.g., winds, topography, and soil) and biotic factors (e.g., individual tree characteristics, tree species, stand attributes). Although wind speeds are the primary determinant of tree damage and mortality, topograph exposure, soil moisture and community attributes are the most important factors under similar wind conditions across landscapes. Exposure to winds, saturated soil, and high stand density are all associated with high tree damage and mortality risks. Tree species mixtures are also important for predicting landscape and stand-level damage severity, but evidence of species-specific damage and mortality can be less clear as species effects often interact with tree size.

Abiotic factors

Wind speed: Various studies have examined the relationship between wind speed and tree damage. In a broad sense, tree damage severity can be considered to be a function of wind speed. Fraser (1962) found that tree damage increases linearly with wind speed. Powell and others (1991) reported that little damage occurred below wind speeds of 17.5 m/s, and that trunk snapping and uprooting generally occurred at wind speeds above 33 m/s. Peltola (1996) found that the wind speed required to uproot a tree was much smaller than that required to cause the stem to break, and wind speeds of 12-14 m/s can be strong enough to uproot Scots pines (slender individuals) located along a stand edge. Since even in flat terrain wind speed can vary substantially at scales of less than a kilometer, the local variation in

wind speeds must be taken into account in examining landscape- and region-level wind damage (Foster and Boose 1992, DeCoster 1996, Peterson 2000).

Topography: Topographic exposure has been shown to have major effects on wind damage at the landscape scale. In a Jamaican forest Bellingham (1991) found higher damage on southern slopes and ridge crests that were exposed to the hurricane-face winds, while minor damage occurred on protected northern slopes. Boose and others (1992) found a similar pattern of hurricane damage in New England, USA; higher damage occurred on southwestern slopes exposed to the hurricane winds, whereas minor damage occurred in a protected deep valley. They concluded that topographic exposure, combined with wind intensity and forest stand attributes could largely explain damage patterns at landscape scale.

Soil features: Pre-hurricane soil moisture has been found to be a major factor in controlling whether uprooting or stem breakage is the dominant damage type (DeCoster 1996). Where the soil is dry, uprooting is more difficult, and trees more commonly experienced stem breakage. When the soil is wet, uprooting is more common (Chapter 2). In the cold temperate forest zone such as in Finland, soil frost can reduce uprooting, and a decrease in the period or depth of frost can make trees more vulnerable to windthrow (Peltola 1996).

Biotic factors

Individual tree architecture: Although not always true, the largest canopy trees often experience the most severe damage. Damage severity tends to increase approximately linearly with increasing tree height (e. g., Putz 1983, Walker et al. 1992). Peltola (1996) found the wind speeds required to blow down a tree or break the stem of a tree located along a stand edge decreased as the height-to-diameter ratio or the crown-to-stem weight ratio of

the trees increased (as well as more generally when the tree size increased). Consequently, pines with tall, slim stems are usually extremely vulnerable (Barry et al. 1998).

Species susceptibility: Tree species vary in their ability to withstand wind damage, their resistance depending on the interaction of several factors such as strength of wood, shape and size of the crown, extent and depth of root systems, shape of the bole (Barry et al. 1998), canopy characteristics, leaf features, and characters of root systems. Species with weaker wood (Webb 1989), low leaf reconfiguration ability (Vogel 1996), and shallower root systems (Lorimer 1977, Whitney 1986, Gresahm et al. 1991, Putz and Sharitz 1991) generally suffer greater damage and mortality, although it is difficult to distinguish the effects of species from effects of tree size (Falinski 1978). In the Duke Forest on the North Carolina Piedmont Hurricane Fran caused a higher incidence of damage in canopy hardwoods than pines. This was because hardwoods usually have broad spreading canopies and flat leaves that can catch the force of the wind much more readily than the smaller canopies and the needle leaves of pine trees. Moreover, hardwoods often have shallow, spreading root systems that increase their susceptibility to uprooting during hurricanes (Chapter 3).

Tree species can be classified into different groups based on their susceptibility to wind disturbance. Bellingham and Tanner (1995) studied tree damage and responsiveness in a Jamaican montane forest following Hurricane Gilbert. Based on indices of hurricane-caused damage (including short-term change in mortality and percent of stem that lost crown) and species response following the hurricane (including change in recruitment rate, change in growth rate, and frequency of sprouting), they classified 20 tree species into four groups: resistant (low damage, low response), susceptible (high damage, low response), resilient

(high damage, high response), and usurpers (low damage, high response). They further predicted that species classified as usurpers would increase their relative abundance in the forest in the next decades, while the susceptible tree species would decrease in relative abundance of adults. Similarly, in an old-growth forest damaged by hurricanes in southeastern USA, Batista and Platt (2003) classified 10 tree species into four similar syndromes of response to disturbance according to observed mortality, recruitment, and growth patterns: resilient, usurper, resistant and susceptible. Barry et al. (1998) have provided a rank of resistance of tree species to hurricane-related damage for the major tree species in the southern United States. Although a more complete classification is needed, these classifications provide helpful information for forest managers.

Community attributes: Community attributes such as stand height and age, stand density, and stand edge inevitably influence tree damage risk. Taller forests are generally subject to greater damage and mortality risk than shorter ones. This increase is thought to be primarily a result of greater exposure to wind in the canopy and the increased leverage achieved with canopy movement. Because wind speeds are much higher at and above the crown level than within the stand, the larger trees are subject to higher damage risk than shorter ones (Fraser 1964, Somerville 1980). Another reason for increasing damage with increasing stand height is that smaller, younger trees are generally more flexible to wind flows (Vogel 1996). Foster (1988, 1992) found where severe windthrow of more than 75% of the trees was reached, it mostly occurred in stands of ≥ 25 m height. Similarly, DeCoster (1996) reported a positive relationship between stand height and tree damage for 1989 Hurricane Hugo in South Carolina and for a separate severe tornado event on the Carolina Piedmont.

Literature reports on the effect of stand density on tree damage risk as have been variable. Most studies have shown a trend of increasing damage with decreasing stand density (Prior 1959, Busby 1965, Thomson 1983, Jane 1986, Foster 1988b, Hook et al. 1991), but there are contrasting results, in part because denser stands often consist of younger and more flexible trees. For example, Fraser (1965) found a dense stand would decrease the lateral spread of roots and therefore increase tree damage. Overall, the comprehensive and complex effect of stand density on tree damage is unclear, perhaps because the confounding effects of stand density, tree size, tree species, and tree architectural characteristics have generally not been adequately separated. These relationships need to be examined through more comprehensive field experiments (e.g., Peltola 1995, Vogel 1996).

Interactions of factors: Much of the complexity of tree damage and mortality are caused by meteorological, topographical, and biological factors simultaneously interacting to form patterns of damage. Consequently, the interactions among factors must to be taken into account to better understand wind-damage relationships. For example, DeCoster (1996) found the interactions between species and sizes were significant in predicting tree mortality risk in a temperate deciduous forest of South Carolina. Wind-induced effects and their interactions (e.g., insect breakouts, subsequent fires) need to be considered in evaluating indirect damage. For example, smaller trees sustain wounds caused by the falling tops of adjacent uprooted trees and the major branch breakages during the windstorm are often attacked by insects or affected by diseases (Barry 1996). Similarly, trees with damaged root systems are often invaded by root rot organisms and subjected to higher risk to subsequent windstorms (Pickett and White 1985).

In temperate forests, large wild fires often interact with hurricanes to cause greater forest damage (Platt et al. 2002). Myers and Lear (1998) in a literature review found that in temperate forests, conditions after exceptionally strong hurricanes promote the occurrence of fires of higher than normal intensity. Paleotempestological records also support this hurricane-fire interaction in the Holocene maritime pine-oak forests of the Gulf coast region (Liu 2003). Conversely, Kulakowski and Veblen (2002), working in montane forests of Colorado, found fire history and topography can influence the severity of wind blowdown and the susceptibility of forest stands to wind damage.

Ackerman and others (1991) developed a graphic model depicting expected variation in forest damage and recovery following hurricanes (Figure 1.2). The force exerted by a hurricane increases as a function of wind velocity and storm duration, and decreases with distance from the eye of the hurricane. Forest damage severity increases with intensity of a hurricane (i.e. wind speed), but the amplitude of the relationship depends on the physical and biotic factors of a given site, such as topography, geomorphology, soil moisture, species composition, vegetation structure, state of recovery since last disturbance, plant architecture, size, age, and anatomy. The influence of site factors on the extent of forest damage decreases as the magnitude of the hurricane increases.

Multiple factors simultaneously interact to contribute the observed damage complexity. Canham and others (2001), for example, examined the specific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. The implications of such interactions are still unclear. In future studies, research should address the interplay of multiple factors pre- and post wind disturbance events through experiments, modeling, and cross-site comparison to separate the confound effects.

FOREST RESPONSES

The distinct feature of wind-damaged forests, as compared with forests that have experienced other large, infrequent disturbances such as wild fires and volcano eruption, is that wind-damaged forests often have relatively rapid recovery through multiple recovery pathways. Foster and others (1991) identify two major regeneration pathways: 1) from surviving vegetation through advanced regeneration (advanced growth) and vegetative reproduction (sprouting), and 2) from seedling dispersal, recruitment and establishment (Figure 1.3). The rapid recovery of wind-damaged forests largely results from stem sprouting and the advanced growth of the surviving trees in the new environment of increased light, soil moisture, and nutrient resources. In addition, windthrow creates more diverse soil substrates and allows active seedling and sapling regeneration. Here I review studies of surviving trees and the understory response to canopy tree gaps and newly available soil.

Regrowth of surviving trees by sprouting

Regrowth plays an important role in tree recovery from catastrophic wind disturbances, especially in temperate hardwood deciduous forests. After damage by intensive winds, a high portion of hardwood trees can regrow from sprouts. Although several researchers have reported differences among species in sprouting ability in both tropical (Walker et al. 1992, Zimmerman et al. 1994, Bellingham et al. 1994) and temperate forests (Perterson and Pickett 1991, DeCoster 1996,), this capability appears common. In Piedmont forests of North Carolina, resprouting of damaged individuals and vegetative production of additional shoots were common for most hardwoods (Chapter 4).

Understory response to canopy gaps

The understory of damaged forests plays a major part in forest response to windstorms in temperate forests (Webb 1999). Three mechanisms have been often reported in the wind disturbance literature include release of understory plants, recruitment, and repression. “Release” refers to the rapid growth of suppressed understory plants following catastrophic disturbances. Strong winds often cause an increased growth of established seedlings and saplings of primarily shade-tolerant species that were present in the understory at the time of disturbance. Most work on plant “release” after catastrophic winds has been done for saplings and small trees, though the release of established seedlings could also be expected. Piedmont forests have remarkable resilience to hurricane damage because of widespread advanced regenerations. In Piedmont North Carolina, most tree seedlings and saplings approximately doubled their relative growth rates after the 1996 Hurricane Fran, although not uniformly across tree species.

Recruitment is the addition of new individuals into a community (Ribbens et al. 1995). Previous post-disturbance observations on seedling establishment have shown an increase in seedling density following hurricanes, due probably to increased light and soil nutrient availability (Guzman-Grajales and Walker 1991). In Puerto Rican forests, recruitment from seeds was promoted by the large increase in area of gaps and the increased understory light following Hurricane Hugo (Everham et al. 1998).

Repression refers to suppression of secondary succession by the establishment or growth of plants that restrict regrowth or recruitment of canopy trees; it also refers to forest succession suppressed by heavy litter. For example, in a New England deciduous forest, George and Bazzaz (1999a, 1999b) found that a fern understory could serve as an ecological filter that decreased establishment, growth, and survivals of canopy-tree seedlings.

Ground features: mounds and pits, leaf litter, and woody debris

In addition to increasing light, windstorms generate a highly diverse substrate with treefall mounds and pits, stumps, leaf litter, and rotting logs. With increased light, the microsites play important roles, influencing understory composition, species diversity, growth, and dynamics (Peterson et al. 1990, Webb 1999). These newly formed microsites often differ from intact forests in their greater soil moisture and nutrient availability, thereby allowing rapid establishment of species that require not only increased light, but also more abundant soil water and nutrients than typically found in an intact stand.

Although several studies have examined the roles of mounds and pits following windstorm disturbance, the results have varied greatly between forests. Walker and others (2000) examined seedling and saplings dynamics in treefall pits in a Puerto Rican rain forest and found that treefall pits significantly alter recruitment and mortality of many understory species, but not species richness. In some cases, mounds support more species than pits or un-damaged forests (e.g., Collin and Pickett 1982). However, Peterson and others (1990), working in a temperate forest, found lower species richness on mounds than in pits.

Increased leaf litter can be an important factor influencing seed germination and seedling establishment after windstorm disturbance. In addition, woody debris can provide important sites for germination and establishment (Webb 1999). Guzman-Grajales and Walker (1991) examined the effects of three litter treatments on seedling emergence, growth, density, and mortality during the year following Hurricane Hugo in a Puerto Rican forest. Their conclusion was that leaf litter is a major constraint to seedling recruitment. The role of leaf litter in temperate forests is still less known.

LONG-TERM EFFECTS OF CATASTROPHIC WIND DISTURBANCE

Despite the fact that much has been learned about immediate damage patterns and short-term impacts of catastrophic winds, less is known regarding long-term effects on forest composition, diversity, and succession. Study of long-term effects of historical wind events is difficult because rarely have ecologists been able to combine long-term pre-event and long-term post-event data. Moreover, the few long-term datasets that are available for this purpose were generally not designed or initiated with disturbance events in mind. Nonetheless, sufficient information is available to indicate that hurricanes can have long lasting effects on tree growth, species composition, diversity, and succession, and that these effects can vary greatly with wind intensities, pre-disturbance community attributes, and the timing of the winds (Figure 1.4).

Long-term effects on species composition and diversity

A widely accepted view among forest ecologists is that severe hurricanes have relatively minor long-term effects on species composition and diversity in tropical forest regions and coastal temperate regions where hurricanes are common. Many case studies in the tropics, including studies in Puerto Rico, Nicaragua, Jamaica, and Kolombangara, support this general conclusion (but see Vandermeer 2000). For example, Burslem and others (2000) found that historical hurricanes only had limited effects on species composition after 60 years of forest recovery.

In contrast with results from most tropical studies, significant but highly variable results regarding long-term change in community composition and species diversity have been reported in temperate forests (Table 1.2). Large, infrequent wind disturbance events have played an important role in shaping regional vegetation and influencing dynamics in many

temperate forests (Foster and Boose 1995, Webb 1999). Change in species diversity following catastrophic wind disturbance ranges from increasing to decreasing to no change, depending on many factors such as damage intensity as well as the scale of the investigation. However, large temperate-zone hurricanes generally have had a stronger impact on species richness in heavily damaged stands (Peet and Christensen 1980, Foster et al. 1998, Boose et al. 2001). For example, Peet and Christensen (1980) reported increased species richness in a comparison study of two hardwood plots in the Duke Forest, North Carolina Piedmont, 23 years after the 1954 Hurricane Hazel. The permanent plots that were severely damaged had twice as many as tree species saplings as compared with the number before Hurricane Hazel. This post-disturbance increase in regeneration of multiple species following an intense windstorm is consistent with a general pattern of dynamic, patch-driven regeneration and diversity maintenance in temperate forests.

Species dominance may shift substantially after wind disturbance because early successional species thrive in the hurricane-created gaps but as long-term term effects are less evident, Nonetheless, the addition of early succession species in those successional patches may lead to short-term increases in landscape diversity. Moreover, the results may be scale dependent. For example, following the 1989 Hurricane Hugo, Everham (1996) found that the number of plant species increased in some sites when observed at an intermediate spatial scale (i.e. hectares), but was essentially constant at both larger and smaller scales. Over the several decades following a hurricane, the short life span of the early successional species, coupled with the self-thinning process may again result in reduced dominance and landscape diversity. Thus, overall, catastrophic wind disturbance may have a limited small-scale effect on species diversity over time, while enhancing diversity at a landscape scale.

The lasting effects of windstorms on forest succession

Extreme windstorms tend to differentially remove the oldest and largest trees in a stand. As a consequence, large, catastrophic wind events has been concluded to significantly change forest structure and alter the rates of various processes in the temperate forests, even though their long-term effects on forest succession is uncertain (Waring and Schlesinger 1985, Foster and Boose 1995). Studies of the long-term wind effects on temperate forest succession to date have shown that windstorms can have all possible effects from setting succession back to advancing successional stages, to initiating multiple-stages of succession depending on wind intensity, frequency, forest types and their pre-disturbance successional stages.

The traditional idea that wind disturbance sets back succession to some earlier seral stage may apply in temperate forests where extreme high winds create large forest openings and initiate secondary succession. The mechanism for this change is that severe windstorms substantially damage the late-successional, canopy-dominant tree species and lead to establishment of early successional species. Therefore, 'setting back of succession' often occurs in the later successional hardwood forests exposed to extreme wind intensity. The New England hurricane of 1938, for example, leveled many thousands of acres of mature and semi-mature hardwood forests and initiated new forest associations over a large area with the long-lasting effects (Wilson et al. 2005).

Wind disturbance can also accelerate succession when early successional canopy tree species are heavily disturbed (White and Jentsch 2004, Chapter 2). In temperate forests where early successional tree species such as various pines and oaks are dominants, instantaneous death of the even-aged canopy by intensive winds tends to advance forest succession and differentially favor the shade-tolerant understory species. Abrams and Scott

(1989) in particular showed that windstorms, among other disturbances, can accelerate forest succession in some North American forest communities. The 1938 hurricane that caused in excess 30% tree mortality and large areas of windthrow in New England heavily damaged the earlier successional *Pinus strobus* forests, accelerating successional turnover to hardwood forests that were in some cases already present in the understory (Foster and Boose 1992). Arevola and others (2000) examined the changes in both pine forest and hardwood stands 14 years following a catastrophic windstorm in Minnesota and concluded that the wind disturbance acted to accelerate the successional process in both forest types by increasing the rate of compositional change from early successional pines and hardwoods to late-successional hardwoods. Although this pattern may be somewhat simplistic, the patterns they found appear common in temperate forests, especially in old-field forests.

When the dominants in temperate forests are damaged by windstorms but are replaced by same type of species, succession can be held at the same stage. In this regard, biotic factors such as propagule supply may strongly influence long-term forest recovery and succession following a large disturbance. In the case of intensive wind, the interactions of survivors and the pre-disturbance understory species (small trees and saplings) may determine the initial state in which the forest develops and the recovery pathways from the catastrophic wind event. Turner and others (1998) have argued that the abundance and spatial arrangement of the survivors and the arrival pattern of propagules may be the pivotal factors determining how succession differs between catastrophic disturbances of large and small extent. However, few studies actually examine this effect and the role of propagule in influencing forest regeneration and succession largely remains a matter of conjecture (Webb 1999).

THE ROLE OF THE PREDICTIVE MODELS FOR EVALUATING WIND IMPACTS

Ecologists and foresters have increasingly used modeling approaches to evaluate damage-risk factors and predict forest responses to large windstorms. The modeling methods combine available techniques from statistics, remote sensing, and GIS (Geographical Information System), and are attractive to ecologists and foresters, largely because they allow efficient and effective prediction of impacts by future windstorms.

A major focus of such modeling work has been integration of remote sensing, aerial photo, and ground field data with GIS software to assess damage risk factors at various spatial scales. For instance, Foster and Boose (1992, 1994) took an integrative approach through analysis of remotely sensed, historical and field data to assess actual forest damage in both tropical and temperate forests. They also developed meteorological and topographic exposure models to reconstruct wind conditions and site exposure to windstorms. Pleshikov and others (1998) developed a computer system for evaluating and predicting pine stand resistance to hurricane-force winds in central Siberia. They attempted to analyze risk factor at landscape, stand, and single-tree scales. Lindemann and Baker (2002) used GIS with CART (Classification and Regression Tree) and logistic regression to analyze a severe forest blowdown in the Southern Rocky Mountains and found that the blowdown was most influenced by the factors pertaining to the physical setting. However, McMaster (2005) suggested that detailed site factors such as average stem diameter, species, canopy height, and stand age are critical for improved accuracy of forest blowdown prediction.

Several studies have focused on modeling forest dynamics after large hurricanes. Doyle (1997) developed the HURISIM model for modeling hurricane effects on mangrove forests. He used historical simulations that included actual hurricane tracks and tree conditions and

found hurricanes account for the structural composition of modern day mangrove forests across south Florida. He suggested that the occurrence of major storms with a contemporary recurrence interval of 30 years may be the most important factor controlling mangrove ecosystem dynamics in south Florida. Canham and others (2001) developed maximum-likelihood models for simultaneously estimating both local storm severity and the parameters of functions that define species-specific variation in susceptibility to windthrow.

Development of spatially-explicit and landscape-scale models is becoming an active research arena of forest disturbance dynamics. These models have proven especially useful for examination of windstorm impacts. Kramer and others (2001) built such a spatially-explicit model to examine abiotic controls on windthrow and forest dynamics in southeast Alaska. More recently, Schumacher and others (2004) developed a modified LANDIS landscape model to examine the interaction among species-specific responses, intra- and inter-specific competition, and exogenous disturbance regimes including winds. Landscape models have an important role as tools for synthesizing existing information and making projections of possible future vegetation dynamics at large spatial scales.

In summary, developing and applying predictive models provides a new promising opportunity for evaluating windstorm-induced forest damage. The predictive models can project the loss/alteration of habitat and the resulting impact on species diversity, thus can be an effective evaluating tool, that when used properly, and in conjunction with other assessment techniques, could be a valuable aid in understanding forest damage patterns and controlling factors at various temporal and spatial scales. These models can also be an effective tool for post-damage forest management decision-making.

SYNTHESIS AND FUTURE DIRECTIONS

A general framework is needed for understanding the complexity of windstorm effects on temperate forests and subsequent forest response. In this paper, I combine illustrative examples to present a conceptual framework and then link them to several important themes that have emerged in recent years. Two relatively separated lines of investigation are apparent in the literature review, one focused on the complexity of forest damage patterns and their risk factors, and the other focused on the high degree of variation among forests in their structural and compositional responses to windstorm disturbances.

The variation among wind regimes and forest responses makes generalization a challenge. The literature here reviewed shows the complexity of pattern in forest damage and tree mortality following catastrophic wind, as well as the significant variation among forests in structural and composition responses. Many factors interact to influence the patterns of damage and dynamics of recovery. Therefore, evaluating the relative importance of multiple-factors and various recovery patterns across the full spectrum of disturbance severity levels will help elucidate these factors and their interactions. Nonetheless, there remains a clear need for additional studies that quantify wind disturbance severity and complexity of impact in high-wind damaged forests.

Windstorm-induced dynamics may vary at the different spatial and temporal scales. The ecological consequences of catastrophic winds are complex, subtle, and at smaller scales relatively unpredictable. Consequently, wind-induced changes must be viewed in the context of interaction and variations among multiple factors, especially species composition resulting from differences in habitat and stand history. Remarkably few studies have actually examined multiple factors and multiple-scale wind damage and forest recovery. Windstorm-

induced effects should be examined across a gradient of spatial and temporal scales. Such studies are needed to explore these complicated and scale-dependent processes and patterns.

Long-term studies of forest response to different combinations of the wind disturbance severity are needed. The variable effects of windstorms on temperate forests largely depend on the wind intensity, size, specificity, frequency of individual windstorms in a given location, pre-disturbance species composition, and successional stage. The complex impacts of winds and variable forest recovery are more readily discerned when detailed, long-term pre-disturbance and long-term post-disturbance data are available. Certainly, more extensive long-term studies on permanent research sites will be very important for understanding the long-term impacts.

Finally, better and more generally applicable models are needed for predicting the impacts of future catastrophic windstorm events on forests. Both population-based gap models and spatially explicit landscape models provide powerful tools for predicting forest disturbance and dynamics. Recent progress has been made in constructing such models applicable to temperate forests (Doyle 1997, Schumacher et al. 2004), but parameterization of these models for species-rich systems presents considerable challenges. Direct estimates of colonization and mortality rates from long-term studies in temperate forests could be highly valuable for improving these models. Predictive models will ultimately provide the knowledge essential for understanding the role of windstorm disturbances in forest communities, in guiding conservation efforts, and in informing forest management decisions.

LITERATURE CITED

- Abrams, M. D. and M. L. Scott. 1989. Disturbance-mediated accelerated succession in 2 Michigan forest types. *Forest Science* **35**:42-49.
- Abrams, M. D., D. G. Sprugel, and D. I. Dickmann. 1985. Multiple successional pathways on recently disturbed jack pine sites in Michigan. *Forest Ecology and Management* **10**:31-48.
- Ackerman, J. D., L. R. Walker, F. N. Scatena, and J. Wunderle. 1991. Ecological effects of hurricanes. *Bulleting of the Ecological Society of America* **72**:178-180.
- Akachuku, A. E. 1993. Recovery and morphology of *Pinus resinosa* trees 50 years after they were displaced by a hurricane. *Forest Ecology and Management* **56**:113-129.
- Allen, B. P., E. F. Pauley, and R. R. Sharitz. 1997. Hurricane impacts on liana populations in an old-growth southeastern bottomland forest. *Journal of the Torrey Botanical Society* **124**:34-42.
- Arevalo, J. R., J. K. Decoster, S. D. Mcalister, and M. W. Palmer. 2000. Changes in two Minnesota forests during 14 years following catastrophic windthrow. *Journal of Vegetation Science* **11**:833-840.
- Baker, G. T. 1915. A windfall problem. *Forestry Quarterly* **13**:317-324.
- Baker, W. L., P. H. Flaherty, J. D. Lindemann, T. T. Veblen, K. S. Eisenhart, and D. W. Kulakowski. 2002. Effect of vegetation on the impact of a severe blowdown in the southern Rocky Mountains, USA. *Forest Ecology and Management* **168**:63-75.
- Barnes, J. 2001. North Carolina's hurricane history. The University of North Carolina Press, Chapel Hill and London. USA.
- Barry, P., C. Doggett, R. Anderson, and K. Swain. 1998. How to evaluate and manage storm-damaged forest areas. United States Forest Service, Southern Region Management Bulletin R8-MB 63. 11 p.
- Batista, W. B. and W. J. Platt. 2003. Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. *Journal of Ecology* **91**:197-212.
- Batista, W. B., W. J. Platt, and R. E. Macchiavelli. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* **79**:38-53.
- Battaglia, L. L., R. R. Sharitz, and P. R. Minchin. 1999. Patterns of seedling and overstory composition along a gradient of hurricane disturbance in an old-growth bottomland hardwood community. *Canadian Journal of Forest Research* **29**:144-156.
- Bazzaz, F. A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. Pages 259-275 in H. A. Mooney and M. Godron, editors.

- Disturbance and Ecosystems -- Components of response. Springer-Verlag, Berlin, Germany.
- Beatty, S. W. and O. D. V. Sholes. 1988. Leaf litter effect on plant-species composition of deciduous forest treefall pits. *Canadian Journal of Forest Research* **18**:553-559.
- Beckage, B. and J. S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* **84**:1849-1861.
- Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research* **30**:1617-1631.
- Bellingham, P. J. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* **89**:409-416.
- Bellingham, P. J., V. Kapos, N. Varty, J. R. Healey, E. V. J. Tanner, D. L. Kelly, J. W. Dalling, L. S. Burns, D. Lee, and G. Sidrak. 1992. Hurricanes need not cause high mortality - the effects of Hurricane Gilbert on forests in Jamaica. *Journal of Tropical Ecology* **8**:217-223.
- Bellingham, P. J., T. Kohyama, and S. Aiba. 1996. The effects of a typhoon on Japanese warm temperate rainforests. *Ecological Research* **11**:229-247.
- Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1994. Sprouting of trees in Jamaican montane forests, after a hurricane. *Journal of Ecology* **82**:747-758.
- Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1995. Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* **76**:2562-2580.
- Boose, E. R., K. E. Chamberlin, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. *Ecological Monographs* **71**:27-48.
- Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* **64**:369-400.
- Boose, E. R., M. I. Serrano, and D. R. Foster. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs* **74**:335-352.
- Bormann, F. H. and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.
- Bormann, F. H. and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist* **67**:660-669.
- Boucher, D. H., J. H. Vandermeer, I. G. De La Cerda, M. A. Mallona, I. Perfecto, and N. Zamora. 2001. Post-agriculture versus post-hurricane succession in southeastern

- Nicaraguan rain forest. *Plant Ecology* **156**:131-137.
- Boucher, D. H., J. H. Vandermeer, K. Yih, and N. Zamora. 1990. Contrasting hurricane damage in tropical rain-forest and pine forest. *Ecology* **71**:2022-2024.
- Brewer, R. A. P. G. M. 1978. Windthrow and tree replacement in a climax beech-maple forest **30**:149-152.
- Brokaw, N. V. L. and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* **23**:442-447.
- Bromley, S. W. 1939. Factors influencing tree destruction during the New England hurricane. *Science* **90**: 15-16.
- Burslem, D. and T. C. Whitmore. 1999. Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *Journal of Vegetation Science* **10**:767-776.
- Burslem, D., T. C. Whitmore, and G. C. Brown. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology* **88**:1063-1078.
- Canham, C. D. and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* **65**:803-809.
- Canham, C. D., M. J. Papaik, and E. F. Latty. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research* **31**:1-10.
- Carlton, G. C. and F. A. Bazzaz. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. *Ecological Monographs* **68**:99-120.
- Carlton, G. C. and F. A. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* **79**:1305-1319.
- Carpino, E. 1998. Ecological determinants of hurricane damage in a southeastern piedmont forest. Master thesis. Duke University, Durham, North Carolina, USA.
- Christensen, N. L. 1988. Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. Page 62-81 *in* J. K. Agee and D. R. Johnson, editors. *Ecosystem Management for Parks and Wilderness*. University of Washington Press, Seattle, Washington, USA.
- Cooper-Ellis, S., D. R. Foster, G. Carlton, and A. Lezberg. 1999. Forest response to catastrophic wind: results from an experimental hurricane. *Ecology* **80**:2683-2696.
- Coutts, M. P. and J. Grace. 1995. *Wind and trees*. Cambridge University Press, Cambridge, UK.

- Curtis, J. D. 1943. Some observations of wind damage. *Journal of Forestry* **41**:877-882.
- DeCoster, J. K. 1996. Impacts of tornados and hurricanes on the community structure and dynamics of north and South Carolina forests. Ph.D. Dissertation. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.
- Denslow, J. S. 1980. Patterns of plant-species diversity during succession under different disturbance regimes. *Oecologia* **46**:18-21.
- Desteven, D., J. Kline, and P. E. Matthiae. 1991. Long-term changes in a Wisconsin *Fagus-Acer* forest in relation to glaze storm disturbance. *Journal of Vegetation Science* **2**:201-208.
- Doyle, T. W. 1997. Modeling hurricane effects on mangrove ecosystems. USGS Biological Resources Division USGS FS-095-97. 2 pp.
- Dunn, C. P., G. R. Guntenspergen, and J. R. Dorney. 1983. Catastrophic wind disturbance in an old-growth hemlock hardwood forest, Wisconsin. *Canadian Journal of Botany* **61**:211-217.
- Elliott, K. J., S. L. Hitchcock, and L. Krueger. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: hurricane opal and salvage logging. *Journal of the Torrey Botanical Society* **129**:48-59.
- Emanuel, K. A., 2005: Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* **436**:686-688.
- Ennos, A. R. 1997. Wind as an ecological factor. *Trends in Ecology & Evolution* **12**:108-111.
- Everham, E. M. and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. *Botanical Review* **62**:113-185.
- Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, southwestern New Hampshire, USA. *Journal of Ecology* **76**:105-134.
- Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology* **76**:135-151.
- Foster, D. R. and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology* **80**:79-98.
- Fraser, A. I. 1964, Wind tunnel and other related studies on coniferous trees and tree crops, *Scottish Forestry* **18**: 84-92
- Fujita, T. T. 1985. The Downburst, Microburst and Macroburst. SMRP Research Paper No. 210 (NTIS No. PB85-148880), University of Chicago, Chicago, Illinois, USA.

- George, L. O. and F. A. Bazzaz. 1999a. The fern understory as an ecological filter: growth and survival of canopy tree seedlings. *Ecology* **80**: 846-856.
- Glitzenstein, J. S. and P. A. Harcombe. 1988. Effects of the December 1983 tornado on forest vegetation of the Big Thicket, southeast Texas, USA. *Forest Ecology and Management* **25**:269-290.
- Glitzenstein, J. S., P. A. Harcombe, and D. R. Streng. 1986. Disturbance, succession, and maintenance of species-diversity in an east Texas forest. *Ecological Monographs* **56**:243-258.
- Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nunez, and W. M. Gray. 2001. The recent increase in Atlantic hurricane activity: causes and implications. *Science* **293**:474-479.
- Greenberg, C. H. and W. H. McNab. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. *Forest Ecology and Management* **104**:179-191.
- Gresham, C. A., T. M. Williams, and D. J. Lipscomb. 1991. Hurricane Hugo wind damage to southeastern united-states coastal forest tree species. *Biotropica* **23**:420-426.
- Guzman-Grajales, S. M. and L. R. Walker. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23**:407-413.
- Harcombe, P. A., C. J. Bill, M. Fulton, J. S. Glitzenstein, P. L. Marks, and I. S. Elisk. 2002. Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. *Journal of Ecology* **90**:947-957.
- Hibbs, D. E. 1983. 40 years of forest succession in central New England. *Ecology* **64**:1394-1401.
- Hook, D. D., M. A. Buford, and T. M. Williams. 1991, Impact of Hurricane Hugo on the South Carolina coastal plain forest: *Journal of Coastal Research* **SI. 8**: 291–300.
- Hubbell, S. P., R. B. Foster, S. T. O'brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. De Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* **283**:554-557.
- Imbert, D., A. Rousteau, and P. Labbe. 1998. Hurricanes and biological diversity in tropical forests - the case of Guadeloupe. *Acta Oecologica-International Journal of Ecology* **19**:251-262.
- Jarrell, J. D., M. Mayfield, and E. N. Rappaport. 2001. The deadliest, costliest, and most intense United States hurricanes from 1900 to 2000. NOAA Technical Memorandum NWS TPC-1.
- Kapustka, L. A. and R. G. Koch. 1979. The acceleration of succession of a birch-maple forest

- due to high wind. *Michigan Botanist* **18**:83-87.
- Kramer, M. G., A. J. Hansen, M. L. Taper, and E. J. Kissinger. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. *Ecology* **82**:2749-2768.
- Kulakowski, D. and T. T. Veblen. 2002. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. *Journal of Ecology* **90**:806-819.
- Kulakowski, D. and T. T. Veblen. 2003. Subalpine forest development following a blowdown in the Mount Zirkel Wilderness, Colorado. *Journal of Vegetation Science* **14**:653-660.
- Kwit, C., W. J. Platt, and H. H. Slater. 2000. Post-hurricane regeneration of pioneer plant species in south Florida subtropical hardwood hammocks. *Biotropica* **32**:244-251.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943-1967.
- Lindemann, J. D. and W. L. Baker. 2002. Using GIS to analyze a severe forest blowdown in the southern Rocky Mountains. *International Journal of Geographical Information Science* **16**:377-399.
- Liu, C. X., J. S. Glitzenstein, P. A. Harcombe, and R. G. Knox. 1997. Tornado and fire effects on tree species composition in a savanna in the Big Thicket National Preserve, southeast Texas, USA. *Forest Ecology and Management* **91**:279-289.
- Liu, K. B. and M. L. Fearn. 2000. Reconstruction of prehistoric landfall frequencies of catastrophic hurricanes in northwestern Florida from lake sediment records. *Quaternary Research* **54**:238-245.
- Lodge, D. J. and W. H. Mcdowell. 1991. Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica* **23**:373-378.
- Loope, L., M. Duever, A. Herndon, J. Snyder, and D. Jansen. 1994. Hurricane impact on uplands and fresh-water swamp forest. *Bioscience* **44**:238-246.
- Lorimer, C. G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. *Ecology* **70**:565-567.
- Lorimer, C. G. and L. E. Frelich. 1994. Natural disturbance regimes in old-growth northern hardwoods - implications for restoration efforts. *Journal of Forestry* **92**:33-38.
- Lugo, A. E. 2000. Effects and outcomes of Caribbean hurricanes in a climate change scenario. *Science of the Total Environment* **262**:243-251.
- Lugo, A. E. and R. B. Waide. 1993. Catastrophic and background disturbance of tropical ecosystems at the Luquillo Experimental Forest. *Journal of Biosciences* **18**:475-481.

- McMaster, K. J. 2005. Forest blowdown prediction: A correlation of remotely sensed contributing factors. *Northern Journal of Applied Forestry* **22**:48-53.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2003. Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a piedmont forest. *Journal of Vegetation Science* **14**:441-450.
- Merrens, E. J. and D. R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. *Journal of Ecology* **80**:787-795.
- Mitchell, S. J. 1995. The windthrow triangle - a relative windthrow hazard assessment procedure for forest managers. *Forestry Chronicle* **71**:446-450.
- Myers, R. K. and D. H. Van Lear. 1998. Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. *Forest Ecology and Management* **103**:265-276.
- Nobel, P. S. 1981. Wind as an ecological factor. Page 475–500 in Lange, O. L., Nobel, P. S., Osmond, C. B. and Ziegler, H, editors. *Physiological plant ecology I: Responses to the physical environment*, Encyclopedia of plant physiology new series vol. 12A. Springer-Verlag, Berlin, Germany.
- Palmer, M. W., S. D. Mcalister, J. R. Arevalo, and J. K. Decoster. 2000. Changes in the understory during 14 years following catastrophic windthrow in two Minnesota forests. *Journal of Vegetation Science* **11**:841-854.
- Pascarella, J. B., T. M. Aide, and J. K. Zimmerman. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. *Forest Ecology and Management* **199**:379-393.
- Peart, D. R., C. V. Cogbill, and P. A. Palmiotto. 1992. Effects of logging history and hurricane damage on canopy structure in a northern hardwoods forest. *Bulletin of the Torrey Botanical Club* **119**:29-38.
- Peet, R. K. and N. L. Christensen. 1980. Succession - a population process. *Vegetatio* **43**:131-140.
- Peet, R. K. and N. L. Christensen. 1987. Competition and tree death. *Bioscience* **37**:586-595.
- Peltola, Heli. 1996. Model computations on the wind flow and turning moment for Scots pine along the margins of clearcut areas. *Forest Ecology and Management* **83** (3): 203-215.
- Peterson, C. J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *Science of the Total Environment* **262**:287-311.
- Peterson, C. J. 2000. Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. *Forest Ecology and Management* **135**:237-252.

- Peterson, C. J. 2004. Within-stand variation in windthrow in southern boreal forests of Minnesota: is it predictable? *Canadian Journal of Forest Research* **34**:365-375.
- Peterson, C. J. and A. J. Rebertus. 1997. Tornado damage and initial recovery in three adjacent, lowland temperate forests in Missouri. *Journal of Vegetation Science* **8**:559-564.
- Peterson, C. J. and S. T. A. Pickett. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *Journal of Vegetation Science* **1**:657-662.
- Peterson, C. J. and S. T. A. Pickett. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock hardwoods forest. *Forest Ecology and Management* **42**:205-217.
- Peterson, C. J. and S. T. A. Pickett. 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. *Oikos* **90**:489-500.
- Pimm, S. L., G. E. Davis, L. Loope, C. T. Roman, T. J. Smith, and J. T. Tilmant. 1994. Hurricane Andrew. *Bioscience* **44**:224-229.
- Platt, W. J., B. Beckage, R. F. Doren, and H. H. Slater. 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna pines. *Ecology* **83**:1566-1572.
- Platt, W. J., R. F. Doren, and T. V. Armentano. 2000. Effects of hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the everglades region of south Florida (USA). *Plant Ecology* **146**:43-60.
- Pleshikov, F. I., V. A. Ryzkova, V. Y. Kaplunov, and J. V. Usoltseva. 1998. A computer system for evaluating and predicting hurricane impact on forest. *Safety Science* **30**:3-8.
- Putz, F. E., P. D. Coley, K. Lu, A. Montalvo, and A. Aiello. 1983. Uprooting and snapping of trees - structural determinants and ecological consequences. *Canadian Journal of Forest Research* **13**:1011-1020.
- Putz, F. E. and R. R. Sharitz. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, USA. *Canadian Journal of Forest Research* **21**:1765-1770.
- Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* **82**: 424-435.
- Reice, S. R. 2001. *The silver lining: the benefits of natural disasters*. Princeton University Press, Princeton, New Jersey, USA.
- Ruel, J. C. 1995. Understanding windthrow - silvicultural implications. *Forestry Chronicle* **71**:434-445.

- Ruel, J. C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. *Forest Ecology and Management* **135**:169-178.
- Ruel, J. C., S. J. Mitchell, and M. Dornier. 2002. A GIS based approach to map wind exposure for windthrow hazard rating. *Northern Journal of applied Forestry* **19**:183-187.
- Ruel, J. C. and M. Pineau. 2002. Windthrow as an important process for white spruce regeneration. *Forestry Chronicle* **78**:732-738.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* **63**:1533-1546.
- Runkle, J. R. 1985. Disturbance regimes in temperate forests. Pages 17-33 *in* S. T. A. Pickett and P. S. White, editors. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida, USA.
- Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1989. Tree uprooting - review of impacts on forest ecology. *Vegetatio* **79**:165-176.
- Schaetzl, R. J., S. F. Burns, T. W. Small, and D. L. Johnson. 1990. Tree uprooting - review of types and patterns of soil disturbance. *Physical Geography* **11**:277-291.
- Schulte, Lisa A. D. J. Mladenoff. 2005. Severe wind and fire regimes in northern forests: historical variability at the regional scale. *Ecology* **86** (2): 431-445.
- Sharitz, R.R., M.R. Vaitkus, and A.E. Cook. 1992. Hurricane damage to an old-growth floodplain forest in the southeast. Seventh Biennial Southern Silvicultural Research Conference, Mobile, Alabama, USA: 203-210.
- Schumacher, S., H. Bugmann, and D.J. Mladenoff. 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecological Modeling* **180**:175-194.
- Seischab, F. K. and D. Orwig. 1991. Catastrophic disturbances in the presettlement forests of western New York. *Bulletin of the Torrey Botanical Club* **118**:117-122.
- Sinton, D. S. and J. A. Jones. 2002. Extreme winds and windthrow in the Western Columbia River Gorge. *Northwest Science* **76**:173-182.
- Sinton, D. S., J. A. Jones, J. L. Ohmann, and F. J. Swanson. 2000. Windthrow disturbance, forest composition, and structure in the Bull Run basin, Oregon. *Ecology* **81**:2539-2556.
- Slater, H., W. J. Platt, D. B. Baker, and H. A. Johnson. 1995. Effects of Hurricane Andrew on damage and mortality of trees in subtropical hardwood hammocks on long pine key, everglades national park, Florida, USA. *Journal of Coastal Research* **21**:197-207.

- Smith, G. F., N. S. Nicholas, and S. M. Zedaker. 1997. Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. *Forest Ecology and Management* **95**:275-283.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353-391.
- Spurr, S. H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* **37**:443– 45.
- Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* **1**:511-523.
- Turner, M. G., V. H. Dale, and E. H. Everham. 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. *Bioscience* **47**:758-768.
- Turton, S. M. 1992. Understorey light environments in a north-east Australian rain-Forest before and after a tropical cyclone. *Journal of Tropical Ecology* **8**:241-252.
- Vandermeer, J., I. G. De La Cerda, D. Boucher, I. Perfecto, and J. Ruiz. 2000. Hurricane disturbance and tropical tree species diversity. *Science* **290**:788-791.
- Vandermeer, J., I. G. Delacerda, and D. Boucher. 1997. Contrasting growth rate patterns in eighteen tree species from a post-hurricane forest in Nicaragua. *Biotropica* **29**:151-161.
- Vandermeer, J., M. A. Mallona, D. Boucher, K. Yih, and I. Perfecto. 1995. 3 years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua - evidence in support of the direct regeneration hypothesis. *Journal of Tropical Ecology* **11**:465-471.
- Veblen, T. T., D. Kulakowski, K. S. Eisenhart, and W. L. Baker. 2001. Subalpine forest damage from a severe windstorm in northern Colorado. *Canadian Journal of Forest Research* **31**:2089-2097.
- Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1989. Blowdown and stand development in a Colorado subalpine forest. *Canadian Journal of Forest Research* **19**:1218-1225.
- Vogel S. 1996. Blowing in the wind: storm-resisting features of the design of trees. *Journal of Arboriculture* **22**: 92–98.
- Uriarte, M., C. D. Canham, J. Thompson, and J. K. Zimmerman 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecological Monographs* **74**(4): 591-614.
- Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo

- Experimental Forest, Puerto Rico. *Biotropica* **23**:379-385.
- Walker, L. R. 1995. Timing of post-hurricane tree mortality in Puerto Rico. *Journal of Tropical Ecology* **11**:315-320.
- Walker, L.R. 2000. Seedling and sapling dynamics in treefall pits in Puerto Rico. *Biotropica* **32**:262-275.
- Walker, L. R., J. Voltzow, J. D. Ackerman, D. S. Fernandez, and N. Fetcher. 1992. Immediate impact of Hurricane Hugo on a Puerto-Rican rain-forest. *Ecology* **73**:691-694.
- Waring, R. H. and W. H. Schlesinger. 1985. *Forest ecosystems: concepts and management*. Academic Press, Orlando, Florida, USA.
- Webb, S. L. 1988. Windstorm damage and microsite colonization in 2 Minnesota forests. *Canadian Journal of Forest Research* **18**:1186-1195.
- Webb, S. L. 1989. Contrasting windstorm consequences in 2 forests, Itasca State Park, Minnesota. *Ecology* **70**:1167-1180.
- Webb, S. L. 1999. Wind disturbances in temperate forests. Page 187-222 *in* L. R. Walker, editor. *Ecosystems of disturbed ground*. Elsevier, Amsterdam, The Netherlands.
- Webb, S. L. and S. E. Scanga. 2001. Windstorm disturbance without patch dynamics: twelve years of change in a Minnesota forest. *Ecology* **82**:893-897.
- Whigham, D. F., M. B. Dickinson, and N. V. L. Brokaw. 1999. Background canopy gap and catastrophic wind disturbance in tropical forests. Pages 223-252 *in* L. R. Walker, editor. *Ecosystems of Disturbed Ground*. Elsevier, Amsterdam, The Netherlands.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229-299.
- White, P. S. and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* **62**:399-450.
- White, P. S. and A. Jentsch. 2004. Disturbance, succession, and community assembly in terrestrial plant communities. Pages 342-366 *in* V. Temperton, R. Hobbs, and S. Halle, editors. *Assembly Rules and Restoration Ecology*. Island Press, California, USA.
- White, R. D. 1999. The impacts of hurricane Fran on a North Carolina piedmont woodland. Master thesis. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.
- Wilkinson, R. C., Britt, R.W., Spence, E.A. And Seiber, S.M. 1978. Hurricane-tornado damage, mortality, and insect infestations of slash pine. *South Journal of Applied*

Forestry **2**:132-134.

Zimmerman, J. K., T. M. Aide, M. Rosario, M. Serrano, and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management* **77**:65-76.

Zhang, Q., Pregitzer, K.S., and Reed, D.D. 1999. Catastrophic disturbance in the presettlement forests of the Upper Peninsula of Michigan. *Canadian Journal of Forest Research* **29**(1) 106-114.

Table 1.1. List of studies of catastrophic windstorms in temperate forests since 1998 by geographic locality, forest type, and windstorm type.

Location	Forest types	Windstorm types	Reference
Asia			
Taiwan (northern)	hardwoods	typhoon	Mabry et al. 1998, Lin et al. 2003
China	northern forests	wind and snow	Zhu et al. 2005
Japan	subtropical	typhoon	Xu et al. 2003b, 2004
New Zealand	planted forests	windstorms	Moore and Quine 2003
Europe			
United Kingdom	spruce forests	windstorm	Quine 2003
Finland	boreal forest	wind and snow damage	Pellikka and Järvenpää 2003
North America			
<i>Canada</i>	boreal forest	windstorm	Mitchell et al. 2001
<i>United States</i>			
Alaska (south)	coastal temperate rainforest	severe windstorm	Kramer et al. 2001
Colorado	subalpine forest	severe windstorm	Veblen et al. 2001
Colorado	<i>Picea-Abies-Pinus</i> forest	severe windstorm	Lidemann and Baker 2002
Florida (northern)	mixed-hardwoods	hurricanes	Batista and Platt 2003
Florida	slash pine savannas	hurricanes	Platt et al. 2000, 2002
Massachusetts	hardwoods	hurricane	Wilson et al. 2005
Michigan	hardwoods	windstorms	Woods 2000, 2001
Minnesota	hardwood	severe windstorm	Peterson 2004
New England	hardwoods	hurricanes	Boose et al. 2001
New York	forests	severe windstorm	McMaster 2005
North Carolina	hardwoods	hurricane	White 1999, Capino 1998
North Carolina	Appalachian hardwoods	hurricanes	Elliott et al. 2002
North Carolina	xeric oak hardwoods	hurricane and downburst	Greenberg and McNab 1998
Pennsylvania	hemlock-hardwoods forest	tornados	Peterson 2000
Texas	southern mixed hardwood forest	hurricane & severe storm	Harcombe et al. 2002

Table 1.2. Comparison of temperate forests and tropical forests, early succession forests and late succession forests in their responses to catastrophic wind disturbance events.

	Damage patterns and forest responses	Citation
Temperate forests	Although geographically variable, generally a low frequency of hurricane damage, but less intense. Windstorms are frequent. Trees are more susceptible to windthrows. In some cases damage severity can be extremely high. Release of advanced regeneration is common. Greater prortion of uprooting than in other types.	Forster 1992, Peterson 2002
Tropical forests	Again geographically variable, but in general more frequent catastrophic hurricanes. Trees are more wind-resistant. Less composition and diversity change; high and relatively stable tree species diversity. Regrowth and sprouting are common.	Walker 2002, Whigham 2003
Early succession forests (Pine forests)	The young trees of secondary forests are typically more resistant to Wind throw than the larger and more brittle trees of old growth. Increased pioneer species in the damaged forests.	Webb 1989, 2000
Late succession forests (Hardwood forests)	Forests are susceptible to windthrows. Diversified forest structure and dynamics; Maintained, increased or lost of tree species.	Mitchell et al. 2004

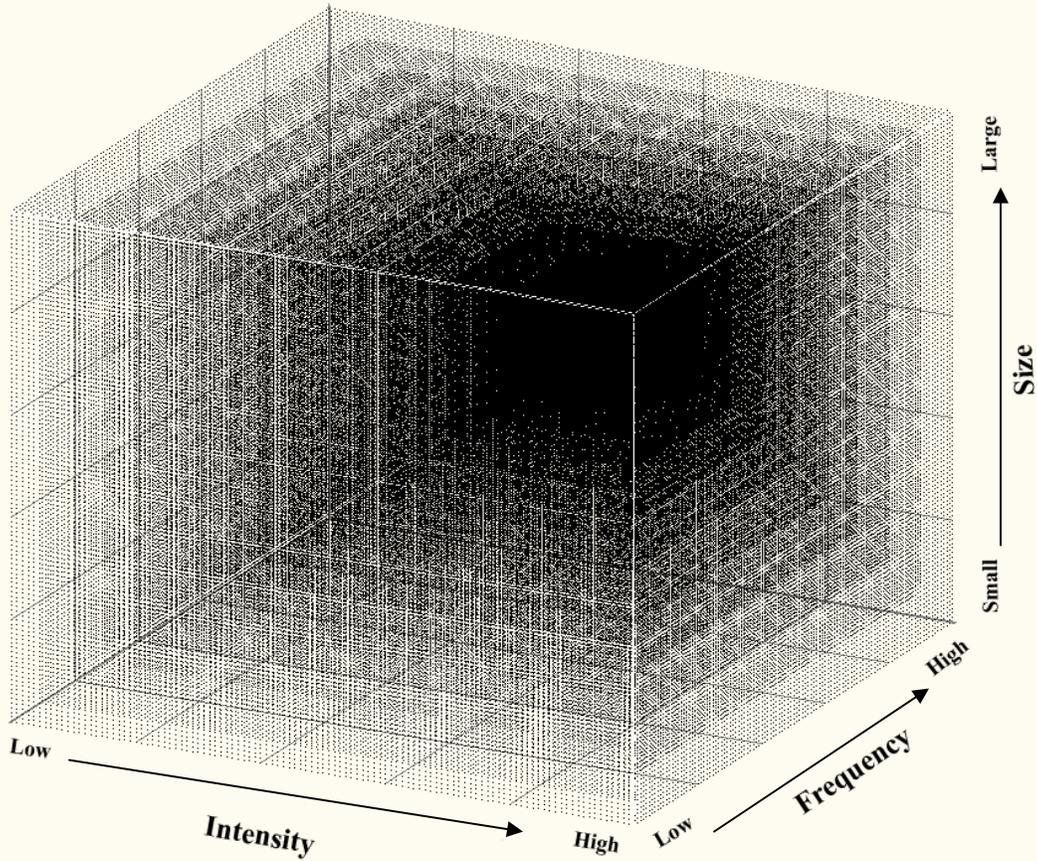


Figure 1.1. Conceptual model of temperate forests in response to varied wind regime (as a function of wind intensity, frequency and size). Forest structure, species composition, and diversity are more predictable when wind frequency is high but wind intensity is low (light portions). Community structure and diversity of the damaged forests become less predictable when intensity increases and frequency decreases, as in the case of large, infrequent hurricanes in temperate forests (dark portions). The importance of pre-disturbance community attributes and site conditions decreases when wind intensity increases.

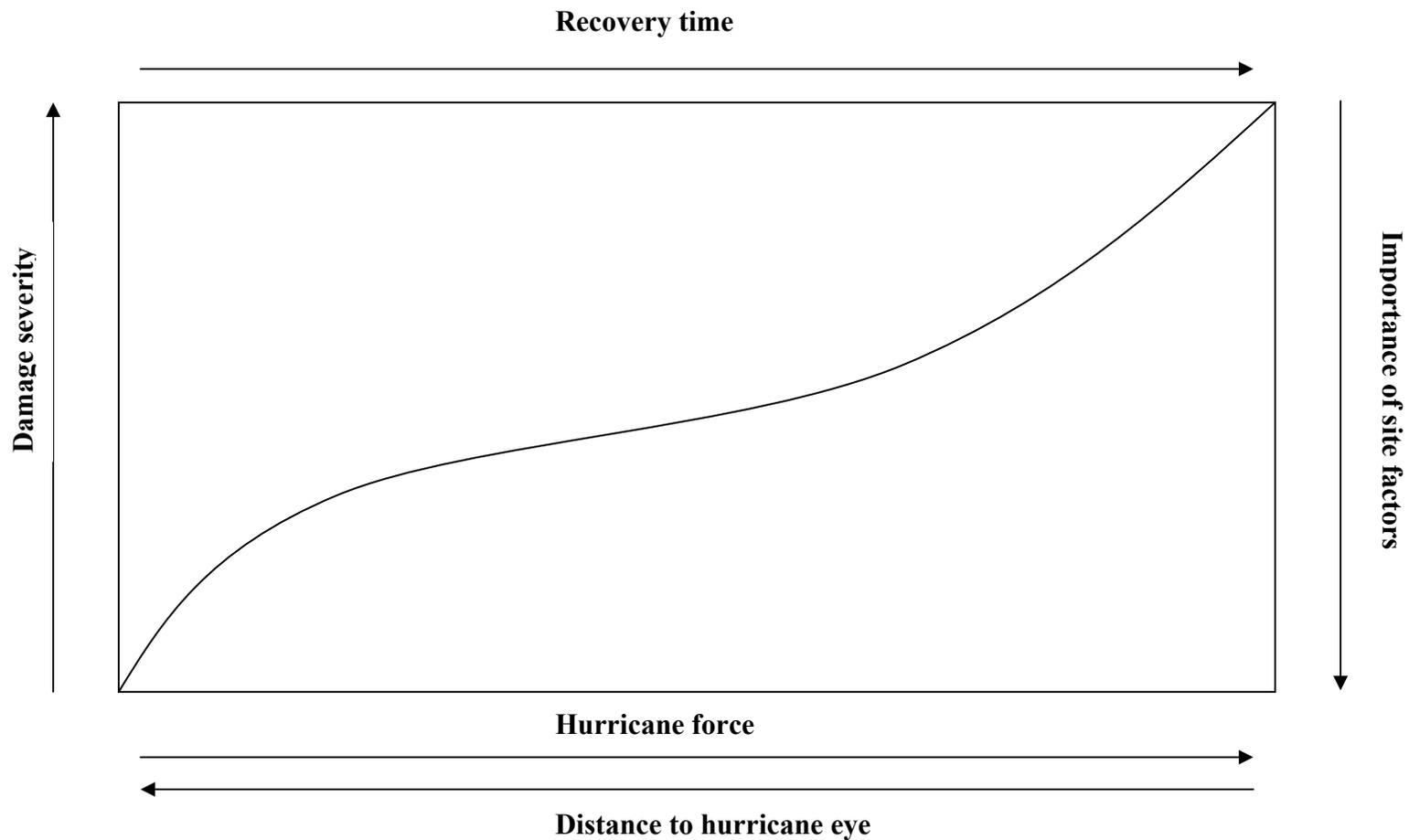


Figure 1.2. Damage severity and importance of site factors vary with wind intensity. Hurricane force is a function of wind speed, duration of storm and rainfall. Vegetation damage is a function of combined progression from defoliation to treefall, and from localized to widespread destruction. (After Ackerman et al. 1991).

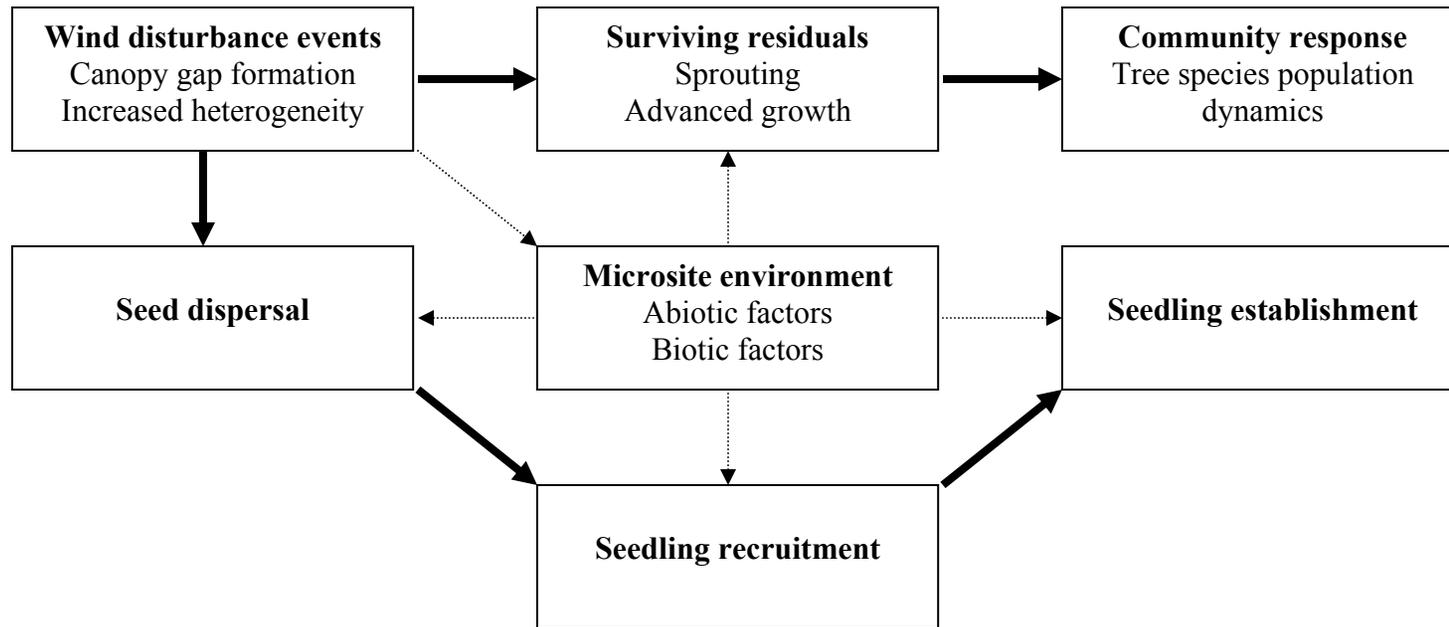


Figure 1.3. Conceptual model of temperate forest regeneration following hurricane disturbance. Two major recovery pathways are represented by large arrows. The microsite environment influences each stage of the pathway of regeneration from seed but exerts less influence on the pathway of regeneration from surviving vegetation (Modified from Foster et al. 1991).

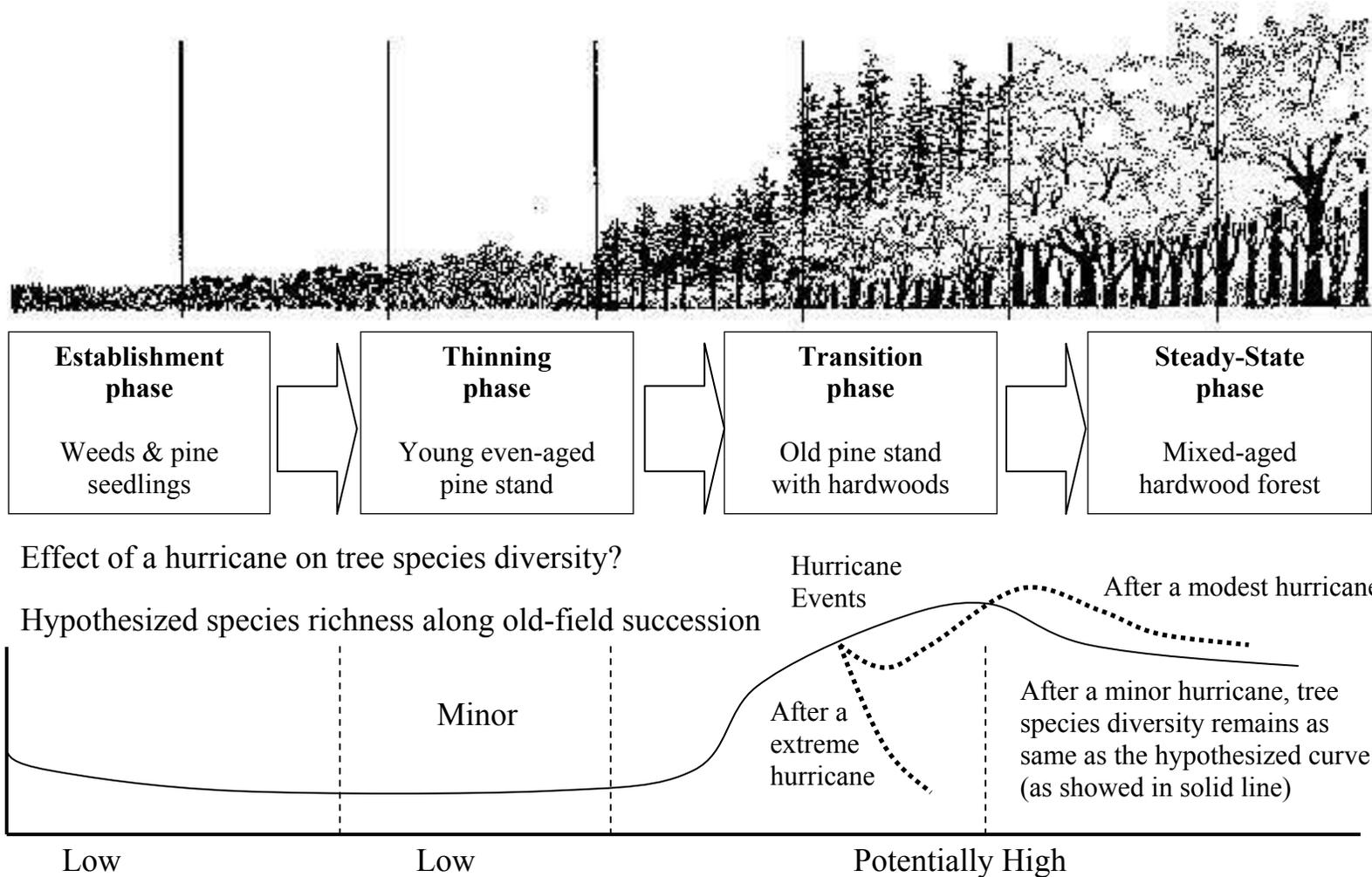


Figure 1.4. Old-field succession on Piedmont and four-stage forest succession model and hypothesized tree species diversity curve (as showed in solid line) over time. The effect of a hurricane on tree species diversity is low during the establishment and thinning phases, impacts are potentially high at the transition and steady-state phases. Changes in species richness impacted by extreme and modest hurricanes are showed as dash-lines. When wind intensity is low, tree richness changes minor. Modest wind intensity may increase tree diversity over time. When extreme winds occur, tree species diversity may decrease.

CHAPTER 2

THE IMMEDIATE IMPACT OF HURRICANE FRAN ON THE STRUCTURE AND TREE SPECIES COMPOSITION OF NORTH CAROLINA PIEDMONT FORESTS

Abstract. In September 1996, Hurricane Fran crossed the central Piedmont of North Carolina and significantly damaged many long-term permanent research plots in the Duke Forest. I surveyed stem damage and tree mortality in 34 long-term permanent plots (ca. 70-year record; 404-1,012 m²) and seven intensive mapped tree stands (ca. 20-year record; 5,250-65,000 m²) representing both transition phase even-aged pine stands mixed-aged upland hardwood forests.

Uprooting was the major damage type for the overstory trees (d.b.h.>10 cm), largely due to the exposure of the crowns to high wind combined with heavy rainfall during and prior to the storm. Uprooting varied greatly among the plots, ranging from 0 to 53.3%. The probability of stem uprooting was positively correlated with pre-hurricane tree size. Saplings, juvenile trees, and small trees (1-10 cm d.b.h.) of the understory and midstory were mainly damaged by being pinned or bent by their large neighbors.

Hurricane-induced tree mortality varied weakly among species, was positively correlated with pre-hurricane tree size, and remained up to two-fold higher five years after the hurricane than pre-hurricane background mortality. Spatial point pattern analysis revealed a patchy distribution of tree mortality during the hurricane sampling interval.

Within-stand damage variation was high. 1000 m² subplots in two large, mapped pine stands had mean damage indices of 0.58 and 0.52, with a standard deviation of 0.42 and 0.47

respectively. The mean damage indices of the five mapped, mixed-aged hardwood plots ranged from 0.07 to 0.64, with the standard deviations either greater than or close to the means. Hurricane Fran resulted in a dramatic increase in average gap size from the pre-hurricane of ca. 400 m² to 1100 m² after the hurricane, whereas maximum gap sizes reached 18-34 times larger than the pre-hurricane levels.

Key-word: wind disturbance, hurricane damage, Hurricane Fran, delayed tree mortality, secondary succession, stand dynamics, structural heterogeneity, Duke Forest.

INTRODUCTION

Hurricanes have long been recognized to have major immediate impacts on forests in both tropical and temperate regions (e.g., Bromley 1939, Spurr 1956), and more recently have been viewed as a potential key factor in long-term variation in vegetation structure, species composition, community dynamics, species diversity, and major ecosystem processes (e.g., Foster 1988, Boucher et al. 1990, Putz and Sharitz 1991, Brokaw and Grear 1991, Hook et al. 1991, Walker 1991, Bellingham et al. 1992, Bellingham et al. 1991, Boose et al. 1994, Foster and Boose 1995, Merrens and Peart 1992, Bellingham et al. 1995, Vandermeer et al. 1995, Imbert et al. 1996, Turner et al. 1997, Allen and Sharitz 1999, Herbert et al. 1999, Burslem et al. 2000, Sinton et al. 2000, Boose et al. 2001, McNulty 2002, Platt et al. 2002, Uriarte et al. 2004).

Hurricanes can have profound impacts on temperate forests, but owing to their infrequent nature, these effects rarely have been examined in detail, especially through a combination of long-term pre-hurricane and post-hurricane data. Such data are undoubtedly important for separating confounding variables to evaluate the true effects of hurricanes. This partitioning of effects, however, has not been well addressed in previous hurricane damage

studies due to the general absence of long-term pre-hurricane data (but see Brokaw and Gears 1991, Zimmerman et al. 1994, Bellingham et al. 1995, Burslem et al. 2000, Platt et al. 2002). Nonetheless, without such partitioning of confounding effects, there is the potential for misunderstanding of the effects of catastrophic wind events (Everham and Brokaw 1996).

In September 1996 Hurricane Fran, a large category-3 hurricane, struck central North Carolina and caused substantial tree damage and mortality in Coastal Plain and Piedmont forests. The storm passed directly over the Duke Forest, an ecological research area for which there are available many years of baseline data on tree, seedling and sapling dynamics, in some cases dating to the early 1930s. The occurrence of Hurricane Fran provides an exceptional opportunity to examine the impacts of a large, infrequent wind event on a series of forest sites varying in species composition, habitats and stand history. I used the available long-term (i.e., over 20 years) baseline information on tree establishment, mortality, and growth, and an additional 5 years of post-hurricane tree recovery data to assess patterns of stem damage, tree mortality, and characteristics of forest recovery in North Carolina Piedmont forests. The time-series data spanning the disturbance event allowed me to separate damage effects from the dynamic baseline.

Hurricanes are the most destructive force of natural disturbance typically encountered on the Piedmont of the eastern United States. Major hurricanes disturb the typical Piedmont forest on average every 50 years. During the 20th century, two major hurricanes crossed central North Carolina and caused extensive tree damage in the Piedmont: Hurricane Fran in 1996 and Hurricane Hazel in 1954. In this chapter I address the influence of these large, infrequent hurricane events on the structure and composition of Piedmont forests by comparison of hurricane-induced structural and compositional changes with the background

forest dynamics. I focus on immediate hurricane damage patterns, hurricane-induced short-term structural and compositional changes of in the tree population (stem d.b.h > 1 cm), as well as the delayed effects evident in the five-year period following the hurricane.

I first quantify stand-level tree damage severity and examine the variance of hurricane damage across the landscape (i.e., among plots), and then estimate the increased spatial heterogeneity by comparing tree gap formation rates and tree spatial point patterns of different strata before and after the hurricane. For the first time, I assess damage variation within large-scale plots to examine the spatial distribution of damage severity. I further assess the changes in tree density and basal area following the hurricane in comparison with their projected level of change without hurricane disturbance. Finally, I examine species-specific and size-specific tree mortality and growth rates over a 5-year period following the disturbance to examine delayed effects.

The specific focus of my study was to examine the immediate and short-term effects of a large hurricane event in terms of damage to structure, composition, and dynamics in the Duke Forest of the North Carolina Piedmont. My specific objectives were to: 1) assess both the landscape-scale and the within-stand forest damage variance; 2) examine species- and size-specific tree mortality and the delayed effects; 3) quantify within-stand hurricane-induced gap formation rates and the changes in forest structural heterogeneity; and 4) examine composition change and predict the dynamic trends in the Piedmont forests. My overall goal was to apply this information to assess 1) variation in stem damage within a stand and across a forested landscape like the Duke Forest, 2) the extent to which tree size distribution and spatial pattern were affected within a relatively homogeneous stand, and 3) stand compositional change over the five years following the hurricane.

METHODS

Study area

The study was conducted in the Duke Forest, Orange and Durham Counties, North Carolina, USA (approximately 35° 52' N, 79° 59' W, Figure 2.1). Varied topography, moderate climate, and a long disturbance history maintain within this research forest a diversity of tree species and forest types. Over 100 species of trees have been identified in the area (Palmer 1990). Particularly prominent major stand types in the Duke Forest include even-aged successional loblolly pine (*Pinus taeda*) forest (ca. 80 to 100 years old) and the mixed-aged mature upland deciduous hardwood forest. The current pine stands in the Duke Forest are the result of reversion from past farmland abandonment, and they are currently in the transition phase of the on-going old-field succession (Peet et al. 1987, Peet and Christensen 1987, 1988, Peet 1992). The mixed-aged hardwood forest type is close to the putative original or 'climax' forest type of the Piedmont. The current mixed-aged hardwood stands are mostly secondary forests that have been variously influenced by the past disturbances (e.g., chronic low-intensity wildfires in the 1700s, and selective cutting and grazing in 1800s, and varied windstorms damage).

The Duke forest has served as a model system and has been home to a wide range of ecological studies on forest succession and productivity since its establishment in early 1930s (e.g., Billings 1938, Korstian and Coile 1938, Oosting 1942, Kozlowski 1949, Keever 1950, Bormann 1953, Christensen 1977, Christensen and Peet 1981, 1984, Peet and Christensen 1979, 1980, 1987, 1988, see review by Peet 1992). More detailed descriptions of site conditions, community types, and successional dynamics can be found in previous research

papers focused on this area (Oosting 1942, Bormann 1953, Peet et al. 1987, Peet and Christensen 1987, 1988, Peet 1992, McDonald et al. 2003, Kaverna et al. 2005).

Vegetation plots

Duke Forest contains a series of long-term permanent plots distributed throughout the forest. A set of 51 permanent sample plots (PSPs, 404 to 1012 m²) was established during the 1930s in an attempt to monitor growth and species composition within stands of various age and site condition, primarily for applied forestry purposes. These sampling plots contain information on all woody stems greater than 1.25 cm diameter at breast height (d.b.h.), stem coordinates, stem d.b.h, tree height, and tree condition (live or dead). Remeasurement of PSPs has been carried out at about 5-year intervals since their establishment. A total of 34 PSPs including 28 even-aged pine stands and six mixed-aged deciduous hardwood stands remain (Figure 2.2).

Seven extensive forest areas of mapped permanent plots (MPPs) were established in the Duke Forest in the late 1970s by Peet and Christensen to study spatial patterns and processes (Table 2.1, Figure 2.2). These large, extensively mapped forest stands vary in size from 5,250 to 65,536 m², and essentially the same information was recorded as with the PSPs except for tree height (Table 2.1). The seven MPPs represent two major forest types of different successional status in North Carolina Piedmont forests: the transition phase of older but even-aged pine stands with a hardwood understory (ca. 80 to 100 years old), and the mature mixed-aged upland deciduous hardwood forest (Peet 1992). As with the PSPs, resurvey of these MPPs has been carried out at about 5-year intervals since their establishment.

Hurricane Fran

Much of the Duke Forest was significantly damaged by Hurricane Fran in 1996. Hurricane Fran was one of the most destructive hurricanes in North Carolina history and the fourth most costly hurricane on the United States mainland in the 20th century (Barnes 2001). Hurricane Fran was a large category-3 hurricane when it made landfall near Cape Fear on the southeast coast of North Carolina. After making landfall, it moved from southeast to the northwest across North Carolina's Coastal Plain and Piedmont (Figure 2.1). On September 6, 1996, Fran struck the Duke Forest and adjacent areas, its eye passing about 24 km to the east of the forest. Although wind intensity had begun to decrease, Hurricane Fran still caused substantial forest damage in these central North Carolina Piedmont forests.

The maximum sustained wind speed at Raleigh-Durham international airport, the nearest official weather station to the Duke Forest, was about 26.82 m/s. The maximum wind gust recorded was 31.85 m/s. Beside the high winds, Hurricane Fran brought a huge amount of rainfall along its path. The total rainfall at Raleigh-Durham International Airport was 224 mm during the two-day hurricane period. In addition, the Duke Forest had received nearly 76 mm of rainfall two days prior to Hurricane Fran and another 51 mm immediately afterward. Overall, this forest region experienced about 423 mm rainfall total for September 1996, the highest ever in a single month since 1908 (The National Hurricane Center, The State Climate Office of North Carolina). The large amount of rainfall softened the soils and greatly facilitated tree blowdown during Hurricane Fran.

Tree stem damage assessment

In the summer of 1997, the first growing season following Hurricane Fran, I resurveyed all of the 34 PSPs and three MPPs in the Duke Forest. Other four MPPs were resurveyed the subsequent summer. During the surveys, in addition to continuing measurement of vitality,

diameter, height (for PSPs only), and survival, I quantified hurricane damage status for each individual stem in the plots with stem damage codes. The stem damage codes I used were uprooting (no such damage, partial uprooting, complete uprooting), breakage (no such damage, < 10%, 10-35%, 35-90%, and > 90% canopy loss), leaning (no such damage, lean over 10%, supported by another tree, down on ground), and leaned on (no such damage, upright, supporting a tree, bent or leaning, pinned). The azimuth of each fallen bole was measured by compass. In all, about 45,800 trees >1 cm in d.b.h. were evaluated for damage status across a total 178,500 m² (17.85 ha) sampling area. All trees in the 34 PSPs and the seven MPPs were remeasured in the summers of 2000 and 2001 for their tree condition, stem d.b.h. and (for PSPs) tree height.

As tree stems often suffered multiple damage types and events, I created an ‘integrated stem damage code’ by combining all the information of uprooting, breakage, leaning and leaned on into a single code ranging from 0-3. I defined a damaged stem as code 3 if a tree sustained severe damage (i.e., completely uprooted, ≥90% canopy lost, or leaned down on the ground), code 2 if a tree sustained substantial damage (i.e., partially uprooted, 35-90% canopy loss, leaned but supported by other trees, or was pinned by neighbors), an code 1 if a tree sustained modest damage (i.e., 10-35% canopy loss, leaning over 10%, or bent > 10% crown displacement. Code 0 is for minor or no damage. These damage codes were then used for generating stand-level damage severity measurements. The ‘integrated stem damage code’ reflects multiple damage attributes for a stem and, therefore, should more accurately to reflect the tree damage status than the individual components.

Stand damage severity and tree mortality analysis

In this study, I examined variation in hurricane-induced, landscape-level damage by comparing the variance in damage severity among the 34 available PSPs and seven MPPs across the Duke Forest. In addition, I focused on two large, severely damaged MPPs (i.e., Graveyard and Bormann plot, see Figure 2.2 for their locations) for analysis of within-stand, species-specific mortality, growth, and spatial point patterns. These two MPPs were substantially damaged in Hurricane Fran (i.e., hurricane-induced plot-level basal area loss 13.88% and 12.86% of previous basal area, respectively) and representative of severely damaged areas in the Duke Forest. Specifically, the Graveyard plot represents the transition phase of older but even-aged pine stands with a hardwood understory (ca. 80-100 years old), and the Bormann plot represents mature, mixed-aged, upland deciduous hardwood forest. This approach of selecting a representative area, although somewhat arbitrary, allows a more focused examination of hurricane-induced within-stand damage variation including species-specific tree mortality, growth, and within-stand spatial change.

I employed three types of damage measures to quantify stand-level damage severity: percentage of stems damaged, percentage of basal area lost, and the 'stand-level damage index'. The percentage of stems damaged was quantified as the percentage of total individuals with damage codes of 3 (severe), 2 (substantial), or 1 (modest damage). The percentage of basal area lost is the percentage difference in stand basal area between the pre-hurricane baseline and post hurricane surveys (not simply basal area of trees lost as this does not include the diameter increments of the surviving trees). I used the projected 1996 stand-level basal area as the pre-hurricane baseline to minimize the influence of pre-hurricane diameter increase between the last survey (i.e., 1992/1993) and the hurricane event in 1996. The annual basal area increase for each plot was derived from pre-hurricane period data (i.e.,

1988/89 to 1992/93) and assumed a constant annual diameter growth for all plots during the pre-hurricane period from 1988/89 to 1996. Stand-level damage index was computed as the average damage codes of all stems within a survey area. I used stem basal area to weight the ‘integrated stem damage code’ before generating the mean stand-level damage index. I first created an ‘integrated stem damage code’ for each stem in the stand by combining all the information of uprooting, breakage, leaning and leaned-on to a single code ranging from 0-3, I then weighted the code by multiplying the stem relative basal area (i.e., the basal area of the stem divided by the sum of all stem in the plot). The stand damage index was the average value of the weighted stem ‘integrated stem damage code’ of all stems in the stand. The range of stand damage index by definition is from 0-3. To minimize the sample size affects, I divided the seven large mapped stands into subplots of approximately 1000 m² before I compared the values across the various sized PSPs and MPPs.

To compare changes in species dominance, I calculated species importance value [IV = (relative density + relative basal area)/2] for all species. To examine population changes of trees in different vertical strata, all tree stems were assigned to strata by diameter class: sapling (1 cm <d.b.h. =< 2.5 cm), juvenile (2.5 < d.b.h =< 5 cm), small (5 cm < d.b.h. =< 10 cm), medium (10 cm< d.b.h. =< 25 cm), and large canopy tree (d.b.h.> 25 cm). I also compared changes of live-tree size distributions over three measurement intervals (the pre-hurricane period, 1989/90-1992/93; the hurricane period 1992/93-1997/98; and the post-hurricane period, 1997/98-2000/01).

I analyzed changes in mortality for the three sampling intervals by calculating the annual mortality rate (*m*) for each of the five size classes by species for those species with 20 or

more individuals in the size class. In this study, the mean annual mortality rate was derived from the exponential model of population growth (or decline) and was calculated as:

$$m = (\ln (N_t/N_0))/t$$

where N_0 and N_t are the number of (alive) stems at the beginning of the interval t (years) and the number of those still alive at the end of the interval. I calculated the stem density for each PSP and each subplot in seven MPPs for each of the three sampling intervals mentioned above. I examined stand-level basal area loss by calculating the percentage difference in stand basal area between the projected 1996 basal area and post hurricane surveys. In addition, I examined the relationships between tree damage and stem size, and tree mortality and stem size for all trees and for major species using logistic analysis (LOGISTIC function, SAS 9.1, SAS Institute Inc. 2003).

Newly created gap number, gap size, and gap formation rate (i.e., (percentage of gap area at the end interval t - percentage of gap area at the beginning of interval)/ t (years)) were measured for two sampling intervals (pre-hurricane 1989-1992 and hurricane period 1992-1997) for all large mapped stands. I used Runkle's (1982) expanded gap concept to define the gap size and adopted 25 cm d.b.h. as the minimum diameter of the trunk of a tree that can form a gap when it dies or falls. I measured gap size in the stem maps by using ArcGIS 9.0 (ESRI Inc. 2004).

Additionally, I investigated pattern in tree mortality in two MPPs based on second order spatial analysis (Ripley's K -function) with SPPA software (Haase 2002). Ripley's K -function is based on the empirical distribution of point-to-point distance (Ripley 1976, 1981, Diggle 1983, Haase 1995, Haase et al. 1995, 2001, Skarpe 1991, McDonald et al. 2003). I started the

analysis at a radius t of 0.25 m with 0.25 m increments up to 40 m. I calculated the sample statistic-based Ripley's K -function:

$$K(t) = \lambda^{-1}E(t)$$

where $E(t)$ is the expected number of points within a distance t from any arbitrary points. λ , the mean intensity, is estimated as n/A , where n is total number of trees and A is total area sampled. I then performed the transformation $\sqrt{[K(t)/\pi]}-t$ to yield a linear plot of the sample statistic against t and a further transformation of a derived K -function $L(t)$:

$$L(t) = \sqrt{[K(t)/\pi]}-t$$

With this transformation, $L(t) = 0$ gives an expectation of *zero* for any value of t when spatial pattern is Poisson randomness (Skarpe 1991). A significant positive sample statistic suggests a clumped distribution of sample points, whereas a significant negative sample statistic suggests a regular (uniform) pattern (Diggle 1983). The K -function $L(t)$ was generated from the survey data and then these data were randomized to generate the test of significance as confidence limits. In this study, I used the lowest and highest of $L(t)$ of 99 randomizations to define the lower and upper bound of a 99% confidence interval. If the sample statistic remains within the bounds of the confidence interval at any given t , the null hypothesis of complete spatial randomness cannot be rejected (Haase et al. 1996).

Compositional trends were assessed with Nonmetric Multidimensional Scaling (NMS) with varimax rotation (Kruskal 1964; Mather 1976) as implemented in version 4.39 of PC-ORD (McCune & Mefford 1999). Data from the 32 PSPs (those with data from 1984-2000, including three measurements prior to the 1996 Hurricane Fran and two measurements after Fran) were used to assess the change of composition and relationships in change between different forest stands (pine stand vs. hardwood stand). Analyses of 1978-2000 data of seven

MPPs were used for more detailed examination of hurricane-induced compositional patterns within upland stands and pine stands. NMS is the most generally effective ordination methods for ecological community data (McCune & Mefford 1999) and has been increasingly used by ecologists for examining composition trends (e.g., McCune et al. 1997a,b, Wood 2000, Kaverna et al. 2005). Ordinations of multiple plot measurements over time allowed examination of plot trajectories in ordination space and patterns of community change (Woods 2000).

RESULTS

Pre-hurricane forest structure and composition

The long-term, detailed demographic data of trees (d.b.h. \geq 1 cm) allowed me to assess the pre-hurricane forest structure and composition of two major forest types in the Duke Forest: successional pines and mixed upland hardwoods. The records showed that the pine stands were even-aged (ca. 80 to 100 years old), secondary forests in their transition phase of old-field succession to late successional hardwood forests (Peet 1992). These pine stands were dominated by loblolly pine in the canopy, along with red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), tuliptree (*Liriodendron tulipifera*) and hickories (*Carya spp.*). The understory, contained few pine saplings, but instead was dominated by hardwoods such as dogwood (*Cornus florida*) and red maple, as well as other hardwoods characteristic of the site, such as sourwood (*Oxydendrum arboreum*) or American hornbeam (*Carpinus carolina*).

The pre-hurricane, mixed-aged, upland hardwood forest stands were mostly in the late successional stage (ca. Bormann's steady-stage phase). Those hardwood stands have been described as characteristic of the original 'climax' forest type of the Piedmont forests

(Oosting 1942, Bormann 1955, Christensen 1978). These mixed-aged hardwood forest stands have been influenced by the past disturbances at various developmental stages (e.g., wildfires in the 1700s, selective cutting and open range grazing in 1800s, plus various windstorms and ice storms throughout). The canopy trees were more diverse than pine stands, and included red oak (*Quercus rubra*), white oak (*Q. alba*), mockernut hickory (*Carya tomentosa*), pignut hickory (*C. glabra*), red hickory (*C. ovata*), red maple, sweetgum, and tuliptree as the most dominant species. The understory of the hardwood forests was characterized by a dominance of dogwood, red maple, ash (*Fraxinus americana*) and hophornbeam (*Ostrya virginiana*).

Stem damage levels

Hurricane Fran caused various forms of damage to trees in the Duke Forest, and the stem damage types appeared to vary in association with pre-hurricane stem size and vertical strata (Table 2.2). The data clearly show that uprooting was the major stem damage type for medium and large trees (d.b.h.>10 cm) during Fran. Categorical logistic regression analysis on the relationship between uprooting and tree size in the two selected MPPs (Graveyard plot, Bormann plot) showed that in both plots the probability of uprooting was positively related to the pre-hurricane tree size (Figure 2.3). Overall, across all MPPs 9.2% of previously existing medium and large trees (n = 605) were either partially or completely uprooted. In the 28 loblolly pine PSPs, 9.7% of the medium and large trees were uprooted. In the six mixed-aged upland hardwood PSPs, an average of 6.6% of existing medium and large stems were uprooted.

Within the two mapped pine stands significantly damaged during the hurricane, 16.1% (Graveyard) and 10.5% (Land's end) of existing medium and large trees were uprooted. In the two significantly damaged upland hardwood plots, 16.5% (Bormann) and 16% (Rocky)

of the large and medium trees were uprooted. The variance of the uproot rate was high among the plots, reflecting the spatial heterogeneity of the storm impacts. In the 34 PSPs, the percentage of uprooting varied from 0 to 53.3%, whereas the percentage of uprooting varied from about 4% to 16.5% in the seven large MPPs.

Large canopy trees (d.b.h.>25 cm) constituted the most damaged tree-size group in both pine and hardwood forests. In the 28 pine PSPs, 11.7% of large canopy trees were uprooted. In the two large mapped pine stands, 22.5% and 13.3% of large trees were uprooted, whereas 24.3% and 27% of large trees were uprooted in the two heavily damaged mapped hardwood plots. In addition, uprooting rates showed the greatest among-plot variation in this size class. The uprooting percentages varied from 0 to 66.7% among 28 pine PSP stands and 10.8% to 24% among the six mixed-aged hardwood PSPs. In the three less damaged hardwood plots, 6.5-9% of large canopy trees were uprooted by the hurricane (Table 2.2).

In contrast to the medium and large trees, the damaged understory saplings, juveniles and midstory small trees (d.b.h. =<10 cm) appeared mostly to be pinned or bent by their large neighbors. The ranking of damage types for the understory saplings, midstory juveniles and small trees decreased in the following order: pinned>bent>breakage>leaning>uprooted. Again, the variation in damage was high among plots. In a large loblolly pine stand (Graveyard), up to 17% of previous saplings, juveniles and small trees were pinned, whereas in another loblolly pine stand (Land's end), the percent of pinned stems was only 2.27%. My results suggested that understory and midstory trees experienced highly uneven indirect damage by their large neighbors during the hurricane.

Among stand variation in damage

I used the weighed mean stem damage index to define stand-level tree damage severity, and examined the degree of variation of hurricane-induced spatial heterogeneity. The index should be a sensitive indicator as it provides an integrated assessment for stand damage. My results show a high degree of variation in forest stand damage severity among the 34 PSPs that span the landscape of the Duke Forest (Table 2.3). Stand-level tree damage severity on the 1-3 index varied significantly both in the PSP pine stands ($n = 28$, mean damage index = 0.34 ± 0.45 standard deviations) and in the PSP hardwood stands ($n = 6$, mean damage index = 0.36 ± 0.36 standard deviations). The mean damage indices of the seven mapped plots divided into $\sim 1000 \text{ m}^2$ subplots (therefore comparable with PSPs), ranged from 0.07 ± 0.11 to 0.64 ± 0.53 . These results suggest a very patchy and complex pattern of hurricane damage across the landscape.

Within stand spatial heterogeneity

There was substantial variation in damage within the seven large, intensively surveyed MPPs, each of which had similar species composition, structure and disturbance history (Table 2.3). The subplots in the two mapped pine stands (Graveyard 1.3 ha, and Land's end ~ 1 ha) had mean damage indices of 0.58 ± 0.42 and 0.52 ± 0.47 . The mean damage indices of the other five large mapped hardwood plots ranged from 0.07 to 0.64, with standard deviations either greater than the mean damage indices or close to their means. This indicated that Hurricane Fran had substantial within-stand spatial heterogeneity, and this small-scale damage heterogeneity needs to be taken into consideration in evaluating hurricane effects on forests and simulating forest recovery from large wind disturbance events.

Second-order spatial point pattern analysis revealed a clumped and patchy distribution of hurricane-induced tree mortality within the damaged forest stands (Graveyard and Bormann,

1.3 and 1.96 ha respectively, Figures 2.5a, 2.5b, and 2.6a). Immediately after Hurricane Fran (ca. one year after the hurricane), the distribution of the dead canopy trees in the Graveyard mapped pine stand become clumping at middle scales (12-38 m) to the whole stand scale (Figure 2.6a.(a)). In this loblolly pine plot, the upper layer tree deaths were becoming clumped at the whole stand level (~1.3 ha) in 2001, five years after the hurricane (Figure 2.6a (b)). The patterns in the mapped hardwood stand (Bormann) appeared patchy in both 1997 and 2000, the mortality patterns of hardwoods were not significant different from each other between two post-hurricane surveys. These results suggested that hurricane-induced tree mortality was largely clumped within a forest stand, probably due largely to the interaction between the less predicable wind gusts at the stand scale and the different abilities of tree species to resist high winds.

The spatial distributions of the residual living overstory trees in the two damaged MPPs clearly become more clumped due to the hurricane damage (Figures 2.6b and 2.6c). This pattern is particularly evident in the Graveyard pine plot in that pre-hurricane upper layer trees (d.b.h.> 25 cm) become clumping from the scale of 6 m to the whole stand after the hurricane. In the mapped upland hardwood plot (Bormann), the pre-hurricane distribution of living upper layer trees was regular at small scales (0-14 m), but became clumped at the whole stand scale after the hurricane. The midstory of both the mapped pine and upland hardwood stands remained visually unchanged with the exception that understory saplings in the hardwood stand become more clumping at scale of 8-40 m. Overall, the sapling and juvenile trees in understory in the mapped pine stand (Graveyard) changed little in spatial distribution, whereas the understory in the mapped hardwood plot became more clumped.

Gap formation rate and gap size

The major source of the increased within-stand and landscape-scale spatial heterogeneity in the Duke Forest was the uneven gap formation caused by uprooting during Fran. Table 2.7 showed the substantially increased but greatly varied average annual gap formation rates of the seven MPPs during the hurricane as compared to the pre-hurricane baseline gap formation rates. The annual tree gap formation rates (GFR) in the two damaged pine MPPs (Graveyard and Land's end) increased about 5-12 fold from the pre-hurricane period (1989-1993) 1.8% and 0.9% to the hurricane period (1993-1997) 97% and 10.8% respectively. The changes in annual gap formation rates in the five mapped hardwoods plots varied greatly, ranging from no significant increase in the less damaged stands (Oosting, Wooden Bridge) to about a 12-fold increase in the substantially damaged stands (Graveyard, Bormann).

The hurricane not only greatly increased the frequency of gap formation in the damaged areas, but also resulted in a greater diversity of tree gap sizes. The maximum sizes of tree gaps in the MPPs after the hurricane increased dramatically, 18-34 fold as compared to the baseline level (Table 2.7). The average gap sizes after the hurricane in the seven mapped plots increased 2-7 fold (ca. 400 to 1000 m²) as compared to the pre-hurricane level (ca. 100 to 250 m²). The minimum sizes of hurricane-induced gaps in the seven MPPs either remained relative similar to pre-hurricane levels or slightly decreased due to that fact of some smaller trees had been uprooted to form a set of smaller tree gaps during the hurricane.

Treefall pattern

In contrast to the observed large variation among plots in damage severity, my data showed striking similarities in treefall orientations among the scattered tree plots in the Duke Forest. The uprooting stems generally fell towards the SSW and the maximum percentage of azimuths in most mapped plots was 200-210° (Figure 2.7), indicating the local surface wind

direction when Hurricane Fran struck the Duke Forest. Azimuths of the fallen trees among the plots were primarily aligned within 45° (Figure 2.7), suggesting that the treefalls were formed within a very short time period during the hurricane, and strong wind gusts may have been the major cause of uprooting of large canopy trees. Interactions between diameter and species showed that the rate of increase in damage with diameter varies among species.

In addition, my finding of a consistent azimuth combined with the patchy nature of damage even on relatively flat uplands could be taken as evidence to support the proposed intense small-scale (sub-kilometer-scale) boundary layer rolling effects found by meteorologists for Hurricane Fran (Wurman and Winslow 1998). I found that despite the fact that there was large spatial damage variation; the azimuths of uprooting boles were strikingly similar in my wide scattered plots across the Duke Forest. This suggests that wind gusts were the major cause of treefall.

Live-tree size structure

As mentioned above, I examined live-tree size structure in Graveyard (an even-aged pine stand) and Bormann (a mixed-aged hardwood plot) in detail. Comparison of the relative size distributions of major species revealed that the tree population structure of the damaged forest stands in the Duke Forest was significantly impacted by the hurricane, although the overall ranking of dominant tree species had not changed five years after Hurricane Fran (Figure 2.8a and 2.8b). For loblolly pine, the most dominant tree species in the Graveyard pine stand, the curve's mode shifted right, plus the entire curve shifted down over time, suggesting that mean size of pine trees in this wind-damaged pine stand was increased by Hurricane Fran, and the density of pines decreased in all size classes. Note that the pines in middle size classes dropped particularly dramatically. Few new pine saplings were available

to fill the small size classes, as other pine stems vacated these size classes. This demographic shift also occurred on another Duke Forest pine stand (Land's end; data not shown). In addition to significantly decreasing pine dominance, Hurricane Fran also greatly affected pine stands by decreasing the relative abundance of small size-class oaks (*Quercus spp.*) and hickories. In the Graveyard plot after Hurricane Fran, red maple increased in density in middle classes, and decreased in both smaller and larger size classes. Dogwood was the most damaged tree in the pine stands and decreased in stem density in all tree sizes, whereas several light-demanding and more shade intolerant hardwood species, such as tuliptree, sweetgum, and hophornbeam had increased in density in the small size class (1-3 cm) dramatically 5 years after the hurricane.

Similar to the fate of dominant loblolly pine in the mapped pine stand, the mean size of the predominant white oak (*Quercus alba*) in the damaged Bormann hardwood mapped plot increased after Hurricane Fran, while the density of the trees decreased in all size classes. Note that the density of small size class (1-3 cm) white oaks dropped particularly dramatically. The pre-hurricane size distribution of red maple in this hardwood plot had an inverse-J shape, and the shape of the curve remained unchanged after Fran, but shifted upwards post-hurricane in all size classes. Particularly conspicuous was the increased stem density of red maple in smaller size classes 5 years after the hurricane. This indicates that the red maple population had considerable demographic momentum to increase its dominance in this oak-dominated community. Hickories and sourwoods (*Oxydendrum arboreum*) increased in smaller class stems. Similarly in pine stands, dogwood decreased in stem density in all size classes, whereas the somewhat light-demanding black cherry (*Prunus serotina*) had increased dramatically in density in all sizes 5-year following the hurricane.

Overall, the predominant tree species of the upper canopy layer in both pine and hardwood forests decreased substantially due to the higher mortality of large-size trees (Figure 2.3). In the Graveyard plot, the dominant loblolly pine decreased in importance value from a pre-hurricane level of 34.5 % in 1992 to 32.0 % in 1997, and continued to decline to 28.3 % in 2000. Red maple had slightly increased its dominance in the plot at the time of the 2000 census, largely due to survival of the advanced regeneration. In the mixed-aged upland oak Bormann plot, the predominant white oak decreased in its importance value from 38.1% in 1993 to 36.6 % in 1997, and continued to decline to 34.0 % in 2000, whereas the light-demanding understory hardwood tree species, including red maple, tuliptree, sweetgum and black cherry had significantly increased their dominance by 5 years after the hurricane.

Species susceptibility and delayed mortality

Hurricane Fran resulted in increased tree death in damaged plots compared to the pre-hurricane background mortality. Table 2.4 shows annual size-specific mean mortality rates of major species in three periods (i.e., pre-hurricane, hurricane period and post-hurricane period) in two selected MPPs (Graveyard loblolly pine and hardwood Bormann plot). Overall, all size classes of trees experienced increased annual mortality. Note that large canopy trees, which normally have the lowest background mortality, become the highest mortality tree group (up about 19 fold from 0.22 to 4.22 %/yr in the pine stand, and up about 5.5 fold from 0.68 to 3.74%/yr in the mixed-aged upland hardwood plot). This clearly suggests that a major consequence of hurricane damage has been an inversion of the ‘normal’ tree mortality pattern where smaller trees usually experience higher mortality than large trees. In the Graveyard plot, the annual mean mortality for all species combined increased from pre-hurricane 2.85 to 3.98 %/yr (Table 2.5). Loblolly pine, red oak, sourwood, black gum,

dogwood and tuliptree experienced significantly higher mortality rates (about doubled), whereas a few trees such as hickories, ash, sweetgum and hophornbeam appeared resistant to hurricane damage and experienced reduced mortality rates in both the hurricane and post-hurricane periods. In the Bormann stand, the annual mean mortality for all species combined increased from pre-hurricane 1.32 to 3.21 %/yr. Most of the trees had a large increase (2-3 fold) in tree mortality with an exception of black gum. Major dominant oak species and dogwood had quite high mortality. The variable degree of increase of tree mortality among tree species indicated uneven tree species susceptibility and tree damage during the severe wind damage (Table 2.5).

In addition to the overall increase in tree mortality immediately after the hurricane, I found substantial delayed tree mortality for loblolly pine and many hardwood species. Mortality rates of several dominant species such as loblolly pine, red maple, tuliptree and black oak in the Graveyard plot, and white oak, red oak and hickories in the Bormann plot, increased substantially in the post-hurricane period. In the Graveyard plot, Hurricane Fran caused about 8.7-fold tree mortality rate increase for the loblolly pine trees and remained 9 fold higher 5 years post-hurricane.

The midstory hardwood species in the mapped pine plots, including dogwood, red maple and black oak (*Quercus velutina*), sustained mortality rates in the post-hurricane period roughly double their rates during hurricane period (Table 2.5). Delayed tree mortality was also found in the understory. Juvenile trees (2.5-5 cm) and small trees (5-10 cm) in the Graveyard plot experienced an increase in the annual mortality rate of 30% from 2.8 %/yr to 3.7 %/yr with the hurricane, but increased even more in the post-hurricane period reaching 3.8%/yr.

In the Bormann plot, which was dominated by oaks, tree mortality of large canopy trees (d.b.h.>25 cm) 5.5-fold that of pre-hurricane period and increased even higher to about a nine-fold increase in the post-hurricane period. In this forest annual mortality rates in the post-hurricane period were roughly tripled for small trees ($5 \leq \text{d.b.h.} \leq 10$ cm) and doubled for juveniles ($2.5 \leq \text{d.b.h.} \leq 5$ cm) compared to the mortality rates of the pre-hurricane period.

Stand density and basal area

The degree of decrease in stand density owing to Hurricane Fran varied significantly among the MPPs from no detectable change in the less damaged plots to 10.5 % in the substantial damaged plots. Density of large trees (> 10 cm d.b.h.) in both heavily damaged pine and hardwood plots was due to the high rate of uprooting during the hurricane. Compared to the projected pre-hurricane stand basal area in 1996, two pine plots (Graveyard, Land's end) had lost 11% and 21.6% of pre-hurricane basal area in 1997. Variances of the basal area loss were high within the plots due to the unevenness of hurricane-induced patchy damage. Moreover, there was a continuous decline in basal area in the damaged stands following the hurricane as a result of the delayed post-hurricane tree mortality. The degree of decline was different between pine and hardwood forests. Two substantially damaged mapped pine plots (Graveyard, Land's end) declined in stand basal area by about 1-2%, whereas the heavily damaged Bormann plot declined an additional 9% in stand basal area by 2001, 5 years after the hurricane damage. The large difference in decline rates in basal area between pine and hardwood stands (1-2% vs. 9%) in large part was the result of differences in post-hurricane mortality characteristics of pine trees (often completely dead within a year of uprooting) and major hardwood trees with delayed mortality.

Tree species composition and relative abundance

Overall, the total number of tree species presented in the plots had increased moderately by 5 years after the hurricane. There were no tree species lost through Hurricane Fran, and 5 years after the hurricane a modest increase in number of exotic species and shrubs was evident in both pine stands and in mixed-aged upland hardwood stands. In the Graveyard pine stand, the light-demanding, fast-growth tree of heaven (*Ailanthus altissima*), along with red hickory and three deciduous shrub species, mapleleaf viburnum (*Viburnum acerifolium*), blackhaw (*Viburnum prunifolium*), and downy arrow-wood (*Viburnum rafinesquianum*), recruited into the stand. The 1.96 ha Bormann oak stand gained four woody species in 2000 including American holly (*Ilex opaca*), hophornbeam, American hornbeam, black walnut (*Juglans nigra*), and slippery elm (*Ulmus rubra*). The major new species in other MPPs were pawpaw (*Asimina triloba*), sugarberry (*Celtis laevigata*), Japanese privet (*Ligustrum japonicum*), Chinese privet (*L. sinense*), and Rhododendron (*Rhododendron periclymenoides*).

Nonmetric Multidimensional Scaling ordinations of observations of 32 PSPs and 7 MPPs before and after the hurricane, and again 5 years later (1978-2000) showed changes in tree species compositional patterns, and to some extent, stand successional trajectory (Figures 2.9 and 2.10). The 26 pine PSPs were generally close to each other in a reduced species space in the early 1980s, strongly associated with *Pinus taeda* (at right side of the Figure 2.9), and moved toward to the right side (upland hardwood forest type) and diverged somewhat over time. The significantly damaged pine PSPs (i.e., PSP 14, PSP 19, PSP 39, PSP 40, and PSP 50) appeared to move towards right side at faster rates in the species space and become more diverse in tree composition after Hurricane Fran. The locations of less or

undamaged PSPs changed little over the 20-year period in a reduced species space, reflecting the gradual nature of natural succession. On the right side of Figure 2.9, the change in tree composition of the six upland hardwood PSPs was less evident in that they moved in a non-directional manner and the dynamic trends were difficult to distinguish.

The seven MPPs were quite distinct in species space. Two large pine stands (Graveyard and Land's end) were at the left side of the Figure 2.10, the three hardwood MPPs were located on the right side of the figure, and another two hardwood plots (Oosting and Wooden Bridge) are located in the middle of the figure. The two pine plots moved further towards the middle near the hardwood plots after Fran (Figure 2.10), indicating increased hardwood dominance and reflecting a trend of continuing directional succession. The three mixed-aged hardwood MPPs (Wooden Bridge, Rocky, Bryan Center plot) slightly changed their locations in the species space, but remained visually unchanged in ordination location over the 20 years, even after hurricane damage. Bormann plot experienced modest compositional change after Fran. This result indicated that the tree species composition remained relatively stable in the late successional hardwood forests. Overall, Hurricane Fran had modest and variable effects on tree composition in the Duke Forest of the Piedmont forests.

DISCUSSION

Hurricane disturbance and major damage types

The primary impact of the intensive disturbance of Hurricane Fran on the Duke Forest was on the large-size canopy trees. Tree damage and stem size showed a strong positive correlation. This finding is consistent with widely observed size-specific damage patterns during strong windstorm events in many tropical and temperate forests (see review by Everham and Brokaw 1996). Hurricane-induced understory damage has been less studied in

the literature. I found that common damage types of understory saplings and small trees included stems that were bent or pinned by their large fallen neighbors and were relatively less damaged, largely due to the possible 'shield effect' from the canopy trees. Studies in French West Indies (Daniel et al. 1996), New Hampshire (Foster 1998) and Minnesota (Webb 1988, Clark and Clark 1991) similarly showed this tendency, although contrasting results have been reported in some tropical forests (e.g., You and Beaty 1995).

The amount of total rainfall associated with the storm events serves as an effective indicator of major tree damage types. In the present study, uprooting was the major damage type for the medium and large trees and the pits and mounds caused by uprooting greatly increased microsite variation and soil dynamics in the damaged stands, providing a diverse habitat for the potential colonization of pioneer herbs, shrub, and trees. This pattern held both in the pine stands and the hardwood forests. The explanation for this pattern was that the high rainfall during the hurricane saturated the soil. Hurricane Fran brought about 224 mm of rainfall to the Duke Forest and adjacent areas during the two-day hurricane period. Perhaps also important was a heavy rainfall (ca. 76 mm) two days before Fran that caused the soil to be already saturated prior to the arrival. Similar patterns have been reported in central New England (Foster et al. 1992), the southern Appalachians (Greenberg and McNab 1998), and in Japan (Naka 1982). In contrast, Hurricane Hugo in 1989, in which the rainfall was much less intense, had more breakage relative to blowdown as compared to Fran, both in bottomland (Sharitz et al. 1992) and upland forests (DeCoster 1996).

Variation in damage

My results are consistent with widely reported patchy damage pattern of hurricanes and other windstorms across forested landscapes (Foster 1988, Brokaw and Walker 1991,

Bellingham et al. 1992). Consequently, I can expect that the wind-damaged Piedmont stands will experience considerable variation in subsequent, post-hurricane successional recovery paths.

A related issue is the hurricane-induced increase in extent and size of gaps. Hurricanes create a complex mosaic of patches within a forest stand by creating canopy gaps. The gaps created by Hurricane Fran have distinctive aspects compared with the gaps created by more frequent, small-scale treefalls. The size of newly formed, hurricane-induced gaps varied dramatically, ranging from about 40 m² to several thousands m² (Table 2.8), whereas in the absence of large hurricanes, the mortality of an aged individual tree or a small group of trees tends to create gaps of limited size (in this case, 100-150 m²). These gaps are critically important for major tree species regeneration in temperate forests since the small gaps created by individual treefalls may not be big enough to maintaining the extant tree species diversity of temperate forests (e.g., Beckage et al. 2000). Large size canopy gaps from severe hurricane damage greatly increase light variability in the understory and have profound effects on tree individual growth and regeneration (Merrens et al. 1992, Runkle 1996).

Increased and delayed tree mortality

The long-term pre-hurricane and post-hurricane data have confirmed the widely-suspected but little known phenomena of delayed tree mortality (see Walker 1995 Sharitz et al. 1992, Allen and Sharitz 1999). One implication is that an immediate post-storm survey of tree mortality is likely to produce an underestimate. Consequently, the effects of hurricane damage on tree mortality and subsequent changes in species diversity and dynamics must be assessed over a longer time scale. For my study area a period of at least 5 years would have

been needed, and another 5 years monitoring period should be ideal to detect the overall tree death process and subsequent compositional changes.

Compositional change

The effects of hurricanes on species composition of temperate forests can be variable between studies as a result of different minimum tree sizes. Consequently, any interpretation of data or comparison regarding the composition needs to be interpreted with caution. In this study of woody species, I failed to detect significant changes in tree (> 1cm d.b.h.) species composition due to either an immediate species loss or a significant increase. The 5-year, post-hurricane data showed that this hurricane event, which had strong impacts on the forest structure, had only modest effects on tree species composition. A few woody, light-demanding, earlier successional shrub and exotic trees species invaded the new gaps. However, I have not yet seen significant increases in exotic tree species. My findings seem to contrast with the more common expectation that a significant change in species composition typically results from catastrophic wind disturbances (e.g., Whigham et al. 1999). This most likely reflects the highly resilient nature of Piedmont forests. From a long-term ecological point of view, Hurricane Fran was still a modest disturbance event for the Piedmont forests. Another possible explanation for this modest composition change is that the damage effect on species composition may be delayed and the compositional changes in tree species may have considerable time lag, reflecting the generally slow seedling and sapling growth rates. I expect that the data in next survey may provide a more complete picture of tree composition change following large hurricanes in this region.

Hurricane effects on forest succession

The disproportionately high tree mortality of large canopy dominants and subsequent structural changes has different effects on the pine forests as compared with the hardwoods of the study area. In particular, the hurricane resulted in a speed up in the rate of succession in the damaged pine stands, and increased diversity in the mixed-aged hardwood forests.

In the absence of severe disturbance, the transition phase, 80 to 100-year-old pine stands will gradually change to the mixed-aged hardwoods (Peet and Christensen 1987, Schultz 1999). Hurricane Fran reduced the dominance of the even-aged pine trees and increased the dominance of hardwood species already presented in the understory, such as red maple and sweetgum. In this regard, Hurricane Fran ‘accelerated’ the succession process of pine forests to late successional stage.

Large, infrequent hurricane events have complex effects on the mixed-aged hardwood forests by substantially increasing the mortality of dominant, late-successional oak trees. The unevenly increased tree mortality among tree species and large gaps created by the hurricane within the hardwood stands together generate complex mosaics that contain simultaneously multiple developmental states, and affect the subsequent structure and dynamics of these hardwood forests. Overall, strong windstorms have profound effects on the structure of the hardwood forest communities in the Piedmont and have, to a certain extent resulted in divergent successional trajectories in various Piedmont forests reflecting species’ differential tolerances to wind damage and differential growth response after the damage.

Historically, disturbance and succession have strongly shaped the structure and composition of Piedmont forests (Christensen 1985, Peet and Christensen 1987, Cowell 1998). Exclusion of wildfires over the last century has been assumed to be one of the major causes for the wide-spread trend toward increase dominance of red maple in the southeastern

United States (Adam 1998, McDonald et al. 2002). Although my data do not allow explicit comparison of the recovery patterns following wind versus fire disturbance, my results showed that large-scale hurricane disturbance appeared to contribute to the trend of increasing red maple dominance due to substantially increased growth of red maple. Although these specific results may not be generalizable to all regions and all forest types within the eastern deciduous forest region, they do provide an alternative for the ubiquitously invoked fire hypothesis for explaining the decline in dominance of oak.

CONCLUSIONS

My study, which was based on an analysis of both long-term baseline data and 5 years of post-hurricane recovery data, has demonstrated the variable effects of hurricanes on the structural attributes in Piedmont forests. The changes in tree species composition, however, were modest. Hurricane Fran significantly altered forest structure by selectively removing larger canopy dominant trees, by increasing both within-community structural heterogeneity and the landscape patchiness, and by unevenly increasing the growth rates of existing midstory and understory tree species. Under the current fire suppression conditions, these hurricane-induced changes will most likely lead to a less predictable successional development in Piedmont forests.

The effects of intensive hurricanes vary greatly among forest types and are closely related to the pre-hurricane community attributes and tree species mixtures in specific stand. For pine forests, Hurricane Fran appeared to accelerate the on-going successional transition process from earlier successional pine forests to the late successional mixed-aged hardwood forests, and therefore sped up the process of reduction of the existing old-field pine forests in the Piedmont. For the mixed-aged hardwood forests, the varied hurricane damage set back

their succession to an earlier hardwood stage with higher variation among patches. This led the whole hardwood forest towards a more diverse forest of greater spatial complexity. Consequently, I anticipate more diverse, dynamic and less predictable hardwood forests in impacted areas of the Piedmont, at least for the near future.

The next 5-10 years of observation of these plots is critical for a better understanding of long-term recovery process, particularly the underlying mechanisms of forest recovery from large disturbances. Nonetheless, the general patterns I report in this paper should be applicable to Piedmont forests and more generally to adjacent areas of the southeastern United States.

LITERATURE CITED

- Abrams, M. D. 1998. The red maple paradox. *Bioscience* **48**:355-364.
- Abrams, M. D. and J. A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Canadian Journal of Forest Research* **20**:1864-1870.
- Abrams, M. D. and M. L. Scott. 1989. Disturbance-mediated accelerated succession in 2 Michigan forest types. *Forest Science* **35**:42-49.
- Abrams, M. D., D. G. Sprugel, and D. I. Dickmann. 1985. Multiple successional pathways on recently disturbed jack pine sites in Michigan. *Forest Ecology and Management* **10**:31-48.
- Ackerman, J. D., L. R. Walker, F. N. Scatena, and J. Wunderle. 1991. Ecological effects of hurricanes. *Bulleting of the Ecological Society of America* **72**:178-180.
- Akachuku, A. E. 1993. Recovery and morphology of *Pinus resinosa* trees 50 years after they were displaced by a hurricane. *Forest Ecology and Management* **56**:113-129.
- Allen, B. P., E. F. Pauley, and R. R. Sharitz. 1997. Hurricane impacts on liana populations in an old-growth southeastern bottomland forest. *Journal of the Torrey Botanical Society* **124**:34-42.
- Arevalo, J. R., J. K. Decoster, S. D. Mcalister, and M. W. Palmer. 2000. Changes in two Minnesota forests during 14 years following catastrophic windthrow. *Journal of Vegetation Science* **11**:833-840.
- Asner, G. P. and G. Goldstein. 1997. Correlating stem biomechanical properties of Hawaiian canopy trees with hurricane wind damage. *Biotropica* **29**:145-150.
- Baker, W. L., P. H. Flaherty, J. D. Lindemann, T. T. Veblen, K. S. Eisenhart, and D. W. Kulakowski. 2002. Effect of vegetation on the impact of a severe blowdown in the southern Rocky Mountains, USA. *Forest Ecology and Management* **168**:63-75.
- Baldwin, A. H., W. J. Platt, K. L. Gathen, J. M. Lessmann, and T. J. Rauch. 1995. Hurricane damage and regeneration in fringe mangrove forests of southeast Florida, USA. *Journal of Coastal Research* **SI**: 169-183.
- Barnes, J. 2001. North Carolina's hurricane history. The University of North Carolina Press, Chapel Hill, USA.
- Basnet, K. 1993. Recovery of a tropical rain-forest after hurricane damage. *Vegetatio* **109**:1-4.
- Basnet, K., G. E. Likens, F. N. Scatena, and A. E. Lugo. 1992. Hurricane Hugo-damage to a tropical rain-forest in Puerto Rico. *Journal of Tropical Ecology* **8**:47-55.

- Batista, W. B. and W. J. Platt. 2003. Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. *Journal of Ecology* **91**:197-212.
- Batista, W. B., W. J. Platt, and R. E. Macchiavelli. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* **79**:38-53.
- Battaglia, L. L., R. R. Sharitz, and P. R. Minchin. 1999. Patterns of seedling and overstory composition along a gradient of hurricane disturbance in an old-growth bottomland hardwood community. *Canadian Journal of Forest Research* **29**:144-156.
- Beckage B, J. S. Clark, B. D. Clinton, B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research* **30**: 1617–1631.
- Bellingham, P. J. 1991. Landforms influence patterns of hurricane damage-evidence from Jamaican montane forests. *Biotropica* **23**:427-433.
- Bellingham, P. J., V. Kapos, N. Varty, J. R. Healey, E. V. J. Tanner, D. L. Kelly, J. W. Dalling, L. S. Burns, D. Lee, and G. Sidrak. 1992. Hurricanes need not cause high mortality - the effects of Hurricane Gilbert on forests in Jamaica. *Journal of Tropical Ecology* **8**:217-223.
- Bellingham, P. J., T. Kohyama, and S. Aiba. 1996. The effects of a typhoon on Japanese warm temperate rainforests. *Ecological Research* **11**:229-247.
- Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1994. Sprouting of trees in Jamaican montane forests after a hurricane. *Journal of Ecology* **82**:747-758.
- Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1995. Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* **76**:2562-2580.
- Bellingham, P. J., E. V. J. Tanner, P. M. Rich, and T. C. R. Goodland. 1996. Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *Journal of Tropical Ecology* **12**:699-722.
- Boose, E. R., K. E. Chamberlin, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. *Ecological Monographs* **71**:27-48.
- Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* **64**:369-400.
- Boose, E. R., M. I. Serrano, and D. R. Foster. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs* **74**:335-352.
- Bormann, F. H. and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, USA.

- Bormann, F. H. A. G. E. L. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist* **67**:660-669.
- Boucher, D. H. 1990. Growing back after hurricanes. *Bioscience* **40**:163-166.
- Boucher, D. H. and M. A. Mallona. 1997. Recovery of the rain forest tree *Vochysia ferruginea* over 5 years following Hurricane Joan in Nicaragua: A preliminary population projection matrix. *Forest Ecology and Management* **91**:195-204.
- Boucher, D. H., J. H. Vandermeer, I. G. De La Cerda, M. A. Mallona, I. Perfecto, and N. Zamora. 2001. Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. *Plant Ecology* **156**:131-137.
- Boucher, D. H., J. H. Vandermeer, M. A. Mallona, N. Zamora, and I. Perfecto. 1994. Resistance and resilience in a directly regenerating rain-forest - Nicaraguan trees of the Vochysiaceae after Hurricane-Joan. *Forest Ecology and Management* **68**:127-136.
- Boucher, D. H., J. H. Vandermeer, K. Yih, and N. Zamora. 1990. Contrasting hurricane damage in tropical rain-forest and pine forest. *Ecology* **71**:2022-2024.
- Bray, J. R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology* **37**:598-600.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* **66**:682-687.
- Brokaw, N. V. L. and J. S. Grear. 1991. Forest structure before and after Hurricane Hugo at 3 elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* **23**:386-392.
- Brokaw, N. V. L. and S. M. Scheiner. 1989. Species composition in gaps and structure of a tropical forest. *Ecology* **70**:538-541.
- Brokaw, N. V. L. and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* **23**:442-447.
- Burslem, D. and T. C. Whitmore. 1999. Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *Journal of Vegetation Science* **10**:767-776.
- Burslem, D., T. C. Whitmore, and G. C. Brown. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology* **88**:1063-1078.
- Canham, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bulletin of the Torrey Botanical Club* **112**:134-145.
- Canham, C. D. 1988. Growth and canopy architecture of shade-tolerant trees - response to canopy gaps. *Ecology* **69**:786-795.
- Canham, C. D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology*

- 70:548-550.
- Canham, C. D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club* **117**:1-7.
- Canham, C. D. and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* **65**:803-809.
- Canham, C. D., M. J. Papaik, and E. F. Latty. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research* **31**:1-10.
- Carlton, G. C. and F. A. Bazzaz. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. *Ecological Monographs* **68**:99-120.
- Carlton, G. C. and F. A. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* **79**:1305-1319.
- Carpino, E. 1998. Ecological determinants of hurricane damage in a southeastern piedmont forest. Master thesis. Duke University, Durham, North Carolina, USA.
- Chesson, P. and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology & Evolution* **4**:293-298.
- Christensen, N. L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in piedmont, North Carolina. *American Midland Naturalist* **97**:178-188.
- Christensen, N. L. 1988. Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. Page 62-81 in J. K. Agee and D. R. Johnson, editors. *Ecosystem Management for Parks and Wilderness*. University of Washington Press, Seattle, Washington, USA.
- Christensen, N. L. and R. K. Peet. 1981. Secondary forest succession on the North Carolina piedmont. Pages 230-245 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest Succession: concepts and application*. Springer-Verlag, New York, USA.
- Christensen, N. L. and R. K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* **72**:25-36.
- Conner, W. H. and A. D. Laderman. 1998. Impact of hurricanes on forests of the Atlantic and Gulf coasts, USA. Pages 271-277 in *Coastally Restricted Forests*. Oxford University Press, New York, USA.
- Cooper-Ellis, S., D. R. Foster, G. Carlton, and A. Lezberg. 1999. Forest response to catastrophic wind: results from an experimental hurricane. *Ecology* **80**:2683-2696.
- Curtis, J. D. 1943. Some observations of wind damage. *Journal of Forestry* **41**:877-882.

- DeCoster, J. K. 1996. Impacts of tornados and hurricanes on the community structure and dynamics of north and South Carolina forests. Ph.D. Dissertation. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.
- Denslow, J. S. 1980. Patterns of plant-species diversity during succession under different disturbance regimes. *Oecologia* **46**:18-21.
- Dunn, C. P., G. R. Guntenspergen, and J. R. Dorney. 1983. Catastrophic wind disturbance in an old-growth hemlock hardwood forest, Wisconsin. *Canadian Journal of Botany* **61**:211-217.
- Elliott, K. J., S. L. Hitchcock, and L. Krueger. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: hurricane opal and salvage logging. *Journal of the Torrey Botanical Society* **129**:48-59.
- Ennos, A. R. 1997. Wind as an ecological factor. *Trends in Ecology & Evolution* **12**:108-111.
- Everham, E. M. and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. *Botanical Review* **62**:113-185.
- Fernandez, D. S. and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica* **23**:393-399.
- Fitzpatrick, P. J. 1999. Natural disasters: Hurricanes. A reference handbook. ABC-CLIO, Santa Barbara, California, USA.
- Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology* **76**:135-151.
- Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1**:497-510.
- Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* **1**:96-119.
- Foster, D. R. and T. M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology* **74**:982-998.
- Frangi, J. L. and A. E. Lugo. 1991. Hurricane damage to a flood-plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* **23**:324-335.
- Frangi, J. L. and A. E. Lugo. 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. *Biotropica* **30**:339-348.
- Frelich, L. E. and C. G. Lorimer. 1991. Natural disturbance regimes in hemlock hardwood forests of the Upper Great-Lakes region. *Ecological Monographs* **61**:145-164.

- Glitzenstein, J. S. and P. A. Harcombe. 1988. Effects of the December 1983 tornado on forest vegetation of the Big Thicket, southeast Texas, USA. *Forest Ecology and Management* **25**:269-290.
- Glitzenstein, J. S., P. A. Harcombe, and D. R. Streng. 1986. Disturbance, succession, and maintenance of species-diversity in an east Texas forest. *Ecological Monographs* **56**:243-258.
- Greenberg, C. H. and W. H. McNab. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. *Forest Ecology and Management* **104**:179-191.
- Gresham, C. A., T. M. Williams, and D. J. Lipscomb. 1991. Hurricane Hugo wind damage to southeastern United States coastal forest tree species. *Biotropica* **23**:420-426.
- Haase P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. *Journal of Vegetation Science* **6**: 575–582.
- Haase, P., Pugnaire, F.I., Clark, S.C. & Incoll, L.D. 1996. Spatial patterns in a two-tiered semi-arid shrubland in south-eastern Spain. *Journal of Vegetation Science* **7**: 527-534.
- Haase, P. 2001. Can isotropy vs. anisotropy in the spatial association of plant species reveal physical vs. biotic facilitation? *Journal of Vegetation Science* **12**: 127–136.
- Haase, P. 2002. SPPA – A Program for Spatial Point Pattern Analysis, Version 2.0.
- Haight, R. G., W. D. Smith, and T. J. Straka. 1995. Hurricanes and the economics of loblolly-pine plantations. *Forest Science* **41**:675-688.
- Halpern, C. B. and D. McKenzie. 2001. Disturbance and post-harvest ground conditions in a structural retention experiment. *Forest Ecology and Management* **154**:215-225.
- Hibbs, D. E. 1983. 40 years of forest succession in central New England. *Ecology* **64**:1394-1401.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. De Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* **283**:554-557.
- Hunter, M. D. and R. E. Forkner. 1999. Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. *Ecology* **80**:2676-2682.
- Imbert, D., P. Labbe, and A. Rousteau. 1996. Hurricane damage and forest structure in Guadeloupe, French West Indies. *Journal of Tropical Ecology* **12**:663-680.
- Imbert, D., A. Rousteau, and P. Labbe. 1998. Hurricanes and biological diversity in tropical forests - the case of Guadeloupe. *Acta Oecologica-International Journal of Ecology* **19**:251-262.

- Jarrell, J. D., M. Mayfield, and E. N. Rappaport. 2001. The deadliest, costliest, and most intense United States hurricanes from 1900 to 2000. NOAA Technical Memorandum NWS TPC-1.
- Kapustka, L. A. and R. G. Koch. 1979. The acceleration of succession of a birch-maple forest due to high wind. *Michigan Botanist* **18**:83-87.
- Keever, K. 1950. Causes of succession on old fields of the piedmont, North Carolina. *Ecological Monographs* **20**:229-250.
- Lertzman, K. P., G. D. Sutherland, A. Inselberg, and S. C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* **77**:1254-1270.
- Liu, C. X., J. S. Glitzenstein, P. A. Harcombe, and R. G. Knox. 1997. Tornado and fire effects on tree species composition in a savanna in the Big Thicket National Preserve, southeast Texas, USA. *Forest Ecology and Management* **91**:279-289.
- Lodge, D. J. and W. H. McDowell. 1991. Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica* **23**:373-378.
- Loope, L., M. Duever, A. Herndon, J. Snyder, and D. Jansen. 1994. Hurricane impact on uplands and fresh-water swamp forest. *Bioscience* **44**:238-246.
- Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* **61**:1169-1184.
- Lorimer, C. G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. *Ecology* **70**:565-567.
- Lorimer, C. G., S. E. Dahir, and E. V. Nordheim. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *Journal of Ecology* **89**:960-971.
- Lugo, A. E. 2000. Effects and outcomes of Caribbean hurricanes in a climate change scenario. *Science of the Total Environment* **262**:243-251.
- Lugo, A. E., C. Rogers, and S. Nixon. 2000. Hurricanes, coral reefs and rainforests: resistance, ruin and recovery in the Caribbean. *Ambio* **29**:106-114.
- Lugo, A. E. and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* **28**:585-599.
- Lugo, A. E. and R. B. Waide. 1993. Catastrophic and background disturbance of tropical ecosystems at the Luquillo Experimental Forest. *Journal of Biosciences* **18**:475-481.
- Mallin, M. A., M. H. Posey, M. R. Mciver, D. C. Parsons, S. H. Ensign, and T. D. Alphin. 2002. Impacts and recovery from multiple hurricanes in a piedmont-coastal plain river system. *Bioscience* **52**:999-1010.

- McDonald, R. I., R. K. Peet, and D. L. Urban. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina piedmont. *Castanea* **67**:84-95.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2003. Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a piedmont forest. *Journal of Vegetation Science* **14**:441-450.
- Merrens, E. J. and D. R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. *Journal of Ecology* **80**:787-795.
- Norton, D. A. 1989. Tree windthrow and forest soil turnover. *Canadian Journal of Forest Research* **19**:386-389.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of piedmont, North Carolina. *American Midland Naturalist* **28**:1-126.
- Palmer, M. W. 1990. Vascular flora of the Duke Forest, North Carolina. *Castanea* **55**: 229-224.
- Palmer, M. W., S. D. Mcalister, J. R. Arevalo, and J. K. Decoster. 2000. Changes in the understory during 14 years following catastrophic windthrow in two Minnesota forests. *Journal of Vegetation Science* **11**:841-854.
- Pascarella, J. B., T. M. Aide, and J. K. Zimmerman. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. *Forest Ecology and Management* **199**:379-393.
- Peart, D. R., C. V. Cogbill, and P. A. Palmiotto. 1992. Effects of logging history and hurricane damage on canopy structure in a northern hardwoods forest. *Bulletin of the Torrey Botanical Club* **119**:29-38.
- Peet, R. K. 1984. 26 years of change in a *Pinus strobus*, *Acer saccharum* forest, Lake Itasca, Minnesota. *Bulletin of the Torrey Botanical Club* **111**:61-68.
- Peet, R. K. and Christensen, N. L. 1980. Hardwood forest vegetation of the North Carolina Piedmont. *Veröff. Geobot.Inst. Eidg. Tech. Hochsch. Stift. Rübel, Zür.* **69**: 14-39.
- Peet, R. K. and N. L. Christensen. 1987. Competition and tree death. *Bioscience* **37**:586-595.
- Peet, R. K. and N. L. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina piedmont. Pages 233-245 *in* H. J. Doring, M. J. A. Werger, and J. Willems, editors. *Diversity and pattern in plant communities*. SPB Publishers. The Hague. The Netherlands.
- Peet, R. K., P. A. Harcombe, and G. R. Parker. 1991. Rates and patterns of mortality in eastern deciduous forests: a comparative study. *Bulletin of the Ecological Society of America* **72**:217.

- Peroni, P. A. 1994. Invasion of red maple (*Acer rubrum*) during old field succession in the North Carolina piedmont - age structure of red maple in young pine stands. *Bulletin of the Torrey Botanical Club* **121**:357-359.
- Perry, D. A. 1997. Disturbance, recovery, and stability. Pages 31-56 *in* *Creating a forestry for the 21st Century: the science of ecosystem management*. Island Press, Washington, D.C. USA.
- Peterson, C. J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *Science of the Total Environment* **262**:287-311.
- Peterson, C. J. 2000. Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. *Forest Ecology and Management* **135**:237-252.
- Peterson, C. J. 2004. Within-stand variation in windthrow in southern boreal forests of Minnesota: is it predictable? *Canadian Journal of Forest Research* **34**:365-375.
- Peterson, C. J. and J. E. Campbell. 1993. Microsite differences and temporal change in plant-communities of treefall pits and mounds in an old-growth forest. *Bulletin of the Torrey Botanical Club* **120**:451-460.
- Peterson, C. J. and W. P. Carson. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. *Canadian Journal of Forest Research* **26**:45-52.
- Peterson, C. J., W. P. Carson, B. C. McCarthy, and S. T. A. Pickett. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* **58**:39-46.
- Peterson, C. J. and S. T. A. Pickett. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *Journal of Vegetation Science* **1**:657-662.
- Peterson, C. J. and S. T. A. Pickett. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock hardwoods forest. *Forest Ecology and Management* **42**:205-217.
- Peterson, C. J. and S. T. A. Pickett. 1995. Forest reorganization - a case-study in an old-growth forest catastrophic blowdown. *Ecology* **76**:763-774.
- Peterson, C. J. and A. J. Rebertus. 1997. Tornado damage and initial recovery in three adjacent, lowland temperate forests in Missouri. *Journal of Vegetation Science* **8**:559-564.
- Philippi, T. E., R. K. Peet, and N. L. Christensen. 1993. Tree seedling demography in old-field *Pinus taeda* and mature mixed hardwoods stands in a piedmont forest. *Bulletin of the Ecological Society of America* **74 (Suppl.)**:393.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways

- of succession. *Botanical Review* **53**:335-371.
- Pielke, R. A. 1990. *The hurricane*. Routledge, New York. USA.
- Pimm, S. L., G. E. Davis, L. Loope, C. T. Roman, T. J. Smith, and J. T. Tilmant. 1994. Hurricane Andrew. *Bioscience* **44**:224-229.
- Pinzon, Z. S., K. C. Ewel, and F. E. Putz. 2003. Gap formation and forest regeneration in a micronesian mangrove forest. *Journal of Tropical Ecology* **19**:143-153.
- Platt, W. J., B. Beckage, R. F. Doren, and H. H. Slater. 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna pines. *Ecology* **83**:1566-1572.
- Platt, W. J. and J. H. Connell. 2003. Natural disturbances and directional replacement of species. *Ecological Monographs* **73**:507-522.
- Platt, W. J., R. F. Doren, and T. V. Armentano. 2000. Effects of hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the everglades region of south Florida (USA). *Plant Ecology* **146**:43-60.
- Platt, W. J. and D. R. Strong. 1989. Special feature - treefall gaps and forest dynamics-gaps in forest ecology. *Ecology* **70**:535-535.
- Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* **64**:1069-1074.
- Putz, F. E., P. D. Coley, K. Lu, A. Montalvo, and A. Aiello. 1983. Uprooting and snapping of trees - structural determinants and ecological consequences. *Canadian Journal of Forest Research* **13**:1011-1020.
- Reilly, A. E. 1998. Hurricane Hugo: winds of change. or not? forest dynamics on St John, US Virgin Islands, 1986-1991. Pages 349-365 *in* F. Dallmeier and J. A. Comiskey, editors. *Forest biodiversity in North, Central and South America, and the Caribbean: Research and monitoring. Man and the Biosphere Series Volume 21*. UNESCO and The Parthenon Publishing Group. Carnforth, Lancashire, UK.
- Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems* **1**:524-534.
- Ruel, J. C. 1995. Understanding windthrow - silvicultural implications. *Forestry Chronicle* **71**:434-445.
- Ruel, J. C., D. Pin, and K. Cooper. 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. *Forest Ecology and Management* **143**:105-113.

- Ruel, J. C. and M. Pineau. 2002. Windthrow as an important process for white spruce regeneration. *Forestry Chronicle* **78**:732-738.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* **63**:1533-1546.
- Runkle, J. R. 1985. Disturbance regimes in temperate forests. Pages 17-33 in S. T. A. Pickett and P. S. White, editors. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida, USA.
- Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1989. Tree uprooting - review of impacts on forest ecology. *Vegetatio* **79**:165-176.
- Schnitzer, S. A. and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* **82**:913-919.
- Sheil, D., D. Burslem, and D. Alder. 1995. The interpretation and misinterpretation of mortality-rate measures. *Journal of Ecology* **83**:331-333.
- Sheil, D. and R. M. May. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* **84**:91-100.
- Sinton, D. S., J. A. Jones, J. L. Ohmann, and F. J. Swanson. 2000. Windthrow disturbance, forest composition, and structure in the Bull Run basin, Oregon. *Ecology* **81**:2539-2556.
- Slater, H., W. J. Platt, D. B. Baker, and H. A. Johnson. 1995. Effects of Hurricane Andrew on damage and mortality of trees in subtropical hardwood hammocks on long pine key, everglades national park, Florida, USA. *Journal of Coastal Research* **21**:197-207.
- Smith, G. F., N. S. Nicholas, and S. M. Zedaker. 1997. Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. *Forest Ecology and Management* **95**:275-283.
- Sousa, W. P. 1980. The responses of a community to disturbance - the importance of successional age and species life histories. *Oecologia* **45**:72-81.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353-391.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 2001. *Categorical data analysis using the SAS system (2ed)*. SAS Institute, Cary, NC, USA.
- Sugden, A. M. 1992. Hurricanes in tropical forests. *Trends in Ecology & Evolution* **7**:146-147.
- Tanner, E. V. J., V. Kapos, and J. R. Healey. 1991. Hurricane effects on forest ecosystems in the Caribbean. *Biotropica* **23**:513-521.

- Tilman, D. 1996. The benefits of natural disasters. *Science* **273**:1518.
- Touliatos, P. A. R., E. 1971. Hurricanes and trees: ten lessons from Camille. *Journal of Forestry* **69**:285-289.
- Trousdell, K. B., Williams, W.C. And Nelson, T.C. 1965. Damage to recently thinned loblolly pine stands by Hurricane Donna. *Journal of Forestry* **63**:96-100.
- Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* **1**:511-523.
- Ulanova, N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management* **135**:155-167.
- Vandermeer, J., D. Boucher, I. Perfecto, and I. G. Delacerda. 1996. A theory of disturbance and species diversity: evidence from Nicaragua after Hurricane Joan. *Biotropica* **28**:600-613.
- Vandermeer, J., A. Brenner, and I. G. De La Cerda. 1998. Growth rates of tree height six years after hurricane damage at four localities in eastern Nicaragua. *Biotropica* **30**:502-509.
- Vandermeer, J., I. G. De La Cerda, D. Boucher, I. Perfecto, and J. Ruiz. 2000. Hurricane disturbance and tropical tree species diversity. *Science* **290**:788-791.
- Vandermeer, J., I. G. Delacerda, and D. Boucher. 1997. Contrasting growth rate patterns in eighteen tree species from a post-hurricane forest in Nicaragua. *Biotropica* **29**:151-161.
- Vandermeer, J., M. A. Mallona, D. Boucher, K. Yih, and I. Perfecto. 1995. 3 years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua - evidence in support of the direct regeneration hypothesis. *Journal of Tropical Ecology* **11**:465-471.
- Veblen, T. T., K. S. Hadley, and M. S. Reid. 1991. Disturbance and stand development of a Colorado sub-alpine forest. *Journal of Biogeography* **18**:707-716.
- Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1989. Blowdown and stand development in a Colorado subalpine forest. *Canadian Journal of Forest Research* **19**:1218-1225.
- Wakimoto, R. M. and P. G. Black. 1994. Damage survey of Hurricane Andrew and its relationship to the eyewall. *Bulletin of the American Meteorological Society* **75**:189-200.
- Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23**:379-385.

- Walker, L. R. 1995. Timing of post-hurricane tree mortality in Puerto Rico. *Journal of Tropical Ecology* **11**:315-320.
- Walker, L. R., J. Voltzow, J. D. Ackerman, D. S. Fernandez, and N. Fetcher. 1992. Immediate impact of Hurricane Hugo on a Puerto-Rican rain-forest. *Ecology* **73**:691-694.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* **35**:1-22.
- Weaver, P. L. 1989. Forest changes after hurricanes in Puerto Rico Luquillo Mountains. *Interciencia* **14**:181-192.
- Webb, S. L. 1988. Windstorm damage and microsite colonization in 2 Minnesota forests. *Canadian Journal of Forest Research* **18**:1186-1195.
- Webb, S. L. 1989. Contrasting windstorm consequences in 2 forests, Itasca State Park, Minnesota. *Ecology* **70**:1167-1180.
- Webb, S. L. 1999. Disturbance by wind in temperate-zone forests. Page 187-222 *in* L. R. Walker, editor. *Ecosystems of Disturbed Ground*. Elsevier, Amsterdam, The Netherlands.
- Webb, S. L. and S. E. Scanga. 2001. Windstorm disturbance without patch dynamics: twelve years of change in a Minnesota forest. *Ecology* **82**:893-897.
- Whigham, D. F., M. B. Dickinson, and N. V. L. Brokaw. 1999. Background canopy gap and catastrophic wind disturbance in tropical forests. Pages 223-252 *in* L. R. Walker, editor. *Ecosystems of Disturbed Ground*. Elsevier, Amsterdam, The Netherlands.
- Whigham, D. F., I. Olmsted, E. C. Cano, and M. E. Harmon. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan peninsula. *Biotropica* **23**:434-441.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229-299.
- White, P. S. and J. Harrod. 1997. Disturbance and diversity in a landscape context. Pages 128-159 *in* J. Bissonette, editor. *Wildlife and landscapes*. Springer-Verlag, New York, USA.
- White, P. S. and A. Jentsch. 2004. Disturbance, succession, and community assembly in terrestrial plant communities. *in* V. Temperton, R. Hobbs, and S. Halle, editors. *Assembly Rules and Restoration Ecology*. Island Press, California, USA.
- White, R. D. 1999. The impacts of Hurricane Fran on a North Carolina piedmont woodland. Master thesis. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.

- Whitmore, T. C. 1984. Gap size and species richness in tropical rain forests. *Biotropica* **16**:239.
- Whitmore, T. C. 1989. Canopy gaps and the 2 major groups of forest trees. *Ecology* **70**:536-538.
- Whitmore, T. C. 1989. Changes over 21 years in the Kolombangara rain forests. *Journal of Ecology* **77**:469-483.
- Wilkinson, R. C., Britt, R.W., Spence, E.A. And Seiber, S.M. 1978. Hurricane-tornado damage, mortality, and insect infestations of slash pine. *South Journal of applied Forestry* **2**:132-134.
- William, J. M. and I. W. Duedall. 1997. Florida hurricanes and tropical storms. University Press of Florida, Gainesville, Florida, USA.
- Wurman, J. and J. Winslow. 1998. Intense sub-kilometer-scale boundary layer rolls observed in Hurricane Fran. *Science* **280**:555-557.
- Zimmerman, J. K., T. M. Aide, M. Rosario, M. Serrano, and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management* **77**:65-76.
- Zimmerman, J. K., E. M. Everham, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico - implications for tropical tree life-histories. *Journal of Ecology* **82**:911-922.
- Zimmerman, J. K., M. R. Willig, L. R. Walker, and W. L. Silver. 1996. Introduction: disturbance and Caribbean ecosystems. *Biotropica* **28**:414-423.

Table 2.1. Characteristics of the seven mapped plots in the Duke Forest, North Carolina, USA.

Name	Size (m ²)	Establishment (yr.)	Habitat	Disturbance history
<u>Pine stands</u>				
Graveyard	13,000	1978	Dry upland	Selective cutting prior to 1930, some salvage cutting following Hurricane Hazel in 1954
Land's end	9,900	1978	Dry upland	Selective cutting prior to 1930
<u>Upland hardwood stands</u>				
Rocky	20,400	1978	Dry upland	Selective cutting prior to 1930
Wooden Bridge	5,250	1984	Dry mesic upland	Selective cutting prior to 1930
Bormann	19,600	1952	Dry upland	Selective cutting prior to 1930
Bryan Center	19,400	1986	Dry mesic upland	Old field, abandoned circa 1780
Oosting	65,536	1990	Dry mesic upland	Selective cutting prior to 1930

Table 2.2. Stem damage (%) by 1996 Hurricane Fran in the seven MPPs in the Duke Forest, North Carolina, USA.

	Uprooting	Breakage	Leaning	Bent	Pinned
<u>Pine stands</u>					
Graveyard					
d.b.h. > 25 cm	22.46	6.15	20.62	0.23	0.46
d.b.h. > 10 cm	16.10	9.09	14.13	3.12	0.86
d.b.h. ≤ 10 cm	3.06	8.50	3.06	3.56	2.27
d.b.h. > 2 cm	7.30	8.69	6.66	2.67	1.90
Land's end					
d.b.h. > 25 cm	13.33	6.64	11.28	0.51	0.00
d.b.h. > 10 cm	10.45	9.15	6.32	2.61	3.05
d.b.h. ≤ 10 cm	1.44	6.48	2.02	4.32	17.13
d.b.h. > 2 cm	3.61	7.00	3.03	3.82	13.38
<u>Upland hardwood stands</u>					
Bormann					
d.b.h. > 25 cm	24.33	4.00	21.33	0.67	2.00
d.b.h. > 10 cm	16.48	8.95	12.64	2.13	4.55
d.b.h. ≤ 10 cm	3.75	7.98	2.90	4.47	13.59
d.b.h. > 2 cm	6.95	8.20	5.34	3.88	11.32
Rocky					
d.b.h. > 25 cm	27.06	5.00	16.76	0.59	4.12
d.b.h. > 10 cm	15.96	5.03	9.07	1.97	3.50
d.b.h. ≤ 10 cm	1.91	3.71	1.01	3.52	8.66
d.b.h. > 2 cm	5.48	4.06	3.06	3.12	7.32
Bryan Center					
d.b.h. > 25 cm	6.58	6.58	0.41	0.00	0.00
d.b.h. > 10 cm	4.02	6.35	0.17	1.34	0.67
d.b.h. ≤ 10 cm	0.28	2.65	0.00	3.11	2.46
d.b.h. > 2 cm	1.09	3.45	0.04	2.73	2.07
Wooden Bridge					
d.b.h. > 25 cm	9.18	1.02	8.16	2.04	2.04
d.b.h. > 10 cm	4.95	4.95	6.31	1.35	4.50
d.b.h. ≤ 10 cm	3.16	3.94	4.47	2.63	6.58
d.b.h. > 2 cm	3.82	3.82	5.15	2.16	5.81
Oosting					
d.b.h. > 25 cm	6.53	2.46	0.92	0.23	0.46
d.b.h. > 10 cm	4.09	1.61	0.04	3.12	0.86
d.b.h. ≤ 10 cm	0.74	2.95	0.21	3.56	2.27
d.b.h. > 2 cm	1.75	3.06	0.44	2.67	1.90

Note: Stem damage percentage was computed as the percent of uprooting, breakage, leaning, bending and pinned stems against their stem number pre-disturbance (1992/1993) in each size category. Uprooting including both partial and complete uprooting stems. Breakage includes stems with over 35% canopy losses.

Table 2.3. With-stand damage variation in two mapped pine and five mapped hardwood plots, and among-stand damage variation in 34 permanent sampling plots in the Duke Forest, North Carolina, USA. The damage severity was examined by using stand damage index.

Plot Names	N	Mean	Std Dev	Minimum	Maximum
<u>Pine stands</u>					
Graveyard	12	0.58	0.42	0.10	1.48
Land's end	9	0.52	0.47	0.12	1.34
PSP pine stands	28	0.34	0.45	0.01	1.54
<u>Upland hardwoods</u>					
Bormann	16	0.50	0.37	0.01	1.22
Rocky	20	0.64	0.53	0.03	1.83
Bryan Center	20	0.11	0.10	0.00	0.39
Wooden Bridge	6	0.24	0.36	0.00	0.96
Oosting	64	0.07	0.11	0.00	0.55
PSP hardwoods	6	0.36	0.36	0.00	0.70

Note: Stand damage index was computed based on all stems >2 cm within a stand. I first created an “integrated stem damage code” for each stem in the stand by combining all the information of uprooting, breakage, leaning and leaned up to a single code ranging from 0-3 (see method section for detailed code criteria), I then weighted the code by multiply the stem relative basal area (i.e., the basal area of the stem divided by the sum of all stem in the plot). The stand damage index was the average value of the weighted stem “integrated stem damage code” of all stems in the stand. The range of stand damage index by definition is from 0-3. N is the number of sub-plot divided in each mapped plot and the amount of the PSPs. The size of sub-plots varied slightly but was generally close to 1000 m².

Table 2.4. Mean annually mortality (%/yr) in the Graveyard and the Bormann plot in the Duke Forest, North Carolina, USA.

	Mean annually mortality (%/yr.)		
	Pre-hurricane (1989-1993)	Hurricane-period (1993-1997)	Post-hurricane (1997-2000)
<u>Pine stand</u> (Graveyard plot)			
2.5-5 cm	2.82	3.67	3.61
5-10 cm	2.86	3.75	3.76
10-25 cm	1.14	1.82	2.28
>25 cm	0.22	4.22	3.18
<u>Upland hardwood</u> (Bormann plot)			
2.5-5 cm	1.52	2.55	4.13
5-10 cm	0.93	2.06	2.74
10-25 cm	0.71	1.87	2.18
>25 cm	0.68	3.74	5.92

Note: Changes in tree mortality for each of the three sampling intervals (i.e., 1989/90 to 1992/93 as pre hurricane period, 1992/93 to 1997 as hurricane period and 1997 to 2000/2001 as post hurricane period). Mean annual mortality rate derived from the common exponential model of population growth (or decline) and was calculated by: $m = (\ln (N_t/N_0))/t$ where N_t and N_0 are the number of (alive) stems at the beginning and end of interval t (years).

Table 2.5. Annual mean mortality rates (m) of tree species in the Graveyard and the Bormann plot in three periods in the Duke Forest, North Carolina, USA.

	No. of initial stems /dead stems			Annual mean mortality rates		
	1989-93	1993-97	1997-2000	1989-93	1993-97	1997-2000
<u>Pine stand (Graveyard plot)</u>						
All species combined	3435/228	3326/479	2666/328	2.86	3.98	3.60
<i>Acer rubrum</i>	927/46	896/74	734/90	1.7	1.72	4.36
<i>Carya</i> spp.	711/53	658/88	501/22	2.58	2.87	1.5
<i>Cornus florida</i>	528/48	563/123	427/128	3.18	4.93	11.88
<i>Fraxinus</i> spp.	18/2	17/3	16/0	3.93	3.88	0
<i>Juniperus virginiana</i>	31/5	25/9	13/0	5.86	8.93	0
<i>Liquidambar styraciflua</i>	346/35	331/48	269/21	3.55	3.13	2.71
<i>Liriodendron tulipifera</i>	150/4	141/11	125/11	0.9	1.62	3.07
<i>Nyssa sylvatica</i>	34/1	33/3	24/2	1	1.91	2.9
<i>Ostrya virginiana</i>	120/3	140/5	147/2	0.84	0.73	0.46
<i>Oxydendrum arboreum</i>	136/3	130/22	104/8	0.74	3.71	2.67
<i>Pinus</i> spp.	274/5	276/64	208/32	0.61	5.28	5.57
<i>Quercus alba</i>	43/7	33/9	21/0	5.92	6.37	0
<i>Quercus rubra</i>	24/2	19/5	12/2	2.9	6.11	6.08
<i>Quercus velutina</i>	60/3	45/4	30/9	1.28	2.33	8.92
<i>Ulmus rubra</i>	33/1	19/1	35/1	1.03	1.08	0.97
<u>Upland hardwood (Bormann plot)</u>						
All species combined	3542/178	3747/400	3388/339	1.32	3.21	3.72
<i>Acer rubrum</i>	1517/41	1643/79	1572/54	0.68	1.23	1.17
<i>Carya</i> spp.	154/5	174/16	160/13	0.83	2.41	2.82
<i>Cornus florida</i>	717/72	804/181	650/183	2.65	6.38	11.02
<i>Juniperus virginiana</i>	35/1	36/4	37/3	0.72	2.94	2.82
<i>Liriodendron tulipifera</i>	19/1	21/3	18/0	1.35	3.85	0
<i>Nyssa sylvatica</i>	192/21	172/16	159/8	2.9	2.44	1.72
<i>Oxydendrum arboreum</i>	494/21	472/42	430/29	1.09	2.33	2.33
<i>Prunus serotina</i>	39/1	55/4	57/4	0.65	1.89	2.43
<i>Quercus alba</i>	283/10	276/42	228/33	0.9	4.13	5.21
<i>Quercus rubra</i>	52/3	53/6	46/7	1.49	3	5.5
<i>Quercus velutina</i>	40/2	41/7	31/5	1.28	4.68	5.8

Table 2.6. Mean diameter growth rate (cm/yr.) of major tree species in the Graveyard and the Bormann plot in three periods (pre-h., h., and post-h; *h = hurricane) in Duke Forest, North Carolina, USA.

Size (cm)	No. of stems 1989	Mean diameter growth rate (cm/yr.)		
		pre-h. (1989-93)	h. (1993-97)	post-h. (1997-2000)
<u>Pine stand (Graveyard plot)</u>				
All species combined	1972	0.14±0.22	0.10±0.14	0.21±0.27
<i>Acer rubrum</i>				
≥25	3	0.42±0.16	0.23±0.09	0.47±0.14
10.0-25	56	0.15±0.49	0.21±0.15	0.30±0.26
5.0-10.0	124	0.12±0.14	0.10±0.09	0.24±0.22
2.5-5.0	163	0.06±0.10	0.05±0.06	0.12±0.17
1.0-2.5	169	0.05±0.07	0.05±0.06	0.09±0.15
Overall	515	0.08±0.19	0.08±0.10	0.16±0.20
<i>Carya spp.</i>				
≥25	0	N/A	N/A	N/A
10.0-25	63	0.23±0.16	0.14±0.10	0.36±0.20
5.0-10.0	125	0.09±0.15	0.06±0.08	0.28±0.22
2.5-5.0	109	0.02±0.08	0.03±0.06	0.11±0.16
1.0-2.5	41	0.05±0.10	0.03±0.06	0.09±0.12
Overall	338	0.09±0.15	0.06±0.09	0.22±0.22
<i>Liquidambar styraciflua</i>				
≥25	22	0.36±0.24	0.26±0.21	0.38±0.19
10.0-25	157	0.12±0.19	0.11±0.16	0.26±0.27
5.0-10.0	49	0.04±0.25	-0.02±0.0	0.11±0.23
2.5-5.0	3	0.01±0.04	-0.01±0.01	0.13±0.14
1.0-2.5	1	0.03±0.00	0.04±0.00	0.03±0.00
overall	232	0.12±0.22	0.10±0.17	0.24±0.27
<i>Pinus spp.</i>				
≥25	157	0.34±0.28	0.23±0.20	0.18±0.26
10.0-25	10	0.08±0.17	0.06±0.10	0.07±0.22
5.0-10.0	0	N/A	N/A	N/A
2.5-5.0	0	N/A	N/A	N/A
1.0-2.5	0	N/A	N/A	N/A
Overall	167	0.33±0.28	0.22±0.20	0.17±0.25
<u>Upland hardwood stand (Bormann plot)</u>				
All species combined	2328	0.13±0.22	0.15±0.16	0.20±0.31
<i>Acer rubrum</i>				
≥25	2	0.13±0.18	0.24±0.16	0.20±0.00
10.0-25	76	0.22±0.16	0.22±0.17	0.33±0.49
5.0-10.0	216	0.17±0.15	0.22±0.14	0.32±0.41

Table 2.6 (Continued). Mean diameter growth rate (cm/yr.) of major tree species in the Graveyard and the Bormann plot in three periods (pre-hurricane, hurricane, and post hurricane) in Duke Forest, North Carolina, USA.

Size (cm)	No. of stems 1989	Mean diameter growth rate (cm/yr)		
		pre-h. (1989-93)	h. (1993-97)	post-h. (1997-2000)
<i>Acer rubrum</i>				
2.5-5.0	363	0.11±0.11	0.13±0.11	0.21±0.27
1.0-2.5	465	0.09±0.10	0.10±0.09	0.14±0.24
Overall	1122	0.12±0.12	0.14±0.12	0.21±0.32
<i>Carya spp.</i>				
≥25	13	0.13±0.15	0.26±0.15	0.06±0.91
10.0-25	33	0.06±0.08	0.11±0.12	0.25±0.30
5.0-10.0	6	0.11±0.13	0.13±0.07	0.38±0.20
2.5-5.0	13	0.04±0.08	0.06±0.05	0.09±0.10
1.0-2.5	33	0.07±0.05	0.06±0.07	0.08±0.12
Overall	98	0.07±0.09	0.11±0.12	0.14±0.39
<i>Cornus florida</i>				
10.0-25	4	0.13±0.13	0.03±0.18	0.15±0.09
5.0-10.0	53	0.10±0.10	0.08±0.10	0.11±0.27
2.5-5.0	102	0.13±0.08	0.09±0.08	0.14±0.16
1.0-2.5	115	0.12±0.11	0.09±0.08	0.14±0.18
Overall	274	0.12±0.10	0.09±0.08	0.14±0.19
<i>Nyssa sylvatica</i>				
≥25	3	0.14±0.15	0.13±0.03	0.12±0.13
10.0-25	22	0.10±0.12	0.15±0.15	0.24±0.32
5.0-10.0	20	0.06±0.10	0.07±0.09	0.22±0.20
2.5-5.0	35	0.06±0.09	0.04±0.06	0.07±0.10
1.0-2.5	41	0.06±0.07	0.07±0.08	0.13±0.22
Overall	121	0.07±0.09	0.08±0.10	0.15±0.22
<i>Oxydendrum arboreum</i>				
10.0-25	142	0.12±0.15	0.16±0.14	0.22±0.58
5.0-10.0	124	0.08±0.11	0.11±0.14	0.21±0.21
2.5-5.0	58	0.09±0.11	0.12±0.11	0.13±0.29
1.0-2.5	25	0.07±0.10	0.12±0.08	0.22±0.25
Overall	349	0.10±0.13	0.13±0.13	0.20±0.41
<i>Quercus alba</i>				
≥25	159	0.38±0.67	0.42±0.31	0.27±0.29
10.0-25	24	0.09±0.11	0.15±0.14	0.14±0.20
5.0-10.0	1	0.03±0.00	0.23±0.00	0.00±0.00
2.5-5.0	3	0.11±0.04	0.12±0.10	0.13±0.09
1.0-2.5	3	0.10±0.09	0.15±0.09	0.20±0.30
Overall	190	0.34±0.62	0.38±0.30	0.25±0.28

Table 2.7. Comparison of gap formation rate for seven mapped plots in the Duke Forest before and after Hurricane Fran.

Period	New gaps	Gap size (m ²)			GFR (%/yr)
		Average	Maximal	Minimal	
<u>Pine stands</u>					
Graveyard					
Pre-hurricane (1989-1992)	2	240.00	352.67	127.33	0.86
Hurricane period (1992-1997)	6	1172.53	4341.65	78.11	10.82
Land's end					
Pre-hurricane (1989-1993)	4	180.84	390.87	86.17	1.83
Hurricane period (1993-1997)	10	382.51	2126.45	45.13	9.66
<u>Upland hardwoods</u>					
Rocky					
Pre-hurricane (1985-1990)	6	187.86	447.77	60.55	3.42
Hurricane period (1990-1997)	10	1084.59	8029.15	64.82	13.29
Wooden Bridge					
Pre-hurricane (1986-1991)	3	75.14	110.64	47.50	0.86
Hurricane period (1991-1998)	6	178.32	260.44	81.77	2.91
Bormann					
Pre-hurricane (1989-1993)	6	145.59	228.56	79.48	1.01
Hurricane period (1993-1997)	9	1092.52	6156.67	47.52	12.54
Bryan Center					
Pre-hurricane (1986-1991)	17	204.08	489.31	66.30	3.58
Hurricane period (1991-1998)	15	357.92	1063.23	72.14	3.59
Oosting					
Pre-hurricane	N/A	N/A	N/A	N/A	N/A
Hurricane period (1990-1998)	53	349.43	1313.71	32.89	3.53

Note: I used Runkle's expanded gap concept to define gap size and adopted 25 cm d.b.h. as the minimum diameter of the trunk of a tree that can form a gap when it dies or falls. The gap size was measured for the stem maps by using ArcGIS 9.0 (ESRI Inc. 2004). The gap formation rate was calculated as the percentage of gap area at the end of an intervals minus the percentage of gap area at the beginning of interval) divided by t (years).

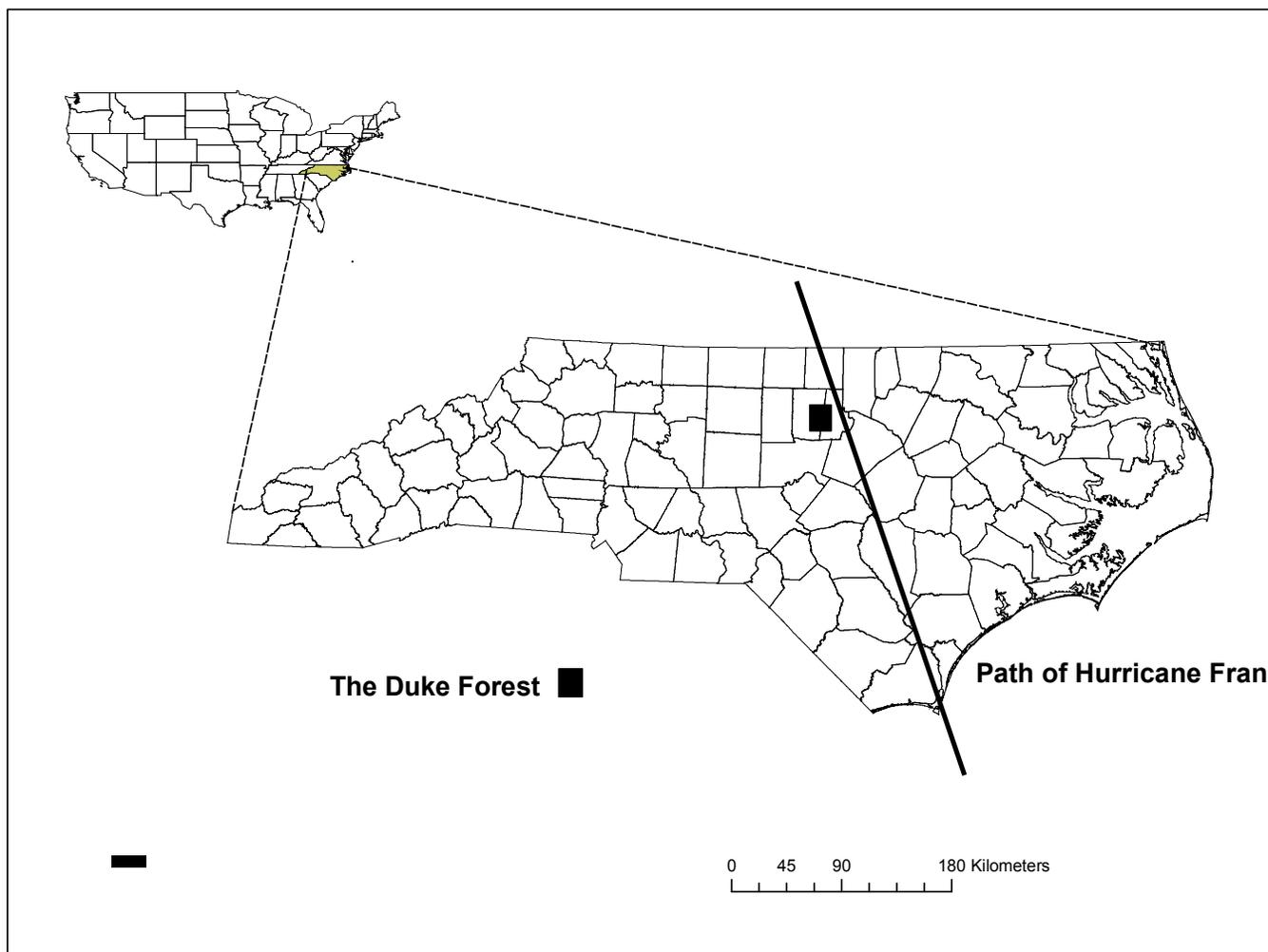


Figure 2.1. The location of the Duke Forest and the path of 1996 Hurricane Fran in North Carolina, USA.

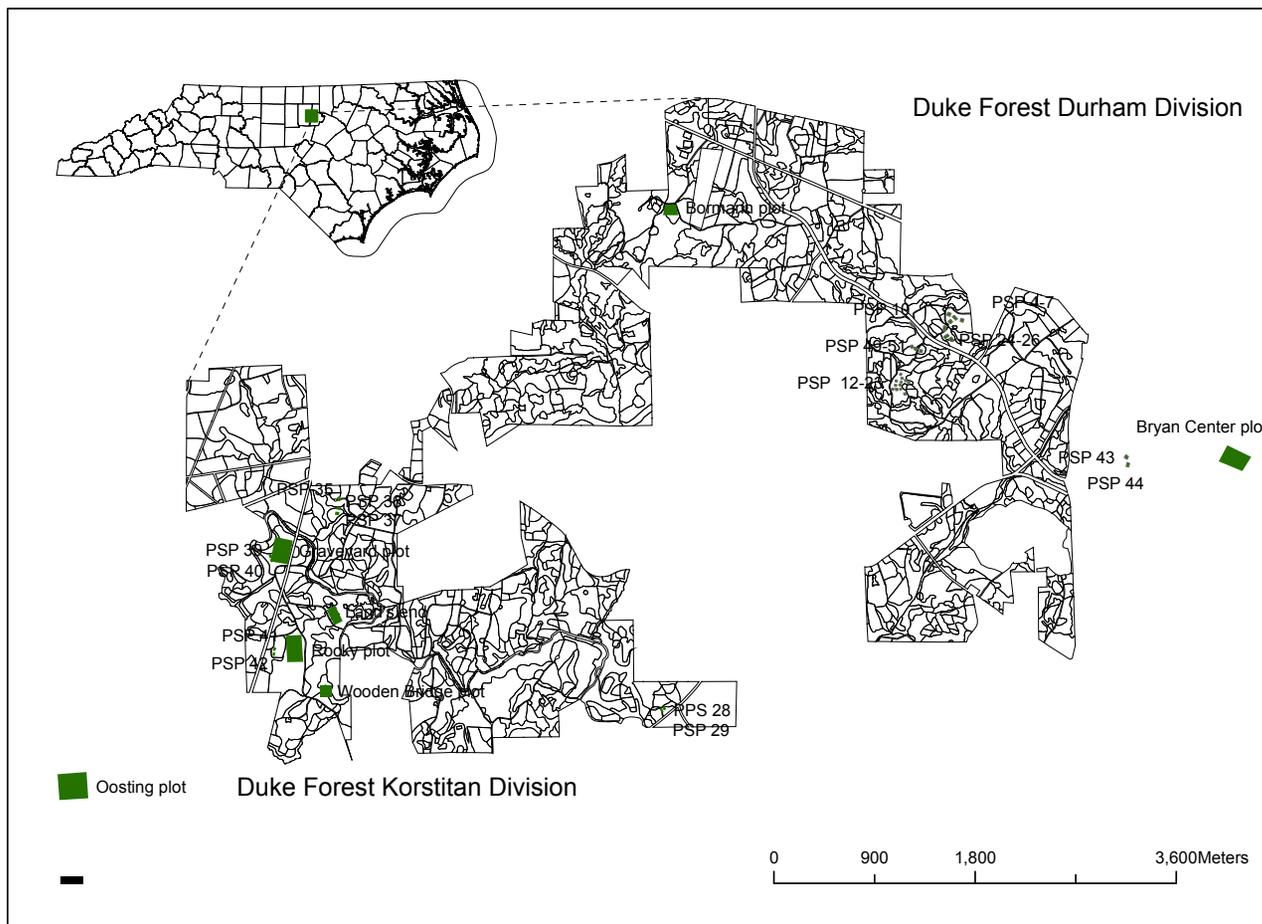
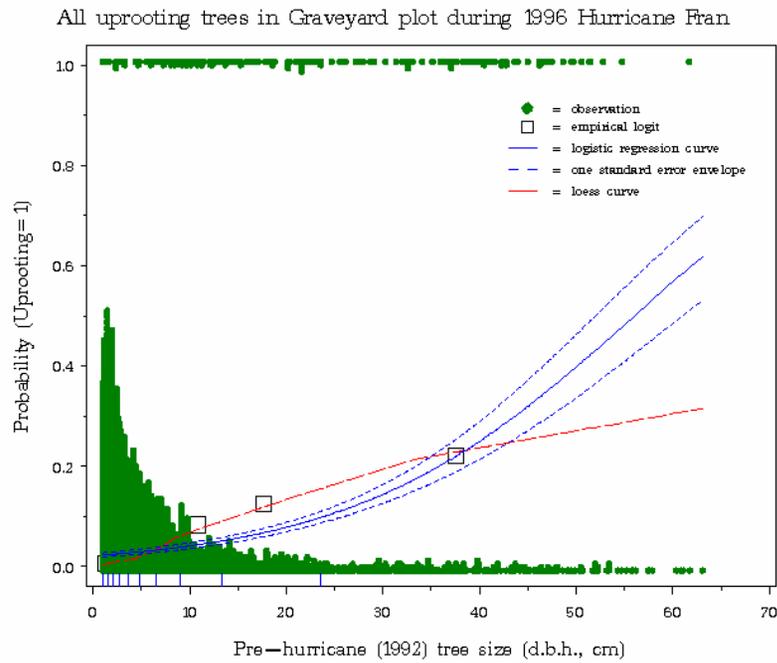
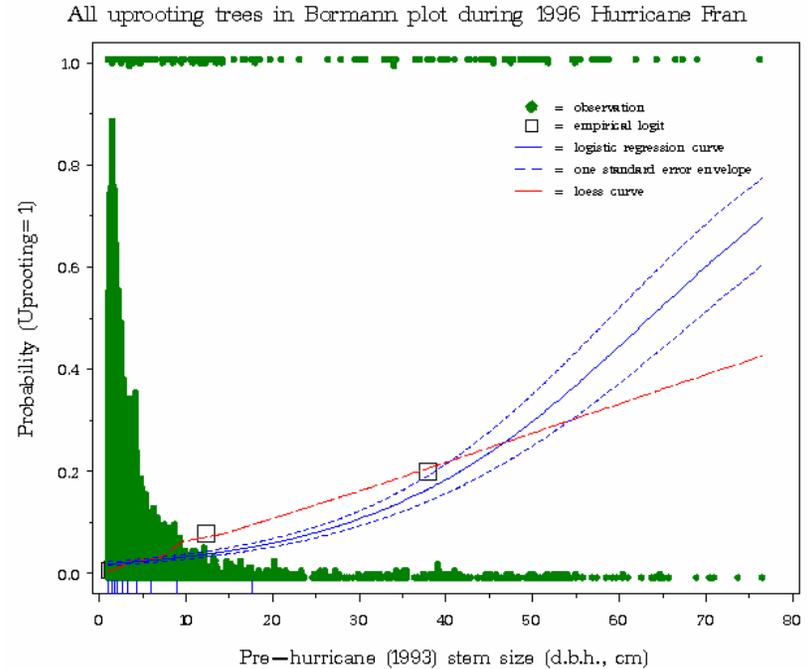


Figure 2.2. The locations of the seven mapped permanent plots (MPPs) and the 34 long-term permanent sample plots (PSPs) used in this study in Durham Division and Korstian Division of the Duke Forest, North Carolina, USA. The sub-areas within the two divisions are the forest cover types. Note the legends of forest cover types are not shown in this figure (Data source: the Duke Forest office, Duke University 2001).

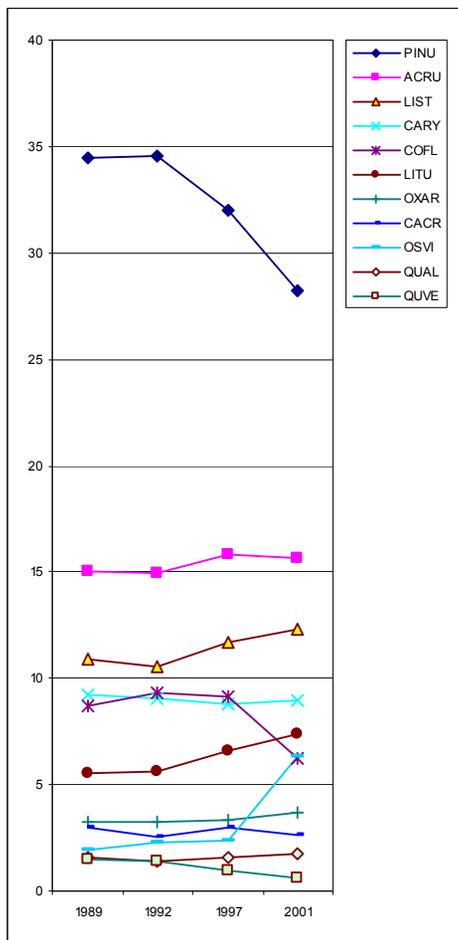


(a) Graveyard Plot

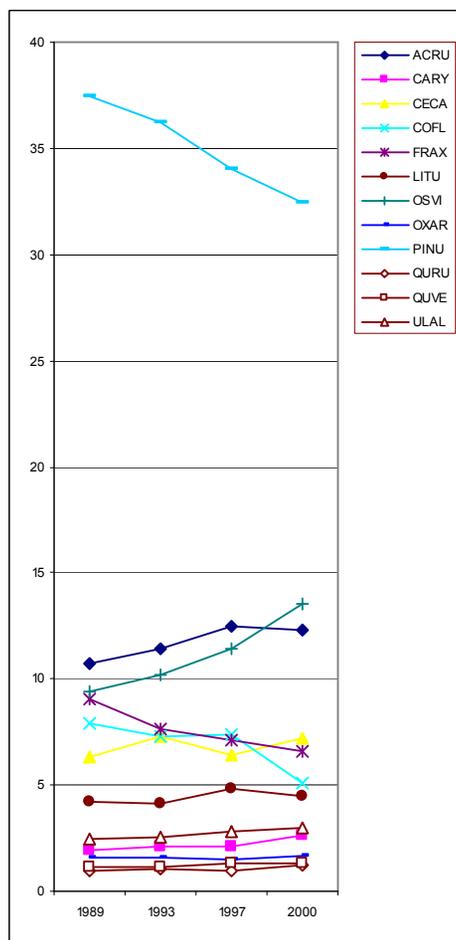


(b) Bormann plot

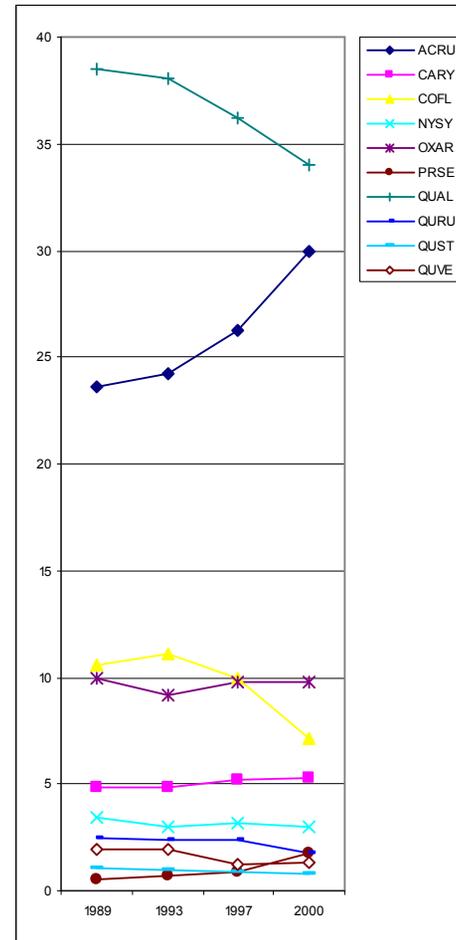
Figure 2.3. The probability of a tree uprooting increased with an increase in tree size in (a) the Graveyard plot and (b) the Bormann plot. Empirical log odds and the probability of uprooting as a function of pre-hurricane tree size are shown. The observed response is plotted as stacked points at the top (i.e., uprooting) and bottom of the figure (i.e. no such type damage). The squares show the empirical sample logits and the analogous adjusted sample probability. The curves on these plots show predicted probabilities and 95% confidence bands.



(A) Graveyard plot



(B) Land's end plot



(C) Bormann plot

Figure 2.4. Change in IV (importance value) of major tree species in three mapped plots in three periods (pre-hurricane, hurricane period and post hurricane) over 10 yr. Data are shown for all species with IV ≥ 1 over the three periods. The total value of IV is 100. The survey years for each plot pre-hurricane vary from 1989–1993, and post hurricane vary from 2000–2001.

Note: Species Abbreviation in **Figure 2.4**:

ACRU - *Acer rubrum*

COFL - *Cornus florida*

JUVI - *Juniperus virginiana*

LITU - *Liriodendron tulipifera*

OSV I - *Ostrya virginiana*

PINU - *Pinus spp.*

QURU - *Quercus rubra*

QUST - *Quercus stellata*

CARY- *Carya spp*

FRAX - *Fraxinus spp.*

LIST - *Liquidambar styraciflua*

NYSY - *Nyssa sylvatica*

OXAR - *Oxydendrum arboreum*

QUAL - *Quercus alba*

QUVE - *Quercus velutina*

QUFA - *Quercus falcata*

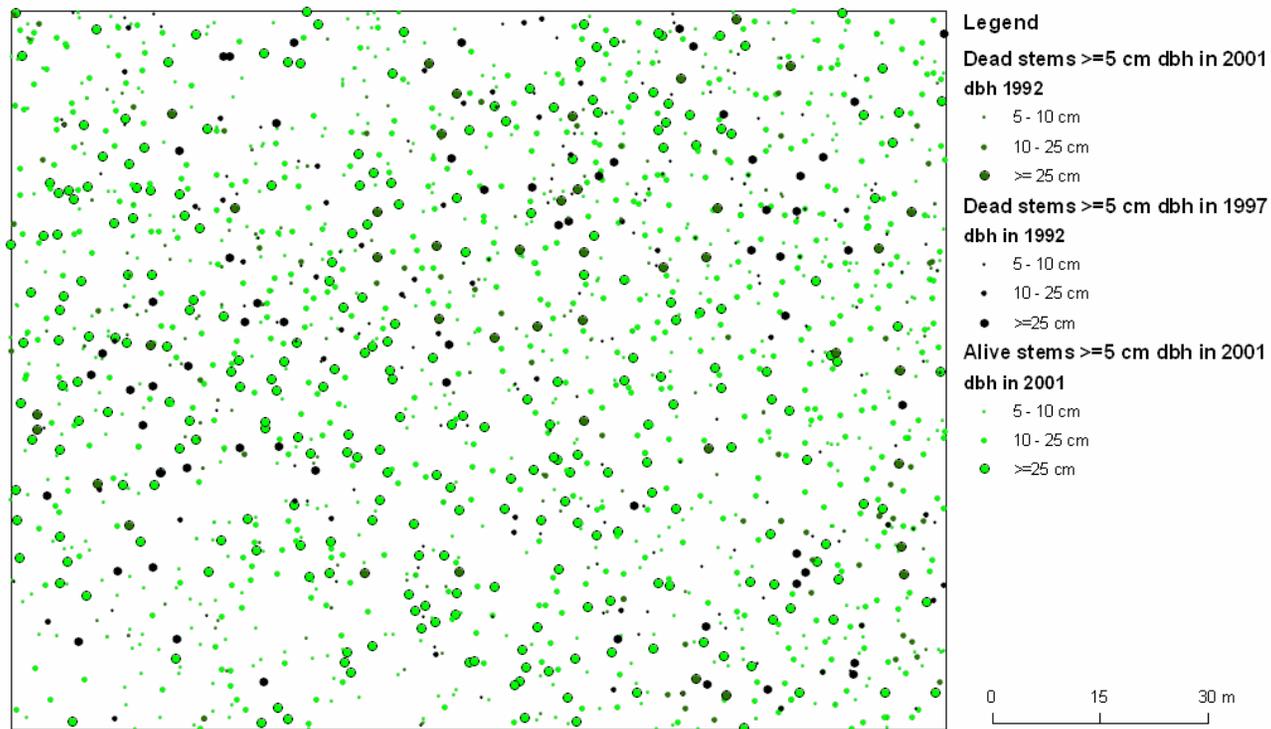


Figure 2.5a. Pattern of tree mortality (Stem d.b.h. ≥ 5 cm) in a loblolly pine stand (Graveyard plot) in the Duke Forest after the 1996 Hurricane Fran, North Carolina, USA.

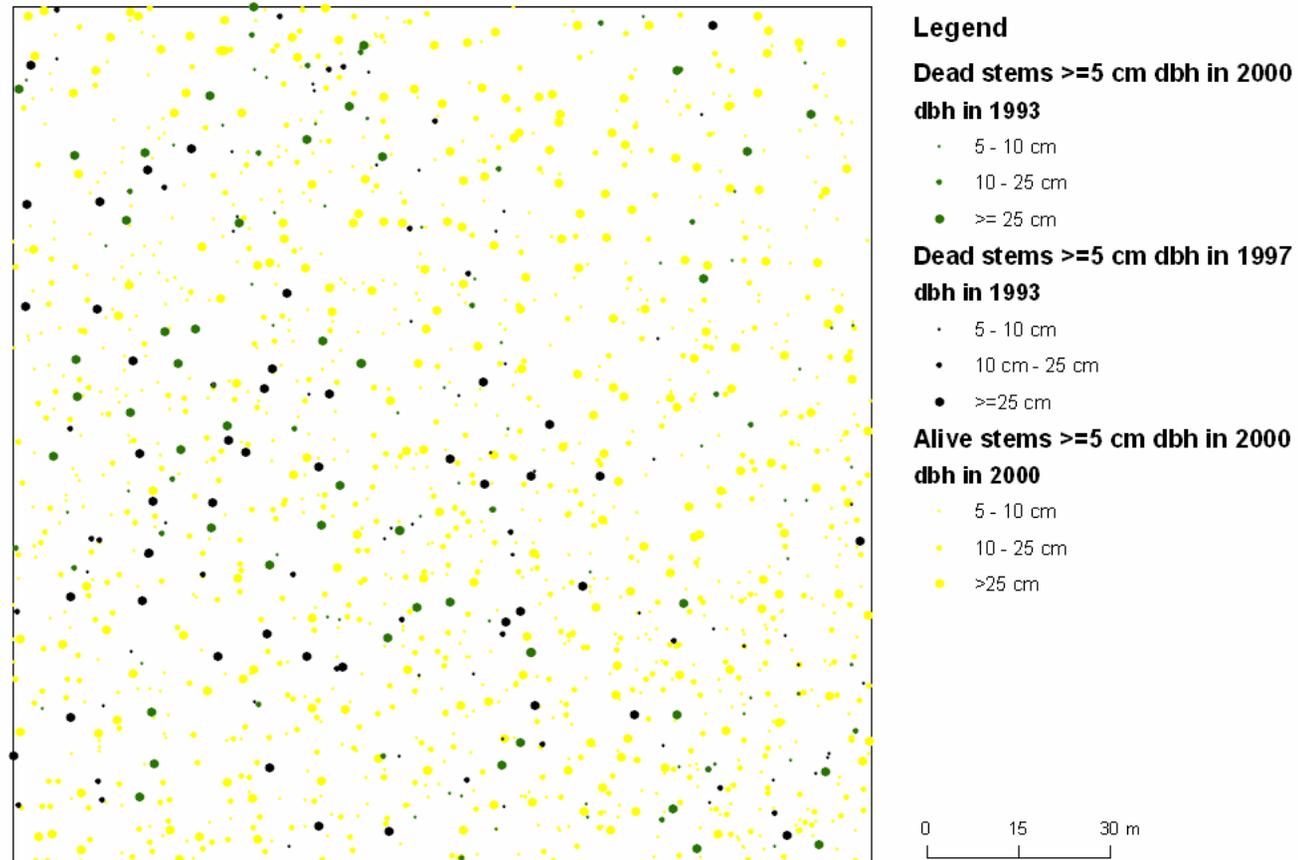


Figure 2.5b. The mortality stem (dbh ≥ 5 cm) maps of Bormann plot in the Duke Forest after the 1996 Hurricane Fran, North Carolina, USA.

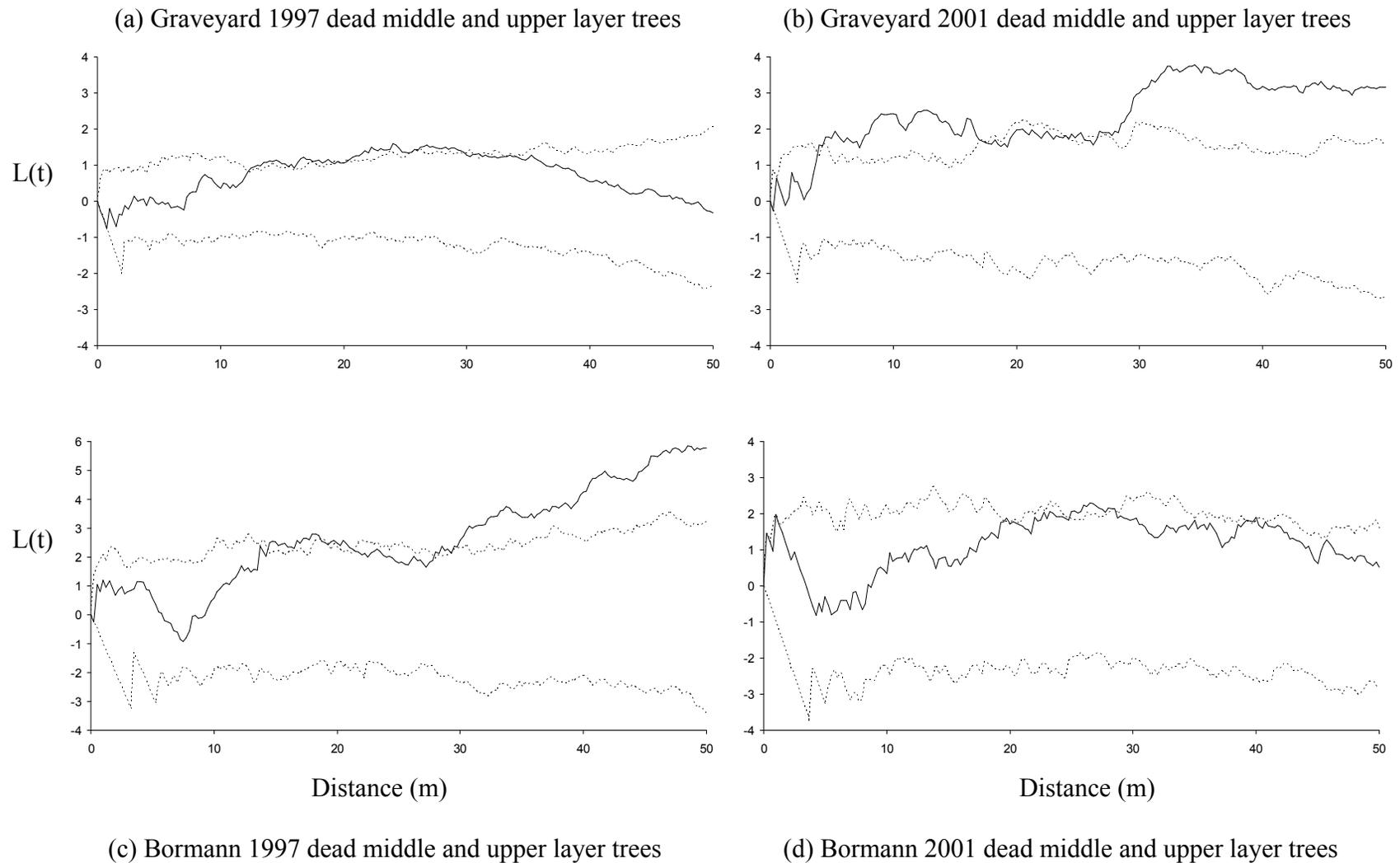


Figure 2.6a. Transformed Ripley's $K(d)$ for tree mortality over time in Graveyard and Bormann plot for the middle and upper layer trees (i.e., d.b.h. >10 cm) in the Duke Forest, North Carolina, USA. The sample statistic $L(t)$ is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness.

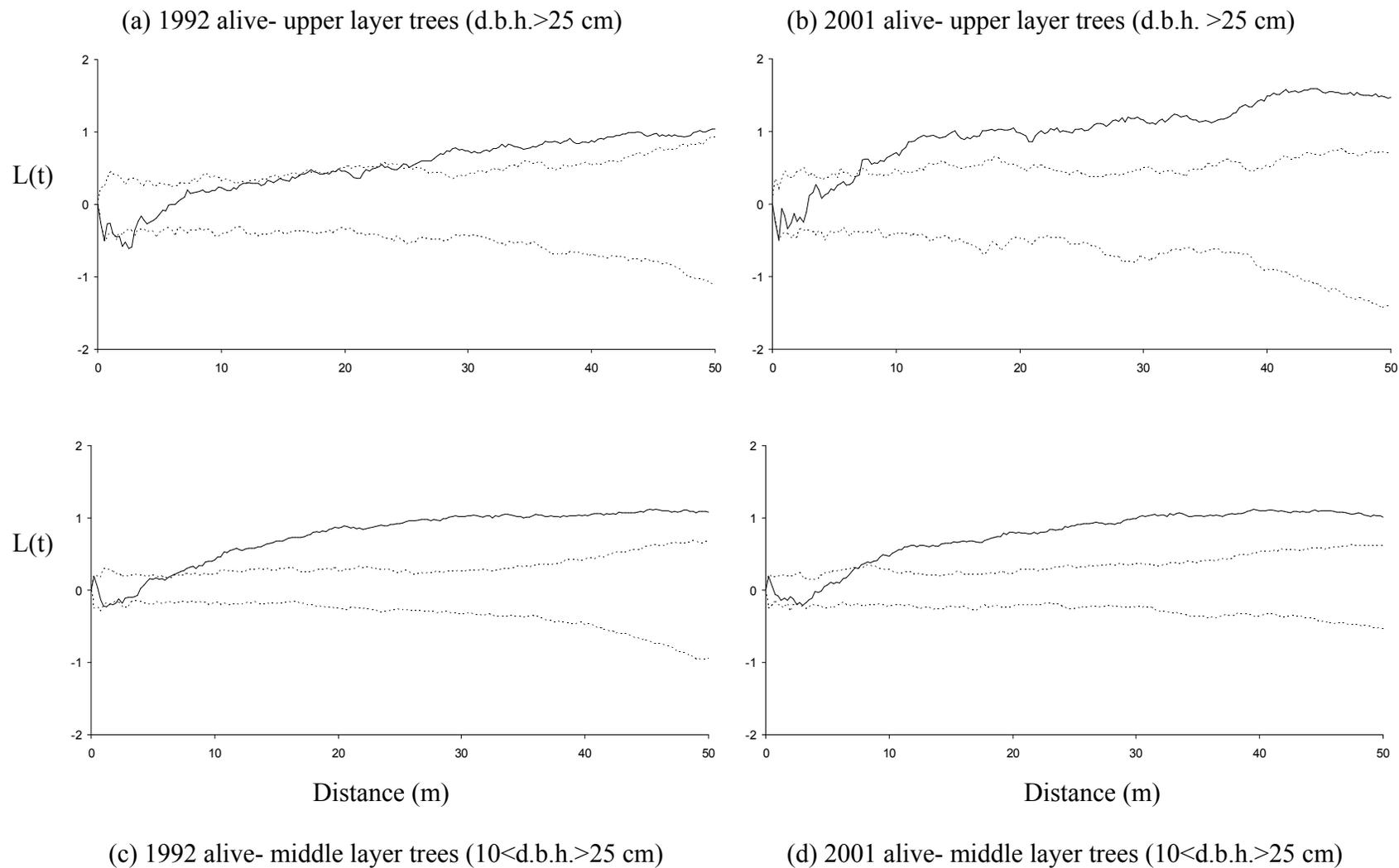


Figure 2.6b. Transformed Ripley's $K(d)$ for alive-trees over time in Graveyard plot in the Duke Forest, North Carolina, USA. The sample statistic $L(t)$ is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness.

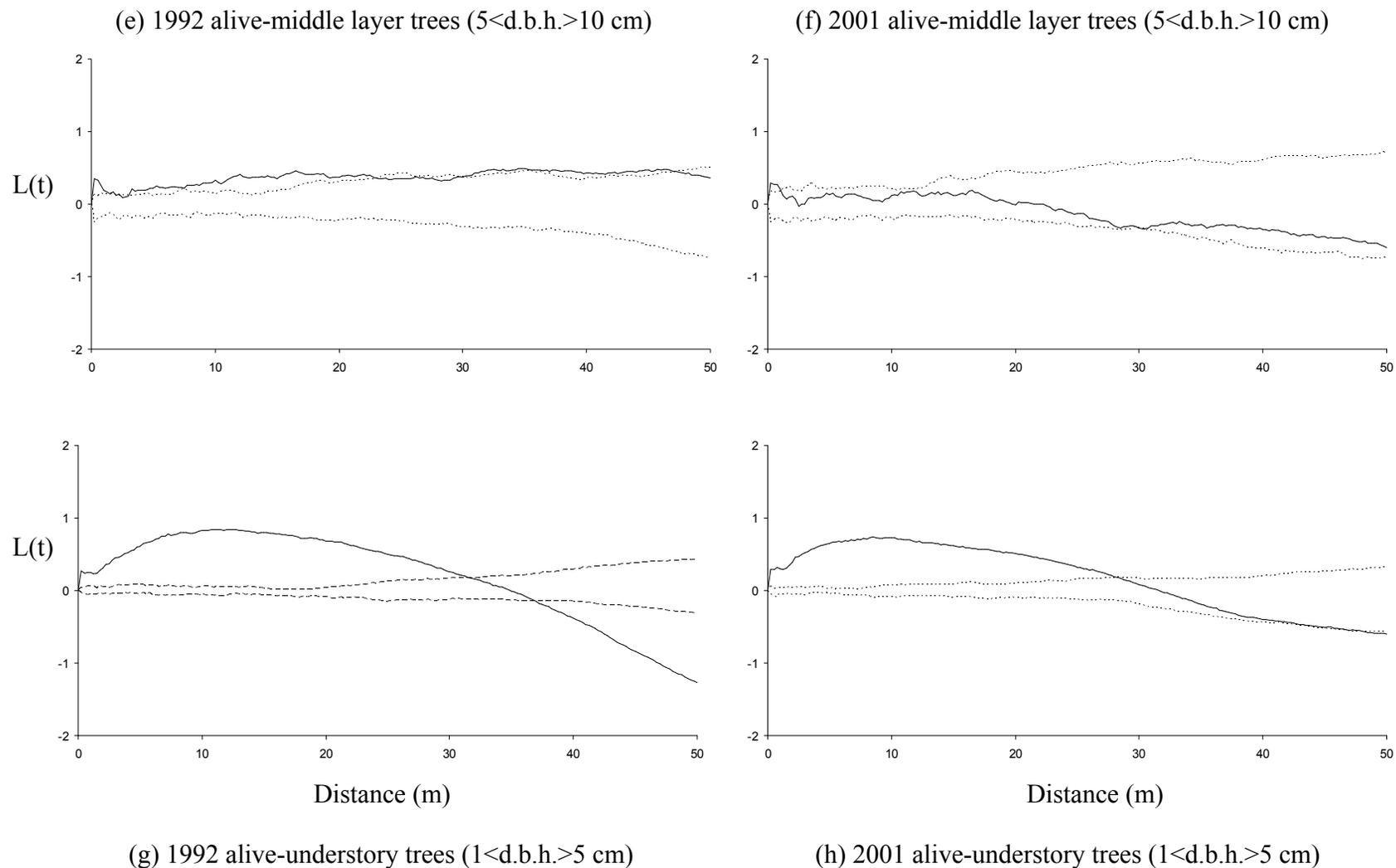


Figure 2.6b (Continued). Transformed Ripley's $K(d)$ for alive-trees over time in Graveyard plot for the major species in the Duke Forest, North Carolina, USA. The sample statistic $L(t)$ is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness.

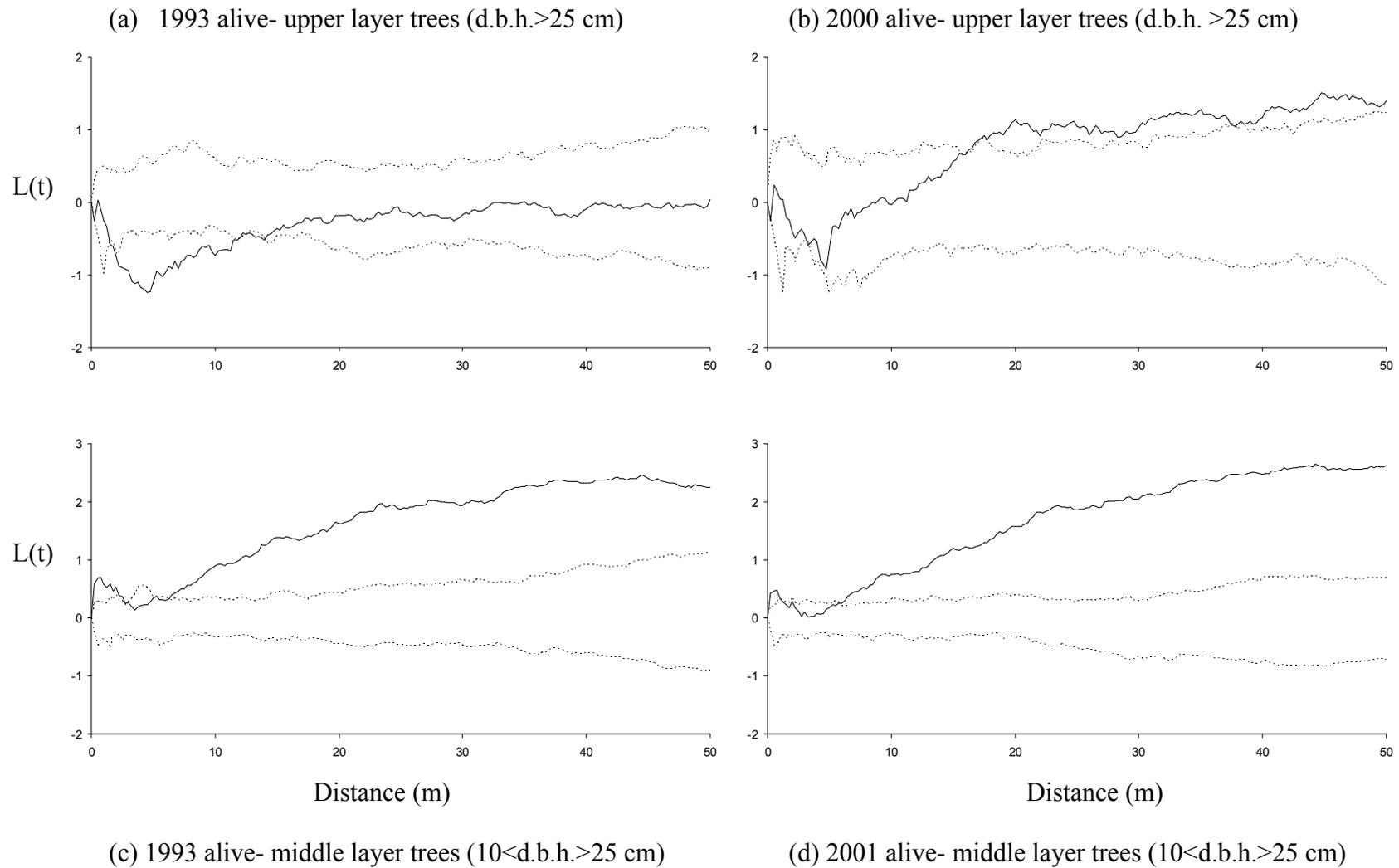


Figure 2.6c. Transformed Ripley's $K(d)$ for alive-trees over time in Bormann plot for the major species in the Duke Forest, North Carolina, USA. The sample statistic $L(t)$ is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness.

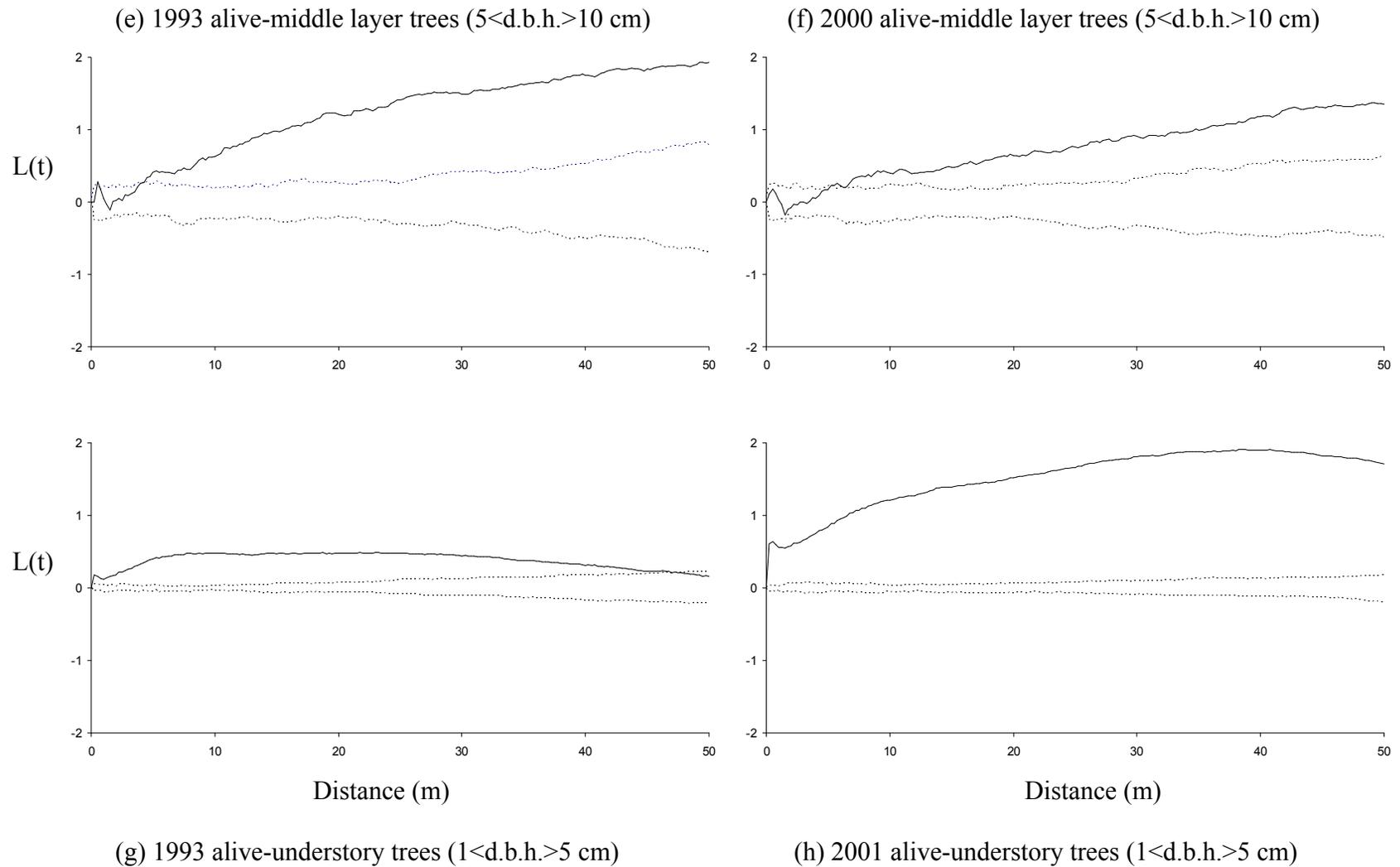
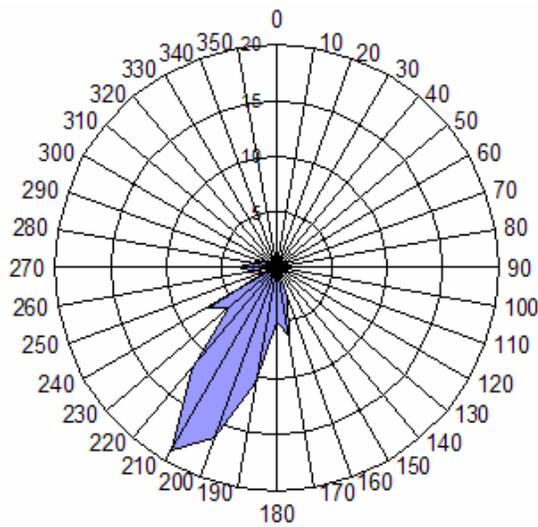
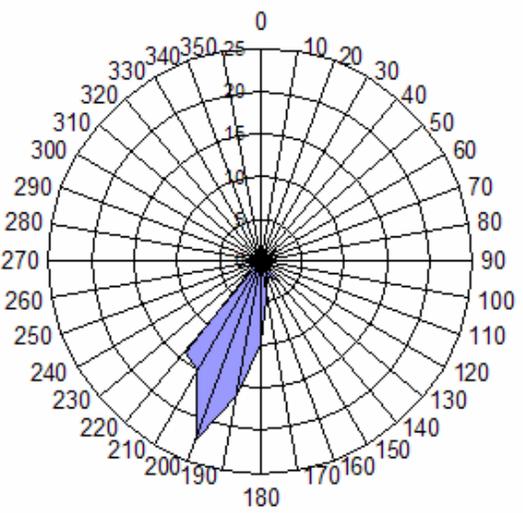


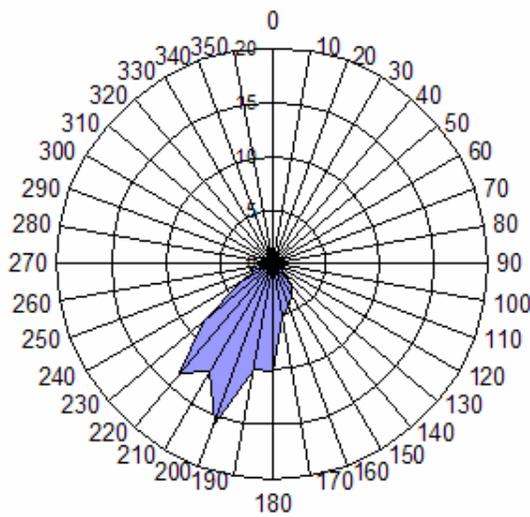
Figure 2.6c (Continued). Transformed Ripley's $K(d)$ for alive-trees over time in Bormann plot for the major species in the Duke Forest, North Carolina, USA. The sample statistic $L(t)$ is plotted against t (solid line). The dotted lines give a 99% confidence envelope for complete spatial randomness.



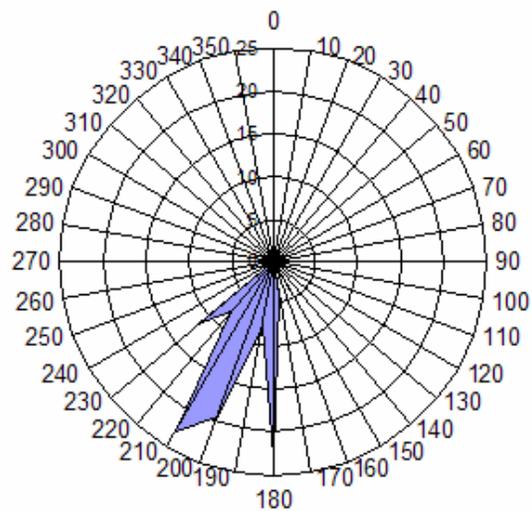
Graveyard plot ($\mu= 216.75 \pm 37.70^\circ$)



Bormann plot ($\mu= 202.85^\circ \pm 36.75^\circ$)

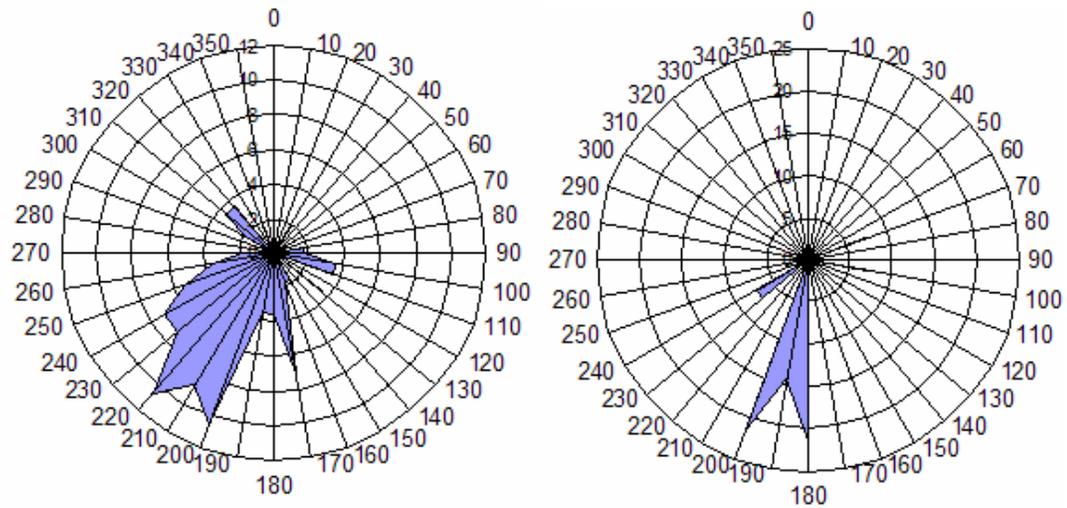


Rocky plot ($\mu= 203.90 \pm 41.80^\circ$)



Land's end plot ($\mu= 205.38 \pm 19.29^\circ$)

Figure 2.7. Percentage of azimuths of uprooting trees in six mapped plots in the Duke Forest, North Carolina, USA.



Oosting plot ($\mu=213.21\pm46.16^\circ$)

Byran Center plot ($\mu=195.29\pm44.50^\circ$)

Figure 2.7 (Continued). Percentage of azimuths of uprooting trees in six mapped plots in the Duke Forest, North Carolina, USA.

Note: Another mapped plot in the Duke Forest (Wooden Bridge plot) is not included due to only three trees were uprooted in the hurricane event. The azimuths of the three trees were 202° and 230° . μ is the mean vector of all fallen tree orientations and values after \pm are circular standard deviations of each plot.

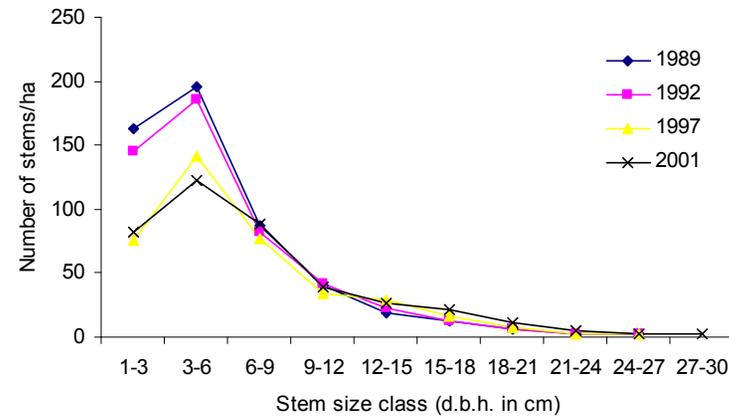
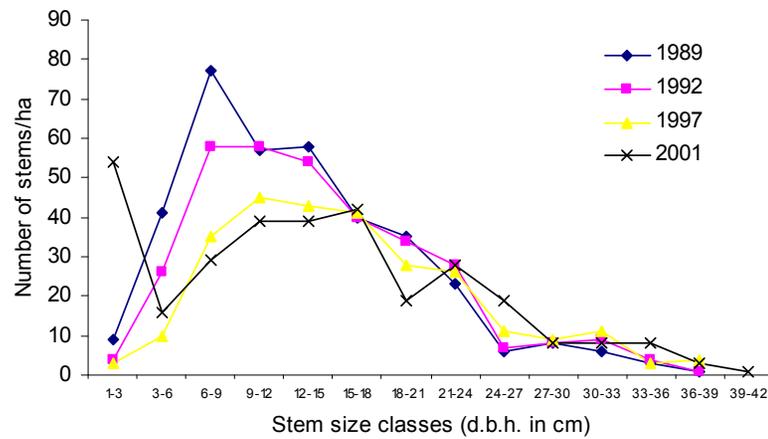
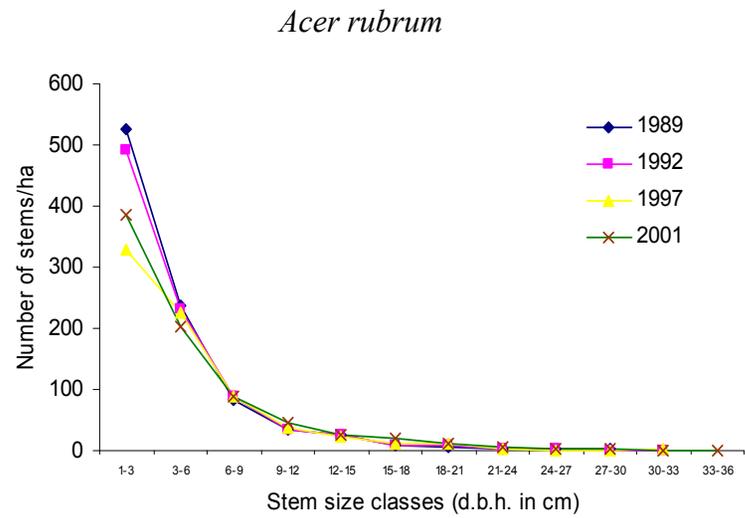
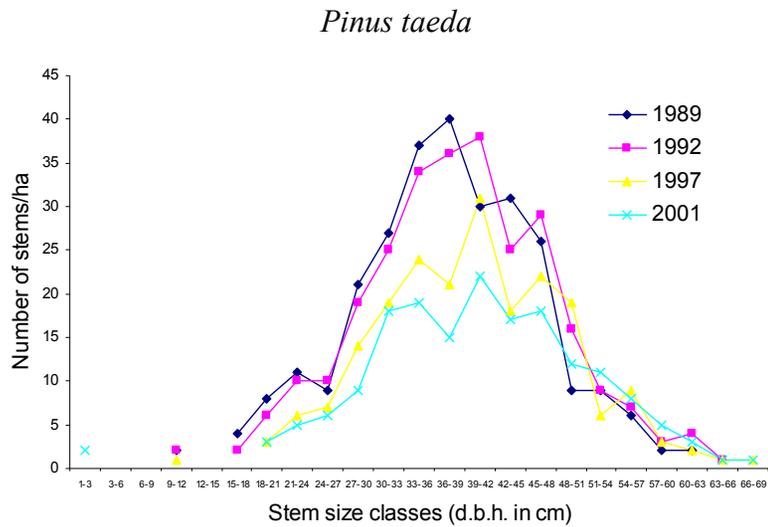
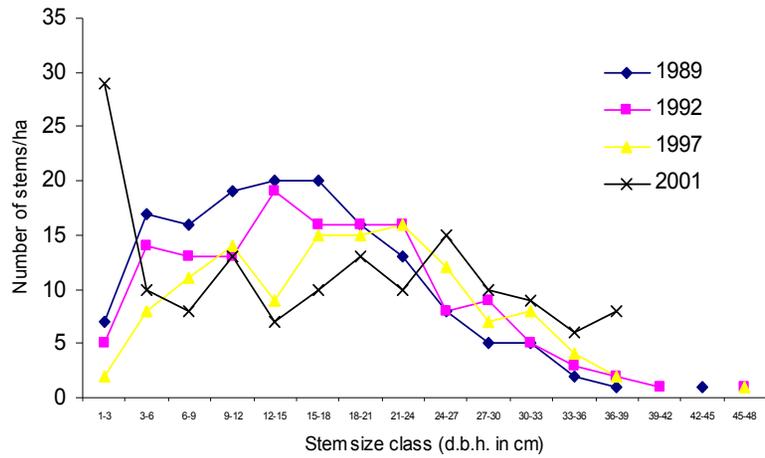
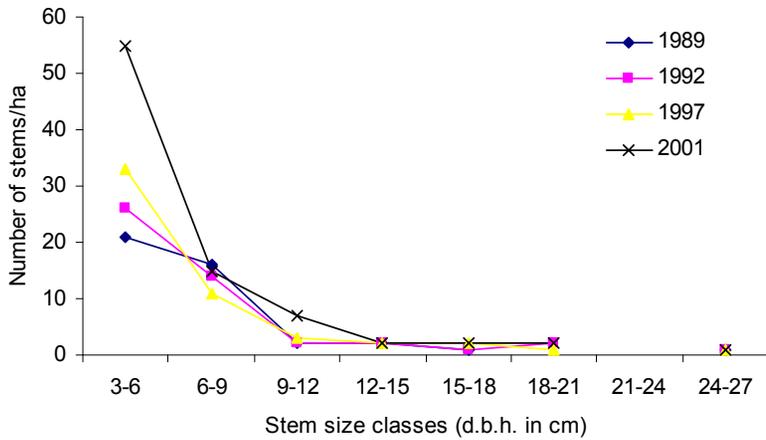
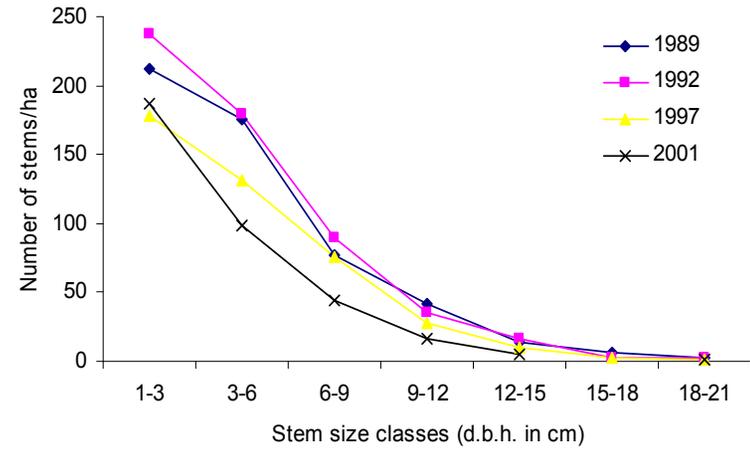


Figure 2.8a. Changes in tree size distribution for major species in the Graveyard plot in the Duke Forest, North Carolina, USA.

Liriodendron tulipifera



Cornus florida



Ostrya virginiana

Quercus velutina

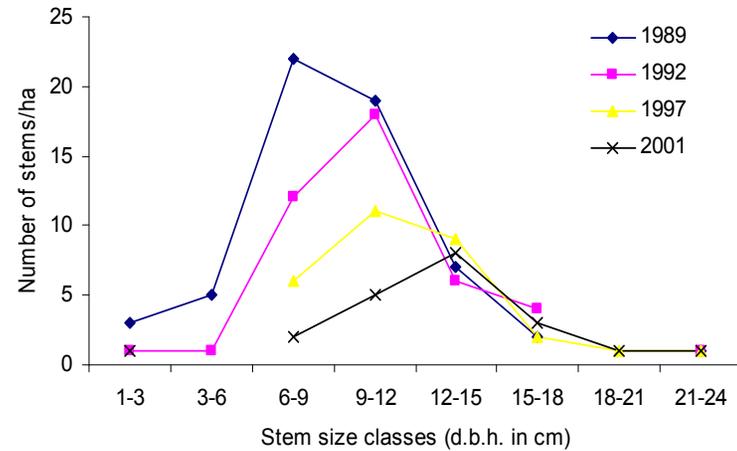


Figure 2.8a (Continued). Changes in tree size distribution for major species in the Graveyard plot in the Duke Forest, North Carolina, USA.

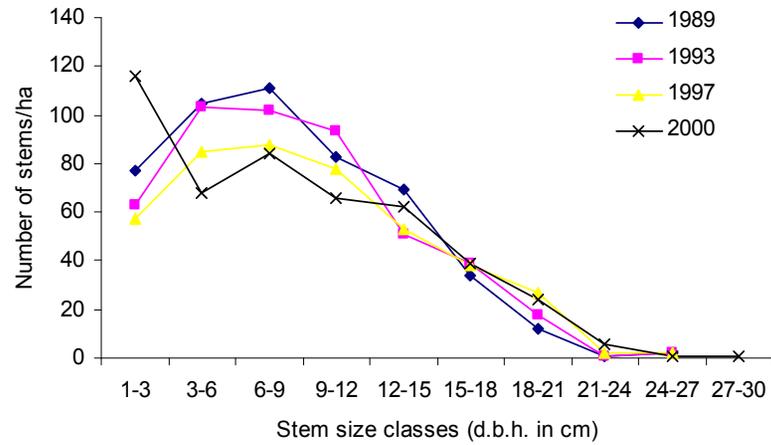
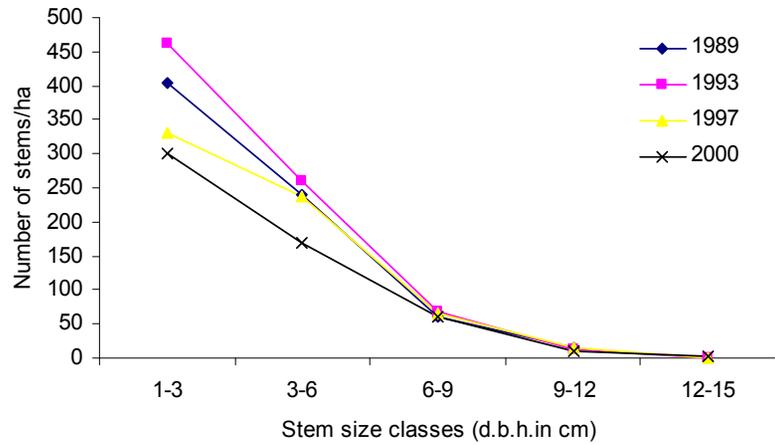
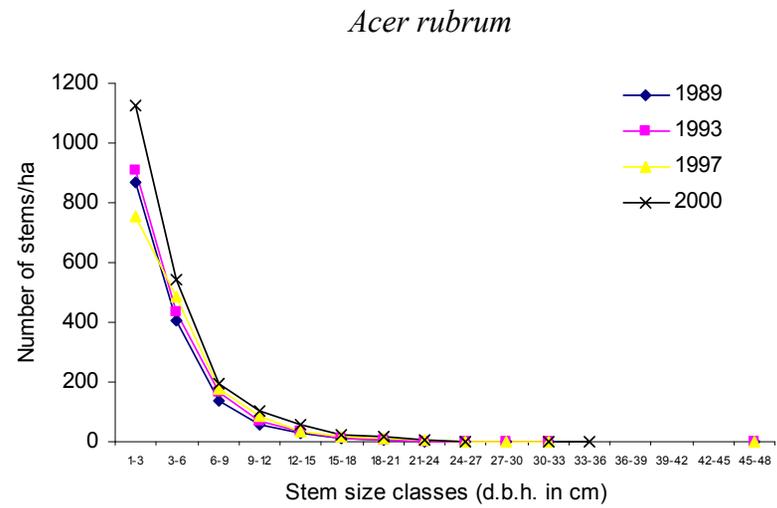
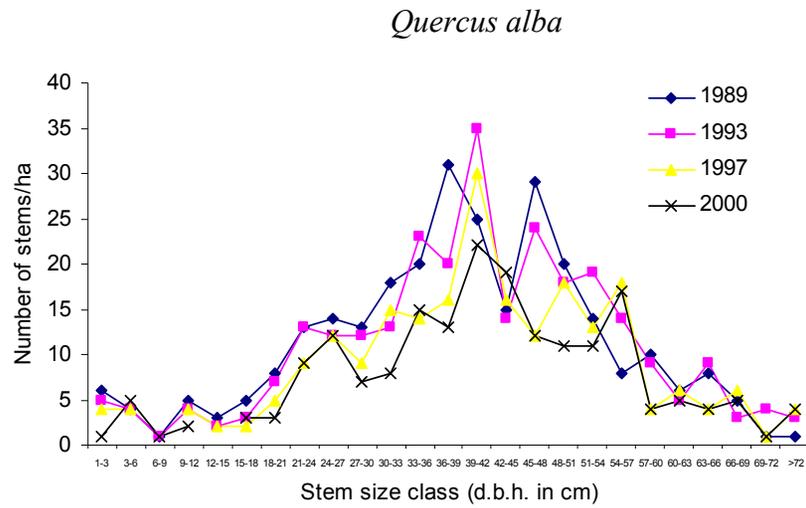


Figure 2.8b. Changes in tree size distribution for 8 manor species in the Bormann plots in the Duke Forest, North Carolina, USA.

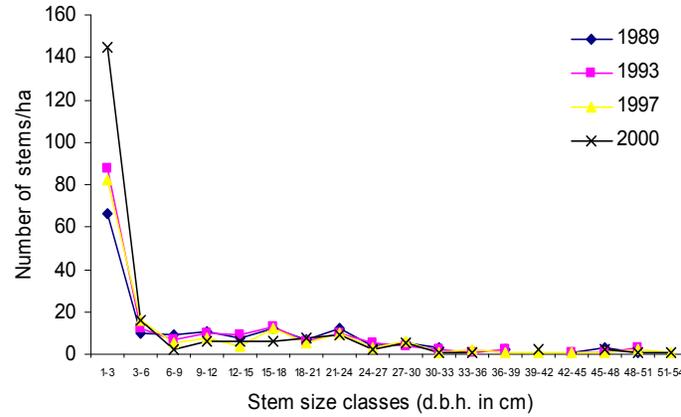
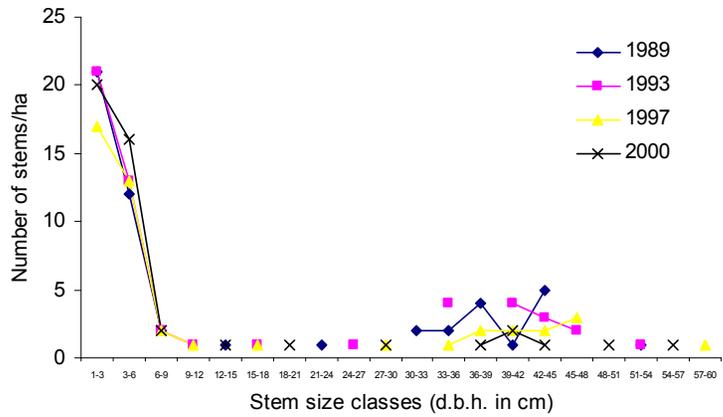
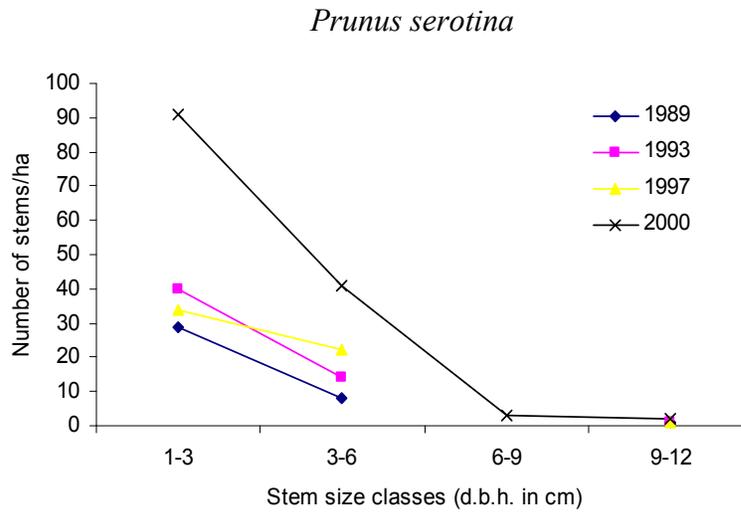
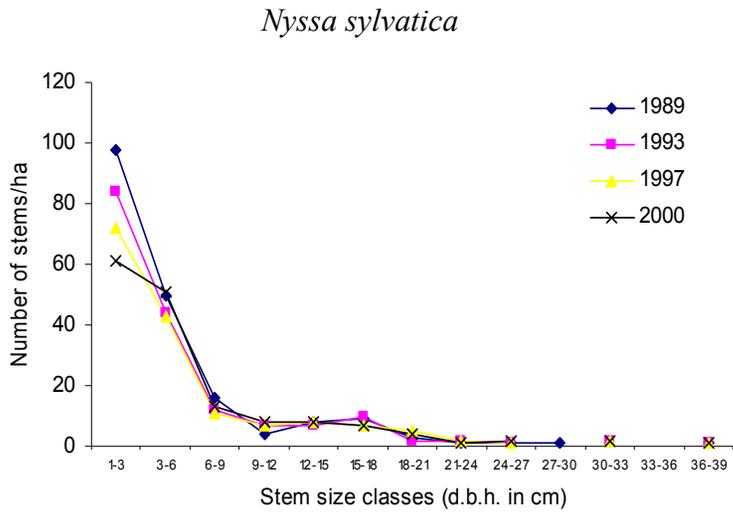


Figure 2.8b (Continued). Changes in tree size distribution for 8 manor species in the Bormann plots in the Duke Forest, North Carolina, USA.



Figure 2.9. Nonmetric Multidimensional Scaling (NMS) ordination of 32 permanent sampling plots in the Duke Forest measured in 1984 through 2000. Squares are plot locations on first axis one and axis two of NMS ordination over time. Crosses show NMS ordination of primary species on same axes. Note labeled PSP10, PSP35, PSP36, PSP37, PSP43, PSP44 are six hardwood PSPs.

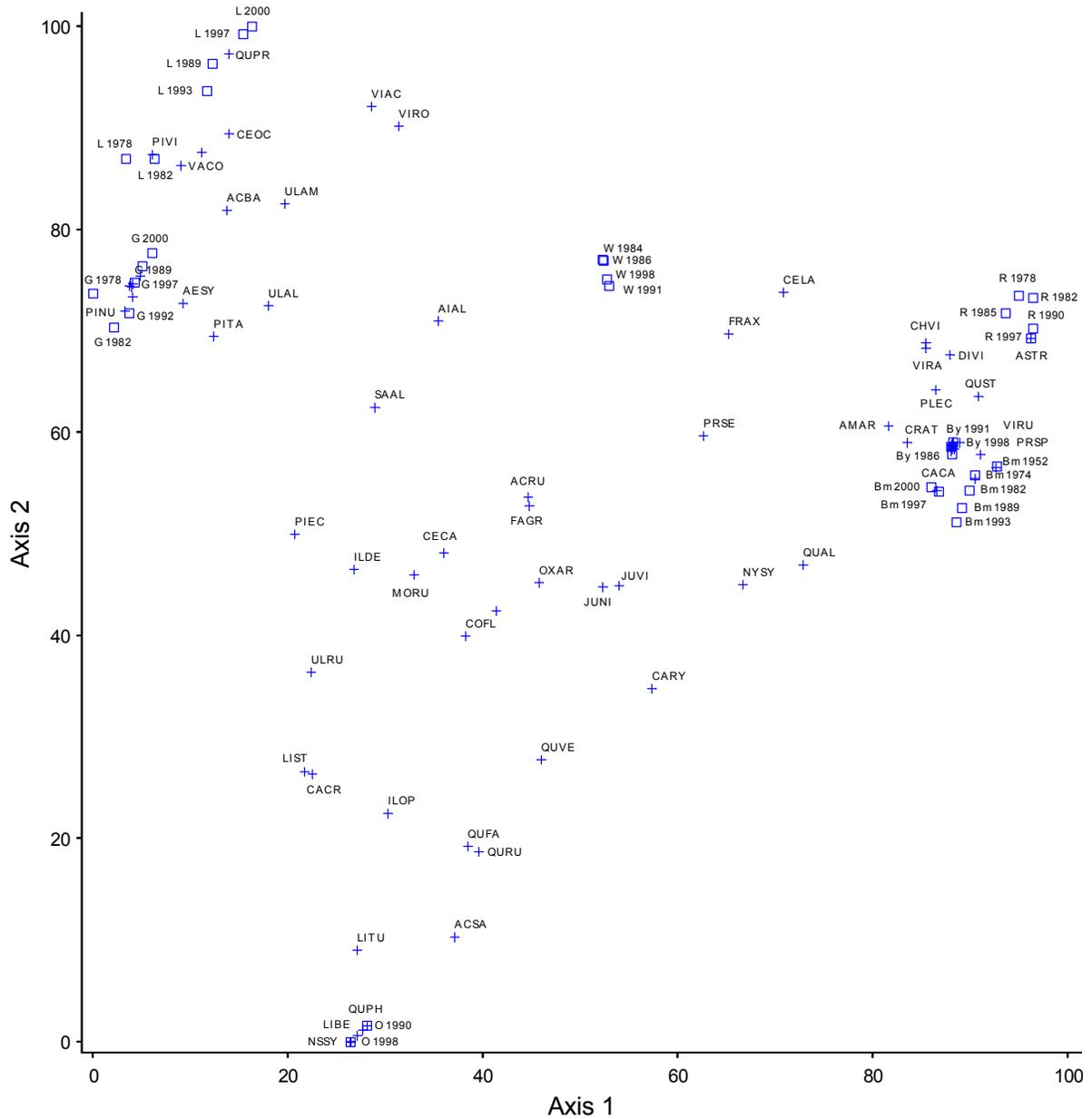


Figure 2.10. Nonmetric Multidimensional Scaling (NMS) ordination of seven mapped plots measured in mostly from 1978 through 2000. Squares are plot locations on first axis one and axis two of NMS ordination over time. Crosses show NMS ordination of primary species on same axes.

Note: Species abbreviation and growth form of the Duke Forest trees in **Figures 2.9** and **2.10**:

Code	Scientific name	Common name	Growth form
ACBA	<i>Acer barbatum</i>	Southern Sugar Maple	Tree
ACRU	<i>Acer rubrum</i>	Red Maple	Tree
AESY	<i>Aesculus sylvatica</i>	Painted Buckeye	Shrub
ALJU	<i>Albizia julibrissin</i>	Silktree	Tree
AMAR	<i>Amelanchier arboretum</i>	Common Serviceberry	Tree
ASTR	<i>Asimina triloba</i>	Pawpaw	Shrub
CACA	<i>Carya caroliniae-septentrionalis</i>	Southern Shagbark Hickory	Tree
CAOL	<i>Carya ovalis</i>	Red Hickory	Tree
CARY	<i>Carya sp.</i>	Hickory	Tree
CELA	<i>Celtis laevigata</i>	Sugarberry	Tree
CEOC	<i>Celtis occidentalis</i>	Common Hackberry	Tree
CECA	<i>Cercis canadensis</i>	Eastern Redbud	Tree
CHVI	<i>Chionanthus virginianus</i>	White Fringetree	Shrub
COFL	<i>Cornus florida</i>	Flowering Dogwood	Tree
CRAT	<i>Crataegus sp.</i>	Hawthorn	Tree
DIVI	<i>Diospyrus virginianus</i>	Common Persimmon	Tree
FAGR	<i>Fagus grandifolia</i>	American Beech	Tree
FRAX	<i>Fraxinus sp.</i>	Ash	Tree
ILDE	<i>Ilex decidua</i>	Possumhaw	Tree
ILOP	<i>Ilex opaca</i>	American Holly	Tree
JUNI	<i>Juglans nigra</i>	Black Walnut	Tree
JUVI	<i>Juniperus virginiana</i>	Eastern Redcedar	Tree
LIJA	<i>Ligustrum japonicum</i>	Japanese Privet	Shrub
LIBE	<i>Lindera benzoin</i>	Northern Spicebush	Shrub
LIST	<i>Liquidambar styraciflua</i>	Sweetgum	Tree
LITU	<i>Liriodendron tulipifera</i>	Tuliptree	Tree
MORU	<i>Morus rubra</i>	Red Mulberry	Tree
NYSY	<i>Nyssa sylvatica</i>	Blackgum	Tree
OSVI	<i>Ostrya virginiana</i>	Hophornbeam	Tree
OXAR	<i>Oxydendrum arboreum</i>	Sourwood	Tree
PATO	<i>Paulownia tomentosa</i>	Paulownia	Tree
PIEC	<i>Pinus echinata</i>	Shortleaf Pine	Tree
PITA	<i>Pinus taeda</i>	Loblolly Pine	Tree
PIVI	<i>Pinus virginiana</i>	Virginia Pine	Tree
PRSE	<i>Prunus serotina</i>	Black Cherry	Tree
QUAL	<i>Quercus alba</i>	White Oak	Tree
QUCO	<i>Quercus coccinea</i>	Scarlet Oak	Tree
QUFA	<i>Quercus falcata</i>	Southern Red Oak	Tree
QULY	<i>Quercus lyrata</i>	Overcup Oak	Tree
QUMA	<i>Quercus marilandica</i>	Blackjack Oak	Tree

Note: Species abbreviation and growth form of the Duke Forest trees in **Figures 2.9** and **2.10**:
(Continued):

Code	Scientific name	Common name	Growth form
QUPR	<i>Quercus prinus</i>	Chestnut Oak	Tree
QURU	<i>Quercus rubra</i>	Northern Red Oak	Tree
QUER	<i>Quercus sp.</i>	Oak	Tree
QURG	<i>Quercus sp.</i>	Red Oak Group	Tree
QUST	<i>Quercus stellata</i>	Post Oak	Tree
QUVE	<i>Quercus velutina</i>	Black Oak	Tree
RHCO	<i>Rhus copulina</i>	Flameleaf Sumac	Shrub
SAAL	<i>Sassafras albidum</i>	Sassafras	Tree
SOAR	<i>Sorbus arbutifolia</i>	Atlantic Goldenrod	Shrub
STGR	<i>Styrax grandifolia</i>	Bigleaf Snowbell	Shrub
ULAM	<i>Ulmus Americana</i>	American Elm	Tree
ULRU	<i>Ulmus rubra</i>	Slippery Elm	Tree
VACO	<i>Vaccinium corymbosum</i>	Highbush Blueberry	Shrub
VIPR	<i>Viburnum prunifolium</i>	Blackhaw	Shrub
VIRA	<i>Viburnum rafinesquianum</i>	Downy Arrowwood	Shrub
VIRU	<i>Viburnum rufidulum</i>	Rusty Blackhaw	Shrub

CHAPTER 3

A COMPARISON OF MORTALITY RISK FACTORS ASSOCIATED WITH LARGE, INFREQUENT WIND DISTURBANCES OF CAROLINA PIEDMONT FORESTS

Abstract. Past studies of large, infrequent wind disturbances have shown that meteorological, topographical, and biological factors interact to generate complex damage patterns, but have left open the extent to which these limited previous findings are representative and can be used to predict damage. I present a multiple-scale comparative analysis and evaluate the consistency in mortality risk factors associated with three major wind events: the Umstead tornado (1988), Hurricane Hugo (1989), and Hurricane Fran (1996). My results reveal distinct differences in the damage caused by hurricanes relative to the tornado, and to some extent consistency between the hurricanes. As compared to hurricanes, the tornado caused significantly greater and less species-specific mortality. Within-stand hurricane damage was patchy, indicating tree mortality risk must be conditioned on occurrence of unpredictable individual gusts. However, tree size, tree species, and growth rates were found to account for most of the within-stand variation in damage. Tree size has been found consistently to be a significant predictor of individual mortality and forest stand damage, although the effect in part was influenced by species. Differences in associated rainfall have strong influences on damage patterns with high rain increasing the risk of blowdown relative to breakage. Landscape-scale analyses show relatively predictable patterns controlled by a combination of topographic position, pre-disturbance species composition,

and tree size, in contrast to local patterns, which can be understood only in the context of site conditions and small-scale wind patterns.

Key words: mortality risk factors, large, infrequent wind disturbances, multiple-scale analysis, the Piedmont forests.

INTRODUCTION

Large hurricanes and other more localized catastrophic high wind events such as tornados and severe windstorms are major natural disturbance agents in the forest regions of the eastern United States and other many areas of the world. They often cause significant and highly variable tree damage across the affected landscape (Foster and Boose 1995, Webb 1999, Whigham et al. 1999). Recognition of the complexity of tree damage and mortality resulting from high wind disturbance events has led to considerable research on the factors generating the observed patterns (e.g. Boose et al. 1994, 1995, Bellingham and Tanner 2000, Platt et al. 2000, Schwarz et al. 2003, Peterson 2000, Boose et al. 2004). It has been well documented that various meteorological, topographical and biological factors simultaneously interact to influence the severity of the damage and associated patterns (see reviews by Evenham and Brokaw 1996, Webb 1999, and Peterson 2000). Past studies on tree mortality risk factors have shown that prediction of tree damage and mortality can be very complex due to the interactions of major abiotic and biotic factors, and have left open the extent to which these limited previous findings are representative and can be used to predict forest damage.

A major objective of wind disturbance studies is to explore factors controlling tree mortality in order to predict the damage risks for future events. Yet these damage patterns and tree mortality risks appear difficult to predict for several reasons. First, wind intensity

varies greatly among different types of windstorms, as well as spatially and temporally during a single windstorm. The complex air flows and tremendous variation in wind gusts during windstorms often make it difficult to accurately determine wind intensity. Second, the predictive power of a given factor may change with increase in wind speed during a wind event (DeCoster 1996) or among different wind events (e.g., hurricanes vs. tornados). Although several researchers have specifically examined major damage factors in various forest ecosystems, the spatial and temporal variation in the relative importance of these tree mortality risk factors across spatial scales has not been well studied. Third, catastrophic wind events are never strictly replicated and therefore ecologists rarely possess the combination of long-term baseline data and long-term post-disturbance records needed to discriminate among risk factors. Moreover, while of the varied impacts single high wind events have been documented, across-scale and across-event comparisons remain rare.

Previous studies of catastrophic wind damage suggest that the relative importance of different factors for predicting mortality risk and forest damage may vary across different spatial scales (Foster and Boose 1992, 1994, Boose et al. 2000). For example, in a detailed study of the 1989 Hurricane Hugo on the South Carolina forests, DeCoster (1996) showed that the predictors of wind damage vary in their relative importance along wind disturbance gradients. Wind intensity and relative site exposure appear to play a more important role in forming regional-scale damage patterns, whereas various biotic factors such as tree size, species identity, and stand density are more meaningful indicators of local-scale mortality risk (Boose and Foster 1992). Tree damage at the stand and landscape scale appears more clumped and therefore is more difficult to predict than across the region. Nonetheless, stand

composition, tree height, stand density, and site exposure, have strong influence on the severity of stand damage (Foster et al. 1992, Peterson 2005).

Tree damage pattern can be better predicted when the consistency of the mortality risk factors are known. To predict damage and mortality risks we must have a sound understanding of (1) the interaction of factors in controlling patterns of damage severity, (2) the relative roles of the different factors at different spatial scales, and (3) the consistency of those mortality risk factors among different wind disturbance events. Although the importance of a comprehensive study in determining tree damage and dynamics of recovery has long been recognized, to date few studies have effectively examined the interactions of various factors across spatial scales, and even fewer studies have compared the consistency of risk factors among different types of windstorms (but see Glitzenstein and Harcombe 1988, Foster and Boose 1992, 1994).

In September 1996 Hurricane Fran, a large, category-3 hurricane passed over the Duke Forest and adjacent Piedmont forest regions in central North Carolina and damaged a series of long-term forest study sites. The occurrence of this hurricane provided an exceptional opportunity to examine the relationship among tree mortality, forest damage, and the various influencing factors. I here present a multi-scale, comparative analysis to evaluate the consistency in mortality risk factors associated with Hurricane Fran and other two major wind events that occurred in Carolina Piedmont forests in the late 1980s: a tornado that occurred in September 1988 and damaged a large portion of Umstead State Park in central North Carolina, and the 1989 Hurricane Hugo, which caused substantial tree damage in the central and eastern South Carolina regions.

In this chapter I focus on the consistency in mortality risk factors among storms and the interaction of relevant biotic and abiotic factors that may predict the damage. At the stand scale I focused on the relationship between tree damage and tree size. The large range of tree sizes (1 cm and up) monitored in the Duke Forest for over 20 years allows detailed examination of the tree size-damage relationship. The Duke Forest long-term data allowed me to provide the first assessment of the relationship between hurricane-induced mortality and tree growth rates and competitive history of individual trees within a stand in an evaluation of tree mortality factors. At the landscape scale, I examined the roles of stand age, height, basal area, density, site exposure, relative topographic position, elevation, slope, and aspect in predicting the damage severity. At a regional scale, I examine the influence of wind speeds, precipitation, pre-disturbance species composition, and proximity to the hurricane path. I then compared the risk factors that influenced tree mortality and forest damage resulting from Hurricane Fran with the factors that have been found previously to be important for predicting wind-induced tree mortality during 1989 Hurricane Hugo and the 1988 Tornado.

The goal of the present study was to better understand the relative role of various meteorological, topographical and biological factors in determining damage and mortality risks at their relevant scales. My focus here is to answer following questions. (1) What are the relative contributions of wind speeds, precipitation, topography, pre-hurricane community attributes, and species characteristics (species, size and growth rate) in determining tree damage risk and the damage patterns at the relevant scales? (2) How does the interaction of site conditions, stand attributes, and tree characteristics relate to the damage patterns and how do their contributions vary with scale of observation? And, (3) are the

mortality risk factors consistent among windstorms and to what extent can damage be predicted? I conclude by arguing that pre-disturbance forest community characteristics and specific site conditions must be taken into account to effectively predict future forest damage and tree mortality risk at all spatial scales.

METHODS

I used four datasets in this multi- windstorm, multi-scale comparative study of tree mortality risk factors. The first dataset is a set of long-term permanent tree census plots in and around the Duke Forest of the North Carolina Piedmont. Many of these plots were significantly damaged by the intensive winds of Hurricane Fran in September 1996. The second dataset included a total 2351 forest inventory plots across South Carolina maintained by USDA with data from before and after Hurricane Hugo of September 1989 (McClure et al. 1979, DeCoster 1996). The third dataset is from a field survey conducted by DeCoster in 1988 and 1992 after a severe (F4) tornado damaged forests of Umstead State Park in central North Carolina. The fourth data set contains results of a statewide forest damage survey for the 1996 Hurricane Fran organized by Coleman Doggett of the North Carolina Department of Environment and Natural Resources. Details of the four dataset are described in the following sections.

Duke Forest and the 1996 Hurricane Fran

The Duke Forest is located near the southeastern edge of the Piedmont plateau in Orange and Durham Counties, North Carolina, USA (35°53'-36°12'N, 78°54-79°3'E, Figure 3.1). Much of the Duke Forest exhibits rolling terrain with the elevation ranging from 85 to 250 m. Major soils belong to common soil series of the Piedmont: Georgeville-Herndon, Tatum-Goldston, Georgeville-Tatum-Herndon, Whitestone Creedmor, and Appling-Cecil. The

annual average temperature is around 15°C. The average temperature in January, the coldest month is about 4°C, while the average temperature in July, the hottest month, is about 26°C. Precipitation averages about 1,118 mm annually and is well distributed throughout the year. July and August are normally the wettest months with an average of 130 mm of rainfall; October and November are normally the driest with an average of 69 mm rainfall.

Rolling topography, moderate climate, and disturbance history together determine that the Duke Forest contains a diversity of plant species and forest types. Over 100 species of trees have been identified in the Duke Forest (Palmer 1990). The major forest types are the even-aged upland loblolly pine (*Pinus taeda*) forest, the upland mixed-aged hardwood forest, and the mixed-aged lowland alluvial hardwood forest (Peet and Christensen 1988). The Duke Forest experienced large-scale land use and anthropogenic disturbance in the 1700s to 1800s. Most of the current pine stands result from reversion of farmland abandoned in early 1900s. A number of hardwood species, such as *Acer rubrum*, *Cornus florida*, *Fraxinus spp*, *Liquidambar styraciflua*, *Carya tomentosa*, *Liriodendron tulipifera* and *Ostrya virginiana* often invaded simultaneously with or slightly after the pines. Some fast-growing hardwood species such as *Liriodendron tulipifera* and *Liquidambar styraciflua* may co-dominate with the pines (Peet et al. 1987).

The majority of upland mixed-aged hardwood forest was significantly influenced by past disturbance. Before Europeans and colonists began to settle the area around 1740, oak-hickory forest with other hardwoods provided the dominant vegetation type. Pine forest (though primarily *Pinus echinata* and *virginiana* rather than *taeda*) had a modest presence on sites with poor soils or in the areas disturbed by such forces as windthrow, wild fires (Oosting 1942). Oak-hickory forest was the most widespread of the upland hardwood types,

but post oak-white oak communities and blackjack-post oak communities were present on edaphically unusual sites. The dominant species of upland hardwoods include *C. glabra*, *C. tomentosa*, *C. ovata*, *Quercus stellata*, *Q. alba*, *Q. rubra*, *Q. velutina*, *Q. falcate*, and *Q. marilandica*. Lowland hardwood forest dominants include *Betula nigra*, *Platanus occidentalis*, *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Fraxinus spp.*, *Acer rubrum*, *Fagus grandifolia*, *Q. alba*, and *Q. rubra*. Particularly wet sites also include such dominants as *Q. michauxii*, *Q. shumardii*, and *Q. phellos*.

The North Carolina Piedmont has experienced occasional intensive, large hurricanes. Historically, hurricanes have been the major natural disturbance factor causing serious forest damage. Since 1900, nine hurricanes have passed through central North Carolina (Barnes 2001). Hurricane Hazel in 1954 caused substantial tree mortality in Piedmont forests and in parts of the Duke Forest. Hurricane Fran in 1996 was the most destructive hurricane of the past century to visit the North Carolina Piedmont region as measured by the amount of forest canopy damage and tree mortality. The total forest damage for North Carolina was estimated as \$ 1,295, 620, 000 (Doggett 1996, Division of Forest Resources, North Carolina Department of Environment and Natural Resources).

Hurricane Fran was a category-3 hurricane when it made landfall near Cape Fear on the southeastern coast of North Carolina. The maximum sustained wind speed was estimated at 51.4 m/s. After making landfall, Hurricane Fran moved from the southeast to the northwest across North Carolina's coastal plain (Figure 3.1). On September 6 1996, Hurricane Fran struck Durham and Orange counties of central North Carolina Piedmont. Hurricane Fran's eye passed about 24 km east of the Duke Forest. Although the wind intensity had begun to decrease to tropical storm levels, Hurricane Fran still caused significant forest damage in

Duke Forest. In a counter-clockwise direction pattern, the maximum sustained surface wind at Raleigh-Durham International Airport, which is the nearest official weather station to the Duke Forest was about 26.8 m/s and maximum wind gusts were 31.6 m/s. The maximum known wind gust in Durham (observation site within Duke University) was 25.93m/s, while the maximum wind gust in Chapel Hill (observation site at the Phillips Middle School) was 11.2 m/s (Figure 3.2, data from Joel Cline in the National Weather Service).

Hurricane Fran brought heavy rainfall along its path. The total rainfall at Raleigh-Durham international airport was 224 mm during the storm period. The Duke Forest had received nearly 76 mm of rainfall two days prior to Hurricane Fran and another 51 mm immediately afterward. Overall, this forest region experienced about 423 mm rainfall total for September 1996, the highest ever in a single month since 1908 (Figure 3.3, data from the State Climate Office of North Carolina and the National Hurricane Center).

Plot description

The Duke Forest contains a series of long-term permanent plots distributed across a range of forest types. A set of 51 permanent sample plots (PSPs) was established within the Duke Forest in the early 1930s in an attempt to monitor growth in stands of varying age, site conditions, and management regime. The sizes of PSPs ranged from 404 to 1012 m². Information was recorded on all woody stems greater than 2.5 cm (1 cm after 1978) diameter at bread height (d.b.h.), including d.b.h, tree height and tree conditions. Stem coordinates were recorded starting in the late 1970s. Remeasurement of the PSPs has been carried out at about 5-year intervals. 20 of PSPs were lost between the 1940s and 1980s. In total, 34 PSPs including 28 PSPs in loblolly pine forest and six PSPs in hardwood forest remain. In

addition, three hardwood plots (4047 m² in size) were located in the Hill Experimental Forest, a research forest area of North Carolina State University located in Durham County.

I also surveyed tree damage in eight large mapped forest permanent plots established in the study area in the late of 1970s (Table 3.1). Those eight plots varied in size from 5250 to 65530 m² and records from them contain the same information as for PSPs except that tree height was not usually recorded. These mapped permanent plots represent three major types of forests in different succession phases: pine forest, upland hardwoods and lowland alluvial hardwoods. The two mapped pine plots are about 80-100 years old, even-aged, old-field pine stands, currently in the transition phase of forest development. The five hardwood plots (Bormann, Rocky, Bryan Center, Wooden Bridge and Oosting plot) represent a broad mix of uneven-aged mixed hardwood forest types. One lowland intensively mapped plot (i.e. Big Oak Woods plot) is located on a moist, semi-alluvial site at North Carolina Botanical Garden Mason Farm Preserve (Table 3.1).

Tree plot damage assessment

From May to October, 1997, the first growing season following the Hurricane Fran, all of the 37 PSPs were resampled, as were four intensively mapped permanent tree plots (Graveyard, Land's end, Rocky, and Bormann) in the Duke Forest, and one mapped plot in the North Carolina Botanical Garden (Big Oak Woods). Other three mapped tree plots (Oosting, Wooden Bridge, Bryan Center) were resurveyed in the summer of 1998. Beside the conventional survey items (d.b.h., tree height, tree conditions), damage was assessed for each individual by using a set of hurricane damage classes. The hurricane damage classes were Uprooted (1 = OK, 2 = partial uproot, 3 = complete uproot), Breakage (1 = OK (< 10% canopy loss), 2 = 10-35% canopy loss, 3 = 35-90% canopy loss, 4 = > 90% canopy loss),

Leaning (1 = OK, 2 = leaning free (lean over 10%), 3 = supported by another tree, 4 = down on ground), and Leaned on (1 = OK, 2 = upright, supporting a tree, 3 = bent or leaning (crown displaced at least 10%), 4 = pinned). In addition, the azimuth of each fallen bole was determined by compass. All of the tree data were compiled and merged with the data set from before Hurricane Fran. Site conditions including elevation, slope, and aspect was measured for each PSP and the eight mapped plots.

North Carolina forest damage and the wind and rainfall data for Hurricane Fran

To evaluate damage risk factors at regional scale (state level) I used a statewide survey of forest damage caused by Hurricane Fran obtained from the Division of Forest Resources of the North Carolina Department of Environment and Natural Resources. Hurricane Fran struck the North Carolina coast and came inland on September 5, 1996, and a survey was conducted on September 9-18, 1996 in order to determine the amount of forest damage caused by the storm (Doggett 1996). The impacted area of North Carolina was first grided into 10 km blocks. Each grid intersection was located on the ground and a plot was established to document forest type and amount of tree damage. The damage was determined by classifying the 20 trees nearest the plot center as windthrown, top completely gone, top broken and undamaged. This dataset also contained an estimation of stand age, average tree size, and the life-form of the 20 trees. A total of 299 plots were collected in the survey.

The wind speed and rainfall data for Hurricane Fran were obtained from the State Climate Office of North Carolina and the National Hurricane Center. All available wind data from weather stations and aircraft reconnaissance were used to create a map of maximum sustained wind velocities as Hurricane Fran moved across the state (Joel Cline 1996, and personal communication). Data on statewide precipitation associated with the hurricane were

obtained from the State Climate Office of North Carolina. I temporal-spatially interpolated these datasets by overlaying the maps on the top of one another, and manually connecting the maxima wind as wind-speed isobars. This provides a map of maximum sustained wind speeds (Figures 3.2 and 3.3). The wind speed data and precipitation records were digitized and merged with the locations of the 299 tree plots to provide wind speed and precipitation estimates for each plot to be related to tree damage.

South Carolina forest damage and the 1989 Hurricane Hugo

I used Forest Inventory and Analysis (FIA) data, collected and maintained by the Southeastern Experiment Station of the US Forest Service. This dataset consists of a large number of permanent plots, mostly established in 1958, and represents a random sample of forests across South Carolina. Hurricane Hugo made landfall near Charleston, South Carolina on September 22, 1989, impacting forests in 17 counties on the Coastal Plain and Piedmont of South Carolina. After Hurricane Hugo, the Forest Service conducted an additional sampling of all plots in the 17 counties most heavily affected by the storm in order to assess the impact of the storm on the forest resources. Numerous variables are typically collected for permanent FIA plots, including both tree and site variables (Sheffield and Thompson 1991). Each plot contains up to 5 sampling points, each of which is the center for a subplot. The sampling design uses the Bitterlich method to sample all trees greater than 12.7 cm d.b.h. (Tansey and Hutchins 1988). Trees between 7.62 and 12.7 cm were measured in circular plots with a fixed area of 0.00135 hectares (1/300 acres). For each tree in the “plot”, diameter, height, crown ratio, canopy position, presence of rot, and other variables were recorded. Site data were collected and including soil texture, hydrology, slope and aspect, and management and site history. In the sampling period following Hurricane Hugo, data

specifically related to tree damage were collected, including presence of root damage, bole missing, terminal shoot missing, percent of crowing missing, and direction of tree fail. Plots not forested at the time of the hurricane were eliminated from the dataset. In total, the dataset contains 29,397 trees from 2,352 plots.

The wind speed data for Hurricane Hugo were obtained from the National Hurricane Center. All of the measured wind data from weather stations and reconnaissance aircraft were used as input for a hurricane model, creating maps of maximum sustained wind velocities for three-hour intervals (Powell et al. 1991). DeCoster (1996) interpolated these datasets by overlaying the maps on the top of one another, and manually connecting the maximum wind in wind-speed isobars. This provides a map of maximum sustained wind speeds in one-minute averages. Data on precipitation associated with the hurricane were obtained from Allis et al. (1991). The wind speed and precipitation data were digitized and merged with the plot locations of FIA forest data to provide wind speed and precipitation estimates for each plot to be related to tree damage.

Umstead State Park and the 1988 Tornado

I used forest damage data from the 1988 William B. Umstead State Park tornado to compare damage risk factors with those found in my hurricane damage analysis. Umstead Park is located in Wake County, North Carolina, between the cities of Raleigh and Durham, about 24 km from the major study sites in the Duke Forest. Elevations range from 75-125 m in those rolling hills of the eastern Piedmont region. The climate is warm temperate, with rainfall varying between 1000 and 1250 mm per year. The upland soils are mostly sandy to Silty loams in the Cecil, Georgeville and Wilkes series, although some fine sandy loams in

the Enon series and gravely loams in Cecil series occur (Cawthron). Creek floodplains are generally Chewlacla soils.

On November 28, 1988, a series of thunderstorms traveled the central and eastern part of the North Carolina, spawning a number of tornados. The strongest of these first touched down in Umstead State Park and carved a discontinuous corridor for 130 km through Wake, Franklin, Nash and Halifax counties (Roth 1990, DeCoster 1996). The tornado was rated F4 on the Fujita scale (Roth 1990), indicating a high intensity storm with winds ranging between 92 and 116 m/s. Throughout the majority of its track, however, including its passage through the Umstead State Park, the tornado only rated F2 on the Fujita scales, indicating wind speeds of 50-70 m/s (Roth 1990).

In the summer following the tornado, five sites were selected by DeCoster for study and eleven transects were established perpendicular to the tornado track, with two or three transects located in each site (DeCoster 1996). Those transects were 10-meters wide, and their ends were determined by the last tree that had sustained severe damage (i.e. snapped, partial snapped or uprooted). With each transect, all trees with pre-tornado diameters at breast height (137 cm) of 4 cm or greater were sampled. For each tree, the position along these transect, species, diameter, type of damage sustained (snapped, partial snapped, uprooted, pinned and leaning), height of breakage, and azimuth of tree fall were recorded. Each portion of each transect was assigned to a slope, on a 6-point scale ranging from no slope (0) to slope greater than 45 degree (6), and a topographic position, on a 5-point scale ranging from ridge (1) to floodplain (5). Soil samples were taken at random locations, one sample for every 35 m of transects. During the summer of 1992, 3½ years following the tornado, these transects were resampled to examine tree growth and mortality. Trees were

considered dead if they had no green foliage on branches attached to the trunk and had no sprouts originating from the base of the tree.

Data analysis

For the Duke Forest plot-level data, I first quantified stand damage by percentage of damage of individuals in each plot. I also created an ‘integrated stem damage code’ to quantify individual damage based on stem uproot, canopy breakage, leaning and leaned on features. One stem was defined as damage code 3 (sustained catastrophic damage) if it was completely uprooted, lost more than 90% of the canopy, or was pinned to the ground. Index 2 was applied if the stem were partial uprooted, canopy loss was 35-90%, the tree was leaning but supported by other trees, or pinned. Index 1 indicating modest damage was applied if the hurricane codes indicated canopy loss 10-35%, leaning over 10% or bent and crown displace >10%. Code 0 was used for no damage. A stand damage index was then computed as the average damage index of all stems within plots. I created an ‘integrated stem damage code’ for each stem in the stand by combining all the information of uprooting, breakage, leaning and leaned-on to a single code ranging from 0-3. I then weighted the code by multiplying by the stem relative basal area (i.e., the basal area of the stem divided by the sum of all stem in the plot). The stand damage index was the average value of the weighted stem ‘integrated stem damage code’ of all stems in the stand. The range of stand damage index by definition was from 0-3.

Logistic regression, a multivariate technique which uses a logit function to predict the outcome a dichotomous event, was used to identify the significant damage risk factors which could explain the observed variation of damage. At the regional scale (i.e., state), the probability of plot-level tree damage was analyzed as a function of stand age, d.b.h., ratio of

pine trees versus hardwoods in the plot, wind speeds, rainfall, and the distance to the path of the hurricane. At the landscape scale, the plot-level damage severity was analyzed as a function of stand density, height, topographic position, aspect, and slope. Within-stand logistic regressions were used to identify the factors that most strongly influenced uprooting and breakage. At this scale I examine the possible risk factors as a function of tree size by different species and included tree growth to examine its ability to predict tree damage. All statistical analyses were performed using SAS 9.0 (SAS Institute Inc, 2003).

RESULTS

Consistency in risk factors that influence regional scale forest damage severity

Hurricane damage generally affects a large region. The plot data used for analysis indicated that at the regional scale a considerable but varied amount of forest damage occurred along the paths of the 1989 Hurricane Hugo and the 1996 Hurricane Fran, reflecting the interactions among wind speed, rainfall level, forest types, complex site conditions, and location relative to the hurricane path.

The primary damage types consisted of windthrow and canopy breakage. For the 1996 Hurricane Fran, 54.5% (n=163) of 299 plots examined contained windthrown trees or trees with the canopy completely broken out. Average percentage of tree destruction (i.e., windthrown or the canopy completely gone) across all plots was 24.6 % (Doggett 1996). When trees were separated into damage classes, 66.3 % of the plots (n=108) had an average destruction in the 1-25% class; 22.7% of the plots had 26-50% damaged; 9.2% of the plots experienced 51-75% destruction and 1.84% plots had 76-100% destruction.

The risk factor comparison indicates that the wind force associated a storm (measured as maximum wind speeds) consistently served as a strong positive indicator of damage severity.

Wind speeds were the dominant factor influencing regional-scale forest damage for both the 1989 Hurricane Hugo and the 1996 Hurricane Fran. In both cases, variation in the maximum wind speeds largely explained the variation in forest damage severity. Wind speeds explained 58.4% of the forest damage in the Hurricane Hugo damage study (DeCoster 1996). In the 1996 Hurricane Fran, stand damage severity was similarly positively related to wind speeds (Table 3.5).

In addition to wind speed, precipitation appeared to be a major factor responsible for the damage type of canopy trees with high rain increasing the risk of blow down relative to breakage. Evaluation of damage to Duke Forest by Hurricane Fran showed most damage to have been caused up uprooting rather than breakage. Hurricane Fran was accompanied by heavy rainfall, especially in the Duke Forest area. The total rainfall at Raleigh-Durham international airport was 224 mm. In addition, the Duke Forest received nearly 76 mm of rainfall two days prior to Hurricane Fran and another 51 mm immediately afterward; overall the region experienced about 423 mm total rainfall for September 1996, the highest in a single month since 1908. Because there was a large volume of rain in the days prior to the hurricane, the soil was saturated by the time the hurricane arrived. Tree root systems were easily separated from the soft soil, allowing the wind to knock the trees down. On the other hand, research by DeCoster (1996) on mortality and damage caused by Hurricane Hugo on the South Carolina Piedmont in 1989 showed breakage to be the major form of damage. Rainfall associated with the 1989 Hurricane Hugo was only half the amount associated with Hurricane Fran.

Distance to windstorm path was a good predictor of wind damage at the regional scale (Table 3.5), but was not consistently useful at the landscape scale in either the South Carolina

or North Carolina study. During Hugo, in topographically gentle region such as coastal plain, winds decreased away from the path in a predictable fashion with the consequence that distance to hurricane path served as a good indicator of forest damage severity. This is consistent with my observation at regional scale in North Carolina during Hurricane Fran (Table 3.5). However, my study showed that a more complex relationship between the distance to the path and forest damage at landscape scale, and therefore distance alone was insufficient to predict damage severity.

In addition to wind, rainfall, and the distance to hurricane path, I found that average tree size was a significant variable for predicting regional-scale forest damage. Moreover, forest types appeared to influence damage risks (Table 3.5).

Consistency of tree risk and mortality factors at the landscape scale

At the landscape scale, the damaged forest sustains relatively consistent overall wind and rainfall conditions with the consequence that site conditions and forest community factors become more important and predictive. The topographic position of the forest stand is particularly predictive of damage. I found that much of the hurricane damage in the Duke Forest concentrated at topographic extremes; particularly hard hit were lower slopes where the wettest soils were located, and ridge tops with the greatest exposure. In addition, stand height was found to be significantly correlated with stand-level damage severity (Table 3.6).

Tree sizes as a consistently strong indicator for all three scales

I found tree size to be a consistently strong predictor of damage severity between different windstorms across scales. The Hurricane Hugo study showed that tree height was a major factor that predicted tree damage at regional scale (DeCoster 1996). My results at the regional scale showed that average tree size of the stand was positively correlated to stand

damage severity. My study of forest damage caused by Hurricane Fran was largely consistent with the results from Hugo due to the positive relation between tree size and tree height. In the landscape-scale analysis of the Duke Forest data, tree height was found to be a significant predictor of stand damage severity (Table 3.5).

Within-stand variation is more difficult to predict due to the stochastic nature of wind gusts and neighborhood effects. However, tree size and species were the most predictive of the variables examined at the within-stand scale. In addition, at the stand scale I found a significant positive relationship between tree size and probability of severe damage. The probability of tree damage during Hurricane Hugo increased with tree height, indicating tree height was a significant factor of tree damage. DeCoster (1996) found that there was an interaction between height and wind such that the probability of damage increased exponentially with wind speed, and the exponent increased with increasing tree height. In summary, pre-hurricane tree size could be used as a common factor for wind damage prediction.

The role of tree species and life-form in determining tree damage and mortality

Tree characters play an important role in their damage risks at smaller scales (i.e., landscape and stand scale). In the three windstorm studies, individual tree damage was shown to vary among species (Figure 3.4 and Figure 3.5). Life-form (pines versus hardwoods) is similarly a factor influencing tree damage. For example, the tornado study found that *Pinus taeda* sustained the highest damage of all species, whereas the two hurricane studies found *Pinus taeda* sustained moderate damage, and that some of the hardwood species were more susceptible. At the landscape scale in the Duke Forest during Hurricane Fran, most of trees that fell were broadleaf deciduous hardwoods species. These

trees have broad spreading canopies and flat leaves that caught the force of the wind much more readily than the smaller canopies and aerodynamic needles of pine trees. Many hardwood trees also have shallow, spreading root systems that increase their susceptibility to tip ups, versus pines which have deep tap roots holding them upright. However, at the regional scale, species or life-form differences may be not significant. For example, analysis of Hurricane Fran on North Carolina forests showed that within 299 plots surveyed, 51.6% of the trees with tops completely out or blown down were pine and 48.4 were hardwood (Doggett 1996).

Although the probability of a tree being uprooted increased with tree size, species vary in their susceptibility to windstorm events. In the Graveyard plot during Hurricane Fran, the dominant loblolly pine experienced a high level of uprooting, whereas the younger, sub-canopy red maple sustained much less damage by uprooting. Sourwood particularly experienced a high level of uprooting, largely due to its leaning tree growth form (Figure 3.5). In the Bormann plot, both the dominant white oak and increasingly dominant red maple sustained high risks of uprooting, while other tree species such as sourwood and hickories sustained modest damage (Figure 3.6). This suggests the damage probability of a same tree species may vary depending on the specific pre-disturbance community attributes.

In addition, I found that pre-hurricane relative growth rates could be to be a significant factor for predicting the probability of tree mortality (Table 3.7). My results showed that pre-hurricane 10-year period relative growth rate was highly significant as an indicator of tree mortality immediate after the hurricane in both pine forest stand and hardwood stand. However, I found this relationship did not significantly predict tree damage such as uprooting and canopy breakage. This results suggest that hurricane-induced tree mortality is not only

correlated with individual and species characteristics, but also to some extent with past disturbance history and stand development.

DISCUSSION

The importance of scale in observation of wind damage pattern and mortality risk factors

My multiple-scale analysis (regional, landscape and stand scale) provides insight into the consistency of possible risk factors and their interactions to explain forest damage. This study has demonstrated that in order to better understand forest damage patterns and mortality risk factors, it is very important to examine possible variables at ecologically relevant scales. Variation in tree damage risk is not only related to multiple factors, but also depends on the scale of the observation. This comparative study examines the consistency in mortality risk factors that influence damage to individual trees and forest stands among two windstorm types (hurricane and tornados) and three events (1989 Hurricane Hugo, 1988 Tornado and 1996 Hurricane Fran), while simultaneously addressing the importance of scale in observation of wind damage pattern and mortality risk factors.

Generally, forest damage patterns result from interaction of disturbance regime, environmental heterogeneity, and vegetation structure (White 1979, Peterson 2000). The damage caused by both hurricanes and tornadoes and its predictability depend on 1) the intensity of the wind and rain, 2) local landscape features, 3) community attributes, and 4) interactions among these factors. The initial results of my analyses at landscape to regional scales suggested that winds, site factors, and tree characteristics may interact with physiographic factors to influence damage severity. This observation is consistent with the results of Foster and Boose who have shown that at the regional scale (~100 km) patterns of damage can be largely explained by patterns in wind force, while at landscape scale (~10 km)

the environmental heterogeneity such as topographic slope and aspect appears responsible for much of the variation of hurricane damage.

My landscape-scale analyses show relatively predictable patterns in small-scale tree mortality and damage controlled by a combination of topography, pre-hurricane species composition, and stand height, in contrast to within stand damage patterns, which can be understood only in the context of tree size and, partially, pre-disturbance growth rates. Although the complexity may lie mostly among stands and less within stands (Peterson 2005), within-stand variation of damage in windthrow in Piedmont forests was proven to be variable and complex.

Wind intensity with rainfall as major factors determining regional-scale tree damage

The two regional-scale comparative hurricane damage studies (i.e., Hurricane Hugo in South Carolina and Hurricane Fran on the North Carolina Piedmont) allowed an unusually thorough analysis in that it included estimates of maximum sustained wind speeds, community characteristics, and site factors that might serve as the damage predictors. Although spatial resolution of the available wind speed data are not sufficient to show individual gusts responsible for damaging individual trees, the maximum sustained wind variable incorporated into a regression model provides an approximation that accounts for the variation in damage pattern at the regional scale. This was not surprising in that wind speeds have long been identified as the primary determinant of large-scale tree mortality and forest damage associated with large wind events (e.g., Anderson 1954, Francis et al. 1993).

The consistency in tree mortality factors between hurricanes at landscape scales

The data on forest damage at various scales associated with Hurricane Hugo, Hurricane Fran, and 1988 Umstead tornado provide an opportunity to examine the consistency of

factors that influence damage. At the landscape scale (in this case, in the Duke Forest), the preliminary assessment on the Duke Forest showed hurricane damage of the forest was very patchy and that stand damage varied significantly over the landscape. I found that of the risk factors controlling forest damage, site conditions and community attributes could explain a large portion of landscape-scale pattern. Variation in damage severity at a given disturbance intensity inevitably occurs and is likely to be result of differential susceptibility of individuals or site factors. When wind intensity is relatively constant at landscape scales, the complexity of the hurricane damage pattern appears strongly mediated by the interaction of suites of ecological factors and community attributes. When wind intensity is constant, the site conditions and community attributes then play a more important role at landscape and stand scales. In most cases, taller stands with larger wind exposure would experience higher forest damage. In all three studies damage was shown to vary among species, and tree height was determined to be a primary determinant of damage, although the effects of height varied among species.

Other comparative studies have also pointed to consistency in factors that influence damage to individual trees. At the landscape scale when wind intensity is presumed more or less constant, site factors increase in relative importance as major predictors. However, previous studies have shown that use of only site factors is insufficient for prediction and must be combined with forest community characters (Capino 1998 and McMaster 2005). Most studies of hurricane damage have reported a positive correlation between severity of tree damage and the tree size as a consequence of increase of exposure area (e.g. Weidman 1920, Runkle 1990, Hook et al. 1991). In a study of Hurricane Fran on the forest damage in part of the Duke Forest (c.a. 226 hectare), Carpino (1998) found that the distribution of

hurricane damage is influenced by fine-scale environmental heterogeneity, and in particular that sites with high-exposure (ridge tops) or highly-saturated soils (low elevations) sustained high damage.

The interactions of site conditions and community attributes, especially relative exposure, mediate tree mortality risk. Greater uprooting was found on exposed sites with high soil moisture. Bormann et al. (1979), for example, found that both abiotic and biotic factors may act to make tree more susceptible to the action of wind force. Boose et al. (1992, 1995) found that wind force, site exposure and tree height can interact to generate extremely complex damage patterns in New England. More recently, Platt et al. (2000) found that the interaction of hurricanes and wild fires drive the complicated damage patterns found in Louisianan coastal forests.

Factors affecting within-stand variation

Within stand variation in forest damage is obviously high and more difficult to predict than large-scale damage because of high variation in wind gusts (Boose et al. 1994). It is easily seen that within-stand hurricane damage was patchy, indicating tree mortality risk must be conditioned on occurrence of unpredictable individual gusts. For instance, in a study of landscape-scale site variables influencing damage by Hurricane Fran in the Duke Forest, Carpino (1998) found that the most intense damage patches were about 0.2 ha in size.

Within-stand variation may be explained by tree size and species susceptibilities. Tree size is consistently found to be a factor that predicts damage severity and type, with large trees being associated with high damage risk. Tree size and species may account for most of the within-stand variation in damage (Peterson 2004). Tree attributes (hardwood versus pine tree) also influence forest damage patterns. Boucher et al. (1990) found a different hurricane

damage patterns in tropical rain forests and pine forests in southeastern coastal Nicaragua, despite similar wind speeds. They found that rain forest and pine forest suffered very different sorts of hurricane damage, and identified a tendency for dicots to survive damage better than conifers.

Species differences in susceptibility to hurricane damage have been documented in literature (Barry et al. 1993). Wind resistance depends on the interaction of five factors: strength of the wood; shape and size of the crown; extent and depth of the root system; previous moisture conditions; and stem biomechanical properties (Asner et al. 1997). Our research on mortality and damage caused by Hurricane Hugo on the South Carolina Piedmont in 1989 and a 1988 Tornado near the Duke Forest showed that tree species and tree height to strongly influence probability of death (DeCoster, 1996). The validity of this correlation has been confirmed both by comparing the distribution of damaged and undamaged trees (e.g. Peterson et al. 1991, Zimmerman et al. 1994) and by applying logistic regression (Webb 1989, Francis et al. 1993, Noel et al. 1995, DeCoster 1996).

Comparison of the effects of hurricane and tornado disturbances

The most distinct difference in the effects of the two hurricanes versus the tornado is the extent of the damage; the tornado had only local impacts, though the tornado was also different in that maximum wind speed was greater such that virtually all trees were damaged over a larger portion of the impacted area. The tornado and the hurricanes were consistent in the importance of tree species and tree size as risk factors. Another factor to be considered is the diameter: height ratio of the tree. The taller the tree, the greater is its chance of breaking, especially if the bole has little taper. For this reason, tall slim pines are extremely vulnerable.

The results from this multiple-windstorm comparison provide evidence of the consistency of and differences among factors that influence tree mortality in different types of windstorms (hurricane vs. tornado) as well as between different windstorm events of same type. The most obvious differences between a hurricane and a tornado are size and intensity. As compared to hurricanes, the tornado caused significantly greater and less species-specific mortality, but over a much smaller area.

Damage resulting from tornadoes may shift forest species composition towards late-successional species, as early successional species often are large and shallow rooted, making individuals more vulnerable. Because late-successional species may share these traits, effects of tornadoes or other catastrophic winds on species composition may be more contingent on forest species and size characteristics (Peterson 2000). Wind disturbances often remove dominant trees from the forest, changing species richness or evenness and potentially altering species diversity (Peterson 2000).

Implications on risk assessment and management practices

Comparative studies on damage risk factors provide information that allows a better understanding of damage patterns of forests and have implications on risk assessment and management practices. In areas at risk for windstorm damage, information on both post-storm actual damage and pre-storm potential damage is needed to determine the risk of future forest damage from storms and priorities for preventive measurements. Post-damage assessment often presents challenges as ground-based intensive plot surveys require large investments in human resources. Knowledge of the interactions among risk factors should aid in developing risk assessment plan for damaged forests of hurricane regions. The forest managers may use this information to both assess the vulnerability of the forest lands to

hurricane damage, and to design efficient campaigns for mapping forest damage after heavy storms.

Ability to predict severity in large, infrequent disturbance events is an important step towards explaining forest composition and dynamics (Turner et al. 1999, Peterson 2004). The information presented in this study may help better understand the impact of large, infrequent wind disturbances on the long-term dynamics of temperate forest ecosystems. In particular, the information is useful for forest ecologists for understanding long-term forest dynamic trajectories in the piedmont region and adjacent southeastern United States, because forest sites in these regions with different combinations of sites conditions can be expected to have different probability of disturbance intensity and frequency and sustained variable amount of damage in the events of catastrophic windstorms.

CONCLUSIONS

This multiple-event and -scale comparative analysis demonstrates the complexity of wind damage in temperate forests. Wind forces and the amount of rainfall associated with large windstorms appeared consistently as the primary determinant of damage severity. Rainfall associated a windstorm has a positive correlation with wind damage severity and type. Differences in associated rainfall have strong influences on damage patterns with high rain increasing the risk of blow down relative to breakage. Trees on sites that have experienced greater recent rainfall often experience higher mortality risk through uprooting.

Landscape-scale analyses show relatively predictable patterns controlled by a combination of topographic position, pre-disturbance composition, and stand height, in contrast to stand-level patterns which can be understood only in the context of site conditions, tree size, and species. Within stand damage is less predictable, but the damage

can be largely explained by tree size and species susceptibilities to winds. Tree size is consistently found to be a major predictor of damage severity as well as damage type, with large trees being associated with a high risk of uprooting or breakage. This study demonstrates the importance of spatial scale in observations of tree damage and mortality risk factors.

Within-stand hurricane damage was patchy; indicating tree mortality risk must be conditioned on occurrence of unpredictable individual gusts. Consequently, local patterns of wind damage can be understood only in the context of site conditions, stand attributes, and tree species. Stand-level variations were largely explained by tree size and species susceptibilities. Nonetheless, a high accuracy of prediction is difficult as the accuracy depends on large-scale, detailed tree data and individual wind gusts. Thus, while certain consistently significant positive or negative correlations were found in this comparative study of forest mortality factors, accurate prediction of tree damage under a range of variable wind conditions is still a challenging task.

LITERATURE CITED

- Allen, B. P., E. F. Pauley, and R. R. Sharitz. 1997. Hurricane impacts on liana populations in an old-growth southeastern bottomland forest. *Journal of the Torrey Botanical Society* **124**:34-42.
- Armesto, J. J. and S. T. A. Pickett. 1985. Experiments on disturbance in old-field plant-communities - impact on species richness and abundance. *Ecology* **66**:230-240.
- Asner, G. P. and G. Goldstein. 1997. Correlating stem biomechanical properties of Hawaiian canopy trees with hurricane wind damage. *Biotropica* **29**:145-150.
- Baker, W. L., P. H. Flaherty, J. D. Lindemann, T. T. Veblen, K. S. Eisenhart, and D. W. Kulakowski. 2002. Effect of vegetation on the impact of a severe blowdown in the southern Rocky Mountains, USA. *Forest Ecology and Management* **168**:63-75.
- Barry, P. J., C. Doggett, R. L. Anderson, and K. M. Swain. 1993. How to evaluate and manage storm-damaged forest areas. USDA Forest Service South Region Management Bulletin R8-MB 63. Atlanta, Georgia, USA.
- Basnet, K. 1993. Recovery of a tropical rain-forest after hurricane damage. *Vegetatio* **109**:1-4.
- Basnet, K., G. E. Likens, F. N. Scatena, and A. E. Lugo. 1992. Hurricane Hugo: damage to a tropical rain-forest in Puerto Rico. *Journal of Tropical Ecology* **8**:47-55.
- Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* **65**:1406-1419.
- Belda, F. and J. Melia. 2000. Relationships between climatic parameters and forest vegetation: application to burned area in Alicante (Spain). *Forest Ecology and Management* **135**:195-204.
- Bellingham, P. J. 1991. Landforms influence patterns of hurricane damage - evidence from Jamaican montane forests. *Biotropica* **23**:427-433.
- Bellingham, P. J. and E. V. J. Tanner. 2000. The influence of topography on tree growth, mortality, and recruitment in a tropical montane forest. *Biotropica* **32**:378-384.
- Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1995. Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* **76**:2562-2580.
- Blennow, K. and L. Lindkvist. 2000. Models of low temperature and high irradiance and their application to explaining the risk of seedling mortality. *Forest Ecology and Management* **135**:289-301.
- Bluhm, A. A. 1997. Response of a mixed-species pine and hardwood forest following a

- tornado disturbance. Master thesis. School of Forest Resources, University of Georgia, Athens, Georgia, USA.
- Boose, E. R., K. E. Chamberlin, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. *Ecological Monographs* **71**:27-48.
- Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* **64**:369-400.
- Boose, E. R., M. I. Serrano, and D. R. Foster. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs* **74**:335-352.
- Boucher, D. H., J. H. Vandermeer, K. Yih, and N. Zamora. 1990. Contrasting hurricane damage in tropical rain-forest and pine forest. *Ecology* **71**:2022-2024.
- Brewer, R. A. P. G. M. 1978. Windthrow and tree replacement in a climax beech-maple forest. **30**:149-152.
- Bruchert, F., G. Becker, and T. Speck. 2000. The mechanics of Norway spruce [*Picea abies* (L.) Karst]: mechanical properties of standing trees from different thinning regimes. *Forest Ecology and Management* **135**:45-62.
- Burslem, D., T. C. Whitmore, and G. C. Brown. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology* **88**:1063-1078.
- Cain, M. D. 1985. Long-term impact of hardwood control treatments in mature pine stands. USDA Forest Service Southern Forest Experiment Station Research Paper: 1-8.
- Canham, C. D., M. J. Papaik, and E. F. Latty. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research* **31**:1-10.
- Carpino, E. 1998. Ecological determinants of hurricane damage in a southeastern piedmont forest. Master thesis. Duke University, Durham, North Carolina, USA.
- Chiba, Y. 2000. Modelling stem breakage caused by typhoons in plantation *Cryptomeria japonica* forests. *Forest Ecology and Management* **135**:123-131.
- Conner, W. H. and A. D. Laderman. 1998. Impact of hurricanes on forests of the Atlantic and Gulf coasts, USA. Pages 271-277 in *Coastally Restricted Forests*. Oxford University Press, New York, USA.
- Coutts, M. P. and J. Grace. 1995. *Wind and trees*. Cambridge University Press, Cambridge, UK.
- Dale, V. H. and R. H. Gardner. 1987. Assessing regional impacts of growth declines using a forest succession model. *Journal of Environmental Management* **24**:83-93.

- DeCoster, J. K. 1996. Impacts of tornados and hurricanes on the community structure and dynamics of north and South Carolina forests. Ph.D. Dissertation. University of North Carolina at Chapel Hill.
- Doggett, C. 1996. North Carolina Forest Damage Appraisal - Hurricane Fran September 1996. Documented by the North Carolina Division of Forest Resources. North Carolina, Raleigh, USA.
- Dunham, R. A. and A. D. Cameron. 2000. Crown, stem and wood properties of wind-damaged and undamaged Sitka spruce. *Forest Ecology and Management* **135**:73-81.
- Dunn, C. P., G. R. Guntenspergen, and J. R. Dorney. 1983. Catastrophic wind disturbance in an old-growth hemlock hardwood forest, Wisconsin. *Canadian Journal of Botany* **61**:211-217.
- Elliott, K. J. and W. T. Swank. 1994. Impacts of drought on tree mortality and growth in a mixed hardwood forest. *Journal of Vegetation Science* **5**:229-236.
- Ellison, A. M. and E. J. Farnsworth. 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. *Biotropica* **28**:549-565.
- Ennos, A. R. 1997. Wind as an ecological factor. *Trends in Ecology & Evolution* **12**:108-111.
- Everham, E. M. and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. *Botanical Review* **62**:113-185.
- Everham, E. M., R. W. Myster, and E. Vandegenachte. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany* **83**:1063-1068.
- Fajvan, M. A., K. E. Knipling, and B. D. Tift. 2002. Damage to Appalachian hardwoods from diameter-limit harvesting and shelterwood establishment cutting. *Northern Journal of Applied Forestry* **19**:80-87.
- Forbes, G. S. and R. M. Wakimoto. 1983. A concentrated outbreak of tornadoes, downbursts and microbursts, and implications regarding vortex classification. *Monthly Weather Review* **111**:220-235.
- Foster, B. L. and D. Tilman. 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. *Plant Ecology* **146**:1-10.
- Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth pisgah forest, southwestern New Hampshire, USA. *Journal of Ecology* **76**:105-&.
- Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England,

- USA. *Journal of Ecology* **76**:135-151.
- Foster, D. R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. *Journal of Ecology* **80**:753-772.
- Foster, D. R., J. F. O'Keefe. 2000. *New England forests through time*. Harvard University Press, USA.
- Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. *Bioscience* **47**:437-445.
- Foster, D. R. and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology* **80**:79-98.
- Foster, D. R., M. Fluet, and E. R. Boose. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological applications* **9**:555-572.
- Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1**:497-510.
- Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* **1**:96-119.
- Foster, D. R., D. A. Orwig, and J. S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution* **11**:419-424.
- Foster, D. R., T. Zebryk, P. Schoonmaker, and a. Lezberg. 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (Hemlock) woodlot in central New England. *Journal of Ecology* **80**:773-786.
- Foster, D. R. and T. M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology* **74**:982-998.
- Foster, J. R. and W. A. Reiners. 1986. Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. *Vegetatio* **68**:109-114.
- Frangi, J. L. and A. E. Lugo. 1991. Hurricane damage to a flood-plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* **23**:324-335.
- Frelich, L. E. and P. B. Reich. 1999. Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems* **2**:151-166.
- Fuller, T. L., D. R. Foster, T. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* **1**:76-95.

- Gardiner, B. A. and C. P. Quine. 2000. Management of forests to reduce the risk of abiotic damage - a review with particular reference to the effects of strong winds. *Forest Ecology and Management* **135**:261-277.
- Garinger, L. P. and K. K.R. 1993. Seasonal tornado climatology for the southeastern United States. Pages 445-452 *in* C. Church, D. Burgess, C. Doswell, and R. Davies-Jones, editors. *The tornado: its structure, dynamics, prediction, and hazards*. Geophysical Monograph, American Geophysical Union, Washington, DC., USA.
- Glitzenstein, J. S. and P. A. Harcombe. 1988. Effects of the December 1983 tornado on forest vegetation of the Big Thicket, southeast Texas, USA. *Forest Ecology and Management* **25**:269-290.
- Gresham, C. A., T. M. Williams, and D. J. Lipscomb. 1991. Hurricane Hugo wind damage to southeastern united-states coastal forest tree species. *Biotropica* **23**:420-426.
- Guariguata, M. R. 1998. Response of forest tree saplings to experimental mechanical damage in lowland Panama. *Forest Ecology and Management* **102**:103-111.
- Harrington, R. A., J. H. Fownes, P. G. Scowcroft, and C. S. Vann. 1997. Impact of Hurricane Iniki on native Hawaiian *Acacia koa* forests: damage and two-year recovery. *Journal of Tropical Ecology* **13**:539-558.
- Harvey, B. D., A. Leduc, S. Gauthier, and Y. Bergeron. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. *Forest Ecology and Management* **155**:369-385.
- Hunter, M. D. and R. E. Forkner. 1999. Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. *Ecology* **80**:2676-2682.
- Imbert, D., P. Labbe, and A. Rousteau. 1996. Hurricane damage and forest structure in Guadeloupe, French West Indies. *Journal of Tropical Ecology* **12**:663-680.
- Jackson, R. G., G. M. Foody, and C. P. Quine. 2000. Characterising windthrown gaps from fine spatial resolution remotely sensed data. *Forest Ecology and Management* **135**:253-260.
- Jalkanen, A. and U. Mattila. 2000. Logistic regression models for wind and snow damage in northern Finland based on the National Forest Inventory data. *Forest Ecology and Management* **135**:315-330.
- Karlsson, K. 2000. Height growth patterns of Scots pine and Norway spruce in the coastal areas of western Finland. *Forest Ecology and Management* **135**:205-216.
- Kato, A. and H. Nakatani. 2000. An approach for estimating resistance of Japanese cedar to snow accretion damage. *Forest Ecology and Management* **135**:83-96.
- King, D. A. 1986. Tree form, height growth, and susceptibility to wind damage in *Acer*

- saccharum*. Ecology **67**:980-990.
- Knowlton, N., J. C. Lang, M. C. Rooney, and P. Clifford. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature **294**:251-252.
- Kramer, M. G., Hansen, Andrew J., Taper, Mark L., Kissinger, and Everett J. 2001. Abiotic controls of long-term windthrow disturbance and temperate rainforest dynamics in Southeast Alaska. Ecology **82**:2749-2768.
- Lassig, R. and S. A. Mocalov. 2000. Frequency and characteristics of severe storms in the Urals and their influence on the development, structure and management of the boreal forests. Forest Ecology and Management **135**:179-194.
- Lawton, R. O. 1982. Wind stress and elfin stature in a montane rain-forest tree - an adaptive explanation. American Journal of Botany **69**:1224-1230.
- Lee, X. 2000. Air motion within and above forest vegetation in non-ideal conditions. Forest Ecology and Management **135**:3-18.
- Lekes, V. and I. Dandul. 2000. Using airflow modeling and spatial analysis for defining wind damage risk classification (WINDARC). Forest Ecology and Management **135**:331-344.
- Lindemann, J. D. and W. L. Baker. 2002. Using GIS to analyse a severe forest blowdown in the southern Rocky Mountains. International Journal of Geographical Information Science **16**:377-399.
- Liu, C. X., J. S. Glitzenstein, P. A. Harcombe, and R. G. Knox. 1997. Tornado and fire effects on tree species composition in a savanna in the Big Thicket National Preserve, southeast Texas, USA. Forest Ecology and Management **91**:279-289.
- Loope, L., M. Duever, A. Herndon, J. Snyder, and D. Jansen. 1994. Hurricane impact on uplands and fresh-water swamp forest. Bioscience **44**:238-246.
- Lugo, A. E., M. Applefield, D. J. Pool, and R. B. McDonald. 1983. The impact of hurricane David on the forests of Dominica. Canadian Journal of Forest Research **13**:201-211.
- Mallin, M. A., M. H. Posey, M. R. Mciver, D. C. Parsons, S. H. Ensign, and T. D. Alphin. 2002. Impacts and recovery from multiple hurricanes in a piedmont-coastal plain river system. Bioscience **52**:999-1010.
- Mallin, M. A., M. H. Posey, G. C. Shank, M. R. Mciver, S. H. Ensign, and T. D. Alphin. 1999. Hurricane effects on water quality and benthos in the Cape Fear watershed: natural and anthropogenic impacts. Ecological applications **9**:350-362.
- Merrens, E. J. and D. R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. Journal of Ecology **80**:787-795.

- Miller, D. R., R. Dunham, M. L. Broadgate, R. J. Aspinall, and A. N. R. Law. 2000. A demonstrator of models for assessing wind, snow and fire damage to forests using the WWW. *Forest Ecology and Management* **135**:355-363.
- Miller, D. R., C. P. Quine, and W. Hadley. 2000. An investigation of the potential of digital photogrammetry to provide measurements of forest characteristics and abiotic damage. *Forest Ecology and Management* **135**:279-288.
- Mitchell, S. J. 2000. Stem growth responses in Douglas-fir and Sitka spruce following thinning: implications for assessing wind-firmness. *Forest Ecology and Management* **135**:105-114.
- Moore, J. and C. P. Quine. 2000. A comparison of the relative risk of wind damage to planted forests in Border Forest Park, Great Britain, and the Central North Island, New Zealand. *Forest Ecology and Management* **135**:345-353.
- Moore, J. R. 2000. Differences in maximum resistive bending moments of *Pinus radiata* trees grown on a range of soil types. *Forest Ecology and Management* **135**:63-71.
- Naka, K. 1982. Community dynamics of evergreen broadleaf forests in southwestern Japan. 1. wind damaged trees and canopy gaps in an evergreen oak forest. *Botanical Magazine-Tokyo* **95**:385-399.
- Nevalainen, S. and H. Yli-Kojola. 2000. Extent of abiotic damage and its relation to defoliation of conifers in Finland. *Forest Ecology and Management* **135**:229-235.
- Ostertag, R., Silver, W.L. & Lugo, A.E. 2005. Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica*, **37**: 16–24.
- Peart, D. R., C. V. Cogbill, and P. A. Palmiotto. 1992. Effects of logging history and hurricane damage on canopy structure in a northern hardwoods forest. *Bulletin of the Torrey Botanical Club* **119**:29-38.
- Peltola, H., B. Gardiner, S. Kellomaki, T. Kolstrom, R. Lassig, J. Moore, C. Quine, and J. C. Ruel. 2000. Wind and other abiotic risks to forests. *Forest Ecology and Management* **135**:1-2.
- Peltola, H., S. Kellomaki, A. Hassinen, and M. Granander. 2000. Mechanical stability of Scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in Finland. *Forest Ecology and Management* **135**:143-153.
- Peterson, C. J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *Science of the Total Environment* **262**:287-311.
- Peterson, C. J. 2000. Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. *Forest Ecology and Management* **135**:237-252.

- Peterson, C. J. 2004. Within-stand variation in windthrow in southern boreal forests of Minnesota: is it predictable? *Canadian Journal of Forest Research* **34**:365-375.
- Peterson, C. J. and A. J. Rebertus. 1997. Tornado damage and initial recovery in three adjacent, lowland temperate forests in Missouri. *Journal of Vegetation Science* **8**:559-564.
- Pleshikov, F. I., V. A. Ryzkova, V. Y. Kaplunov, and J. V. Usoltseva. 1998. A computer system for evaluating and predicting hurricane impact on forest. *Safety Science* **30**:3-8.
- Putz, F. E. and R. R. Sharitz. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, USA. *Canadian Journal of Forest Research* **21**:1765-1770.
- Ruel, J. C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. *Forest Ecology and Management* **135**:169-178.
- Ruel, J. C., D. Pin, and K. Cooper. 1998. Effect of topography on wind behavior in a complex terrain. *Forestry* **71**:261-265.
- Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1989. Tree uprooting - review of impacts on forest ecology. *Vegetatio* **79**:165-176.
- Schnitzer, S. A., J. W. Dalling, and W. P. Carson. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* **88**:655-666.
- Seischab, F. K., J. M. Bernard, and M. D. Eberle. 1993. Glaze storm damage to western New York forest communities. *Bulletin of the Torrey Botanical Club* **120**:64-72.
- Shelton, M. G. and M. D. Cain. 2002. Recovery of 1-year-old loblolly pine seedlings from simulated browse damage. *Canadian Journal of Forest Research* **32**:373-377.
- Skatter, S. and B. Kucera. 2000. Tree breakage from torsional wind loading due to crown asymmetry. *Forest Ecology and Management* **135**:97-103.
- Slater, H., W. J. Platt, D. B. Baker, and H. A. Johnson. 1995. Effects of Hurricane Andrew on damage and mortality of trees in subtropical hardwood hammocks on long pine key, everglades national park, Florida, USA. *Journal of Coastal Research* **21**:197-207.
- Spatz, H. C. and F. Bruechert. 2000. Basic biomechanics of self-supporting plants: wind loads and gravitational loads on a Norway spruce tree. *Forest Ecology and Management* **135**:33-44.
- Stokes, A. and S. Berthier. 2000. Irregular heartwood formation in *Pinus pinaster* is related to eccentric, radial, stem growth. *Forest Ecology and Management* **135**:115-121.

- Sutinen, M. L., T. Repo, S. Sutinen, H. Lasarov, L. Alvila, and T. T. Pakkanen. 2000. Physiological changes in *Pinus sylvestris* needles during early spring under sub-arctic conditions. *Forest Ecology and Management* **135**:217-228.
- Talkkari, A., H. Peltola, S. Kellomaki, and H. Strandman. 2000. Integration of component models from the tree, stand and regional levels to assess the risk of wind damage at forest margins. *Forest Ecology and Management* **135**:303-313.
- Trousdell, K. B., Williams, W.C. And Nelson, T.C. 1965. Damage to recently thinned loblolly pine stands by Hurricane Donna. *Journal of Forestry* **63**:96-100.
- Ulanova, N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management* **135**:155-167.
- Urban, D. L. 2000. Using model analysis to design monitoring programs for landscape management and impact assessment. *Ecological applications* **10**:1820-1832.
- Vandermeer, J., A. Brenner, and I. G. De La Cerda. 1998. Growth rates of tree height six years after hurricane damage at four localities in eastern Nicaragua. *Biotropica* **30**:502-509.
- Vandermeer, J., M. A. Mallona, D. Boucher, K. Yih, and I. Perfecto. 1995. 3 years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua - evidence in support of the direct regeneration hypothesis. *Journal of Tropical Ecology* **11**:465-471.
- Veblen, T. T., D. Kulakowski, K. S. Eisenhart, and W. L. Baker. 2001. Subalpine forest damage from a severe windstorm in northern Colorado. *Canadian Journal of Forest Research* **31**:2089-2097.
- Wakimoto, R. M. and P. G. Black. 1994. Damage survey of Hurricane Andrew and its relationship to the eyewall. *Bulletin of the American Meteorological Society* **75**:189-200.
- Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23**:379-385.
- Walker, L. R., J. Voltzow, J. D. Ackerman, D. S. Fernandez, and N. Fetcher. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rainforest. *Ecology* **73**:691-694.
- Walker, L. R., J. K. Zimmerman, D. J. Lodge, and S. Guzmangrajales. 1996. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. *Journal of Ecology* **84**:877-889.
- Watson, A. 2000. Wind-induced forces in the near-surface lateral roots of radiata pine. *Forest Ecology and Management* **135**:133-142.

- Webb, S. L. 1988. Windstorm damage and microsite colonization in 2 Minnesota forests. *Canadian Journal of Forest Research* **18**:1186-1195.
- Whigham, D. F., I. Olmsted, E. C. Cano, and M. E. Harmon. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan peninsula. *Biotropica* **23**:434-441.
- White, R. D. 1999. The impacts of hurricane Fran on a North Carolina piedmont woodland. Master thesis. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.
- Wilkinson, R. C., R. W. Britt, E. A. Spence, and S. M. Seiber. 1978. Hurricane-tornado damage, mortality, and insect infestations of slash pine. *South Journal of Applied Forestry* **2**:132-134.
- Woodley, J. D., E. A. Chornesky, P. A. Clifford, J. B. C. Jackson, L. S. Kaufman, N. Knowlton, J. C. Lang, M. P. Pearson, J. W. Porter, M. C. Rooney, K. W. Rylaarsdam, V. J. Tunnicliffe, C. M. Wahle, J. L. Wulff, A. S. G. Curtis, M. D. Dallmeyer, B. P. Jupp, M. A. R. Koehl, J. Neigel, and E. M. Sides. 1981. Hurricane Allens impact on Jamaican coral reefs. *Science* **214**:749-755.
- Zhu, J., T. Matsuzaki, and K. Sakioka. 2000. Wind speeds within a single crown of Japanese black pine (*Pinus thunbergii Parl.*). *Forest Ecology and Management* **135**:19-31.

Table 3.1. Characteristics of the eight mapped tree census plots in the Duke Forest of Piedmont region, North Carolina, USA.

Name	Location	Size (m ²)	Year*	Habitat	Disturbance history
<u>Pine stands</u>					
Graveyard	Korstian Division	13,000	1978	Dry upland	Selective cutting prior to 1930, some salvage cutting lowing Hurricane Hazel in 1954
Land's end	Korstian Division	9,900	1978	Dry upland	Selective cutting prior to 1930
<u>Upland hardwood stands</u>					
Rocky	Korstian Division	20,400	1978	Dry upland	Selective cutting prior to 1930
Wooden Bridge	Korstian Division	5,250	1984	Dry mesic upland	Selective cutting prior to 1930
Bormann	Durham Division	19,600	1950	Dry upland	Selective cutting prior to 1930
Bryan Center	Duke Univ. Campus	19,400	1986	Dry mesic upland	Old field, abandoned circa 1780
Oosting	Duke Forest Nat. area	65,536	1990	Dry mesic upland	Selective cutting prior to 1900
Big Oak Woods	NC Bot. Garden	23,550	1986	Alluvial lowland	Natural disturbance by beaver and flooding

* The years of which the mapped tree plot was established.

Table 3.2. Characteristics of the 22 pine permanent sampling plots (PSPs) in the Duke Forest, North Carolina, USA.

Plot #	Damage Index*	Age (yr.)	Density (100m ²)	Height (m)	BA (m ² /ha)	Elevation (m)	Slope†	Aspect‡	Topographic position
Plot 4	0.01	72	6.92	22.96	4144.75	117.69	1	4	Lower slope
Plot 5	0.05	72	16.6	23.25	9050.00	120.24	1	4	Lower slope
Plot 6	0.02	72	9.09	20.68	4591.76	117.85	1	4	Lower slope
Plot 7	0.01	72	7.02	24.38	4104.87	114.34	2	4	Lower slope
Plot 12	0.24	71	7.16	26.53	5811.98	117.83	2	3	Mid-slope
Plot 13	0.04	71	5.68	26.01	4730.55	123.45	2	7	Lower slope
Plot 14	1.01	71	6.67	23.67	3900.55	128.23	2	3	Ridge
Plot 15	0.03	71	7.41	25.3	4837.46	123.13	1	5	Lower slope
Plot 16	0.61	71	6.42	25.67	4842.53	123.34	2	3	Mid-slope
Plot 17	0.01	71	6.17	25.79	3764.59	125.14	2	4	Ridge
Plot 18	0.29	71	5.19	28.31	4157.16	122.04	3	4	Lower slope
Plot 19	1.26	71	5.19	25.46	3568.87	118.82	3	3	Ridge
Plot 20	0.04	71	7.41	22.5	4294.34	126.37	1	5	Lower slope
Plot 21	0.13	71	7.41	26.47	3935.21	126.42	2	4	Lower slope
Plot 22	0.28	71	5.68	23.06	3760.98	129.34	1	4	Mid-slope
Plot 23	0.02	71	4.2	22.19	2695.59	130.00	1	1	Lower slope
Plot 24	0.06	81	6.32	23.61	4059.00	116.62	1	3	Lower slope
Plot 25	0.04	81	7.11	25.18	5262.30	112.91	1	3	Lower slope
Plot 26	0.33	81	8.5	22.08	4773.45	110.43	1	3	Mid-slope
Plot 49	1.43	90	5.14	25.77	4427.60	120.00	3	1	Ridge
Plot 50	1.48	90	5.24	27.92	4465.01	120.00	3	4	Ridge
Plot 51	2.03	90	4.45	28.1	4845.57	121.52	3	4	Ridge

Note: * Stand damage index was computed as the average damage index of all stems >2 cm within plots. The index was weighted by stem basal area for all stems. The range of damage index by definition is 0-3. †Slope class: 1=0-5°, 2=5.1-10°, and 3=>10.1°. ‡Aspect class: 1=0-45°, 2=46-90°, 3=91-135°, 4=135-180°, 5=181-225°, 6=226-270°, 7=271-315°, 8=316-360°.

Table 3.3. Comparison of stand level damage of the eight mapped plots and three groups of PSPs according to their locations i.e. (1) PSP 12-23, 49,50,51; (2) PSP 4,5,6,7,24,25,26 and (3) Hill Forest 23, 24 25 vs. their distances to hurricane path.

	Damage index (weighted by BA) (All stems)	Distance to hurricane path (km)
Graveyard	0.70	15.3
Land's end	0.39	15.2
Bormann	0.87	11.3
Rocky	0.87	15.5
Big Oak Woods	0.28	16.5
Bryan Center	0.23	6.0
Wooden Bridge	0.26	15.5
Oosting	0.07	17.5
Hill 23, 24, 25	0.02	3.5
PSP 12-23, 40-51	0.59	9.8
PSP 4-7, 24-26	0.07	9.0

Table 3.4. Mean damage and standard deviation for mapped plots in the Duke Forest.

Plot	Mean damage*	Standard deviation	Minimum	Maximum
<u>Pine stands</u>				
Graveyard	0.8923	0.6090	0	2.3333
Land's end	0.5096	0.4373	0	0.2353
<u>Hardwoods</u>				
Bormann	0.7347	0.6149	0	2.5385
Rocky	0.4526	0.4380	0	2.2692
Wooden Bridge	0.3667	0.4924	0	2.2308
Oosting	0.1929	0.2585	0	1.3390
Big Oak Woods	0.1911	0.3093	0	1.7419

Note: Most mapped plots are divided into about 10*10 blocks. The blocks in Oosting plot are 16*16 m and in Land's end plot is 10*12.5 m. * Mean damage is the average damage value of all blocks within plot.

Table 3.5. Logistic regression models of hurricane damage during Hurricane Fran at a regional scale. Heavily damaged trees are examined as a function of wind speed, the amount of rainfall, tree size (d.b.h.), tree species composition ratio and the distance to the hurricane path. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Variables	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > ChiSq	
d.b.h.	0.0576	0.0150	14.6852	0.0001	***
Pine ratio	-0.8893	0.3106	8.1975	0.0042	***
Wind Speed	0.0772	0.0160	23.1965	<0.0001	***
Rain	-0.1330	0.0500	7.0661	0.0079	**
Distance to path	-0.0257	0.0063	16.5021	<0.0001	***

Note: tree species composition ratio is the ration of the number of pine trees of each plot which included total 20 trees.

Table 3.6. Logistic regression models of hurricane damage during Hurricane Fran for 22 pine stands in the Duke Forest. Plot-level damage severity was examined as a function of stand density, height, topographic position, aspect, slope, site exposure. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Variables	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > ChiSq	
Height	0.4660	0.2198	4.4943	0.0340	*
Ridge	2.8176	0.9502	8.7918	0.0030	**
Lower slope	-3.0750	0.8480	13.1477	0.0003	***

Table 3.7. Logistic regression models of hurricane mortality during Hurricane Fran in a pine stand and hardwood stand in the Duke Forest. Tree mortality was examined as a function of pre-hurricane d.b.h. and tree growth rates. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Variables	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > ChiSq	
<u>Pine stand (Graveyard plot)</u>					
10-yr relative growth	-5.3370	1.8524	8.3004	0.004	***
<u>Hardwood stand (Bormann plot)</u>					
Pre-hurricane d.b.h	0.0335	0.0075	19.7420	<.0001	***
10-yr relative growth	-11.9284	2.6686	19.9804	<.0001	***

Note: 10-yr relative growth is defined as the diameters increase of ca.10-year period from 1982 to 1992 for the trees (d.b.h >10 cm) in the Graveyard plot (pine stand), and from 1982 to 1993 for trees (d.b.h. >10 cm) in the Bormann plot (hardwood stand) divided by the tree diameter in 1982.

Table 3.8. Factors that were significantly related to wind damage at three relevant scales (i.e. regional, landscape and stand).
 *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Damage risk factors	Hurricanes			Tornado
	Regional	Landscape	Stand scale	
<u>Abiotic</u>				
Wind speed	***	n/a	n/a	n/a
Rainfall	**	n/a	n/a	*
Position	*	***	n/a	n/a
Slope	n/a	n/a	n/a	*
Aspect	n/a	n/a	n/a	*
<u>Biotic</u>				
Tree size	***	***	***	*
Species	*	*	**	**
Growth rates	n/a	n/a	***	n/a
Stand density	n/a	*	*	*
<u>Others</u>				
Distance to path	***	n/a	n/a	n/a

Table 3.9. Wind speed variation largely explains the variation in tree damage during 1989 Hurricane Hugo. Note that species characters play an important role in damage risk.

Relative importance of variables during 1998 Hurricane Hugo

Variables	% Variation Explained
Wind speed	58.39
Tree size/height	6.37
Other tree characters	12.13
Species	9.30
Site variables	0.56
Community attributes	0.98
Interactions	11.81

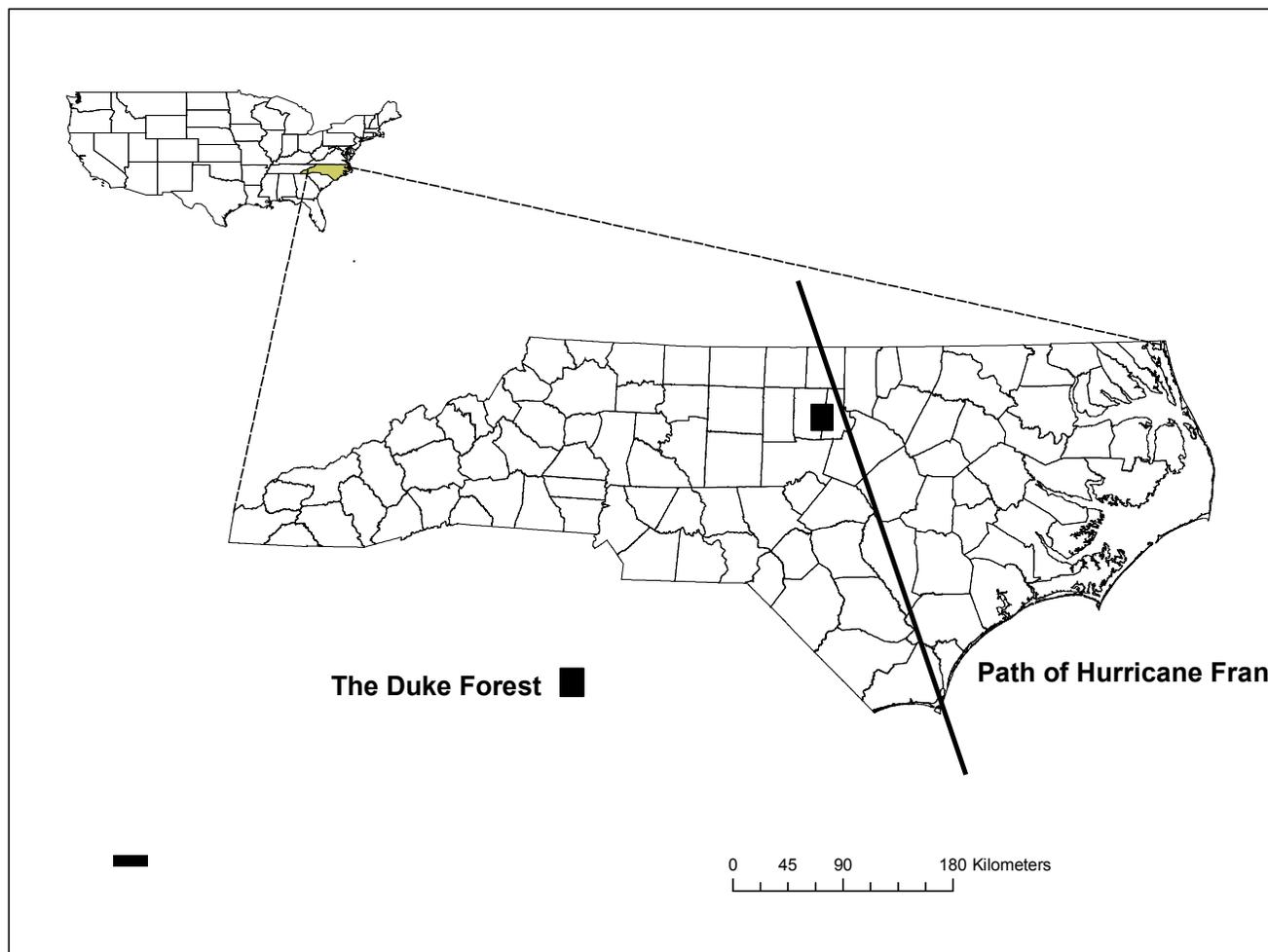


Figure 3.1. The location of the Duke Forest and the path of 1996 Hurricane Fran in North Carolina, USA

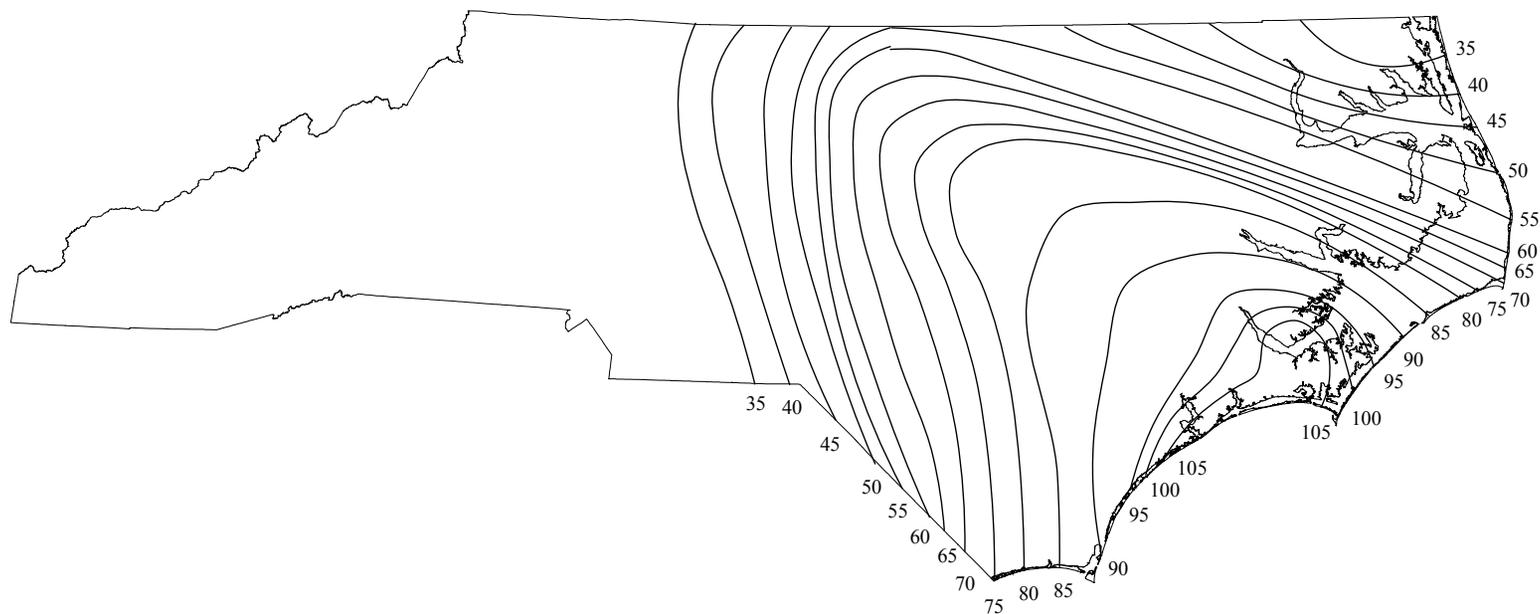


Figure 3.2. Map of estimated maximum sustained wind speeds across North Carolina during the 1996 Hurricane Fran. Wind speed data are from Joel Cline in National Weather Service (1996). Isobars indicated wind speeds intervals of mile/hour. The estimated maximum sustained wind speeds do not take into account fine-scale variation in wind speeds due to gusts, downburst and tornados which can greatly exceed the values presented here.

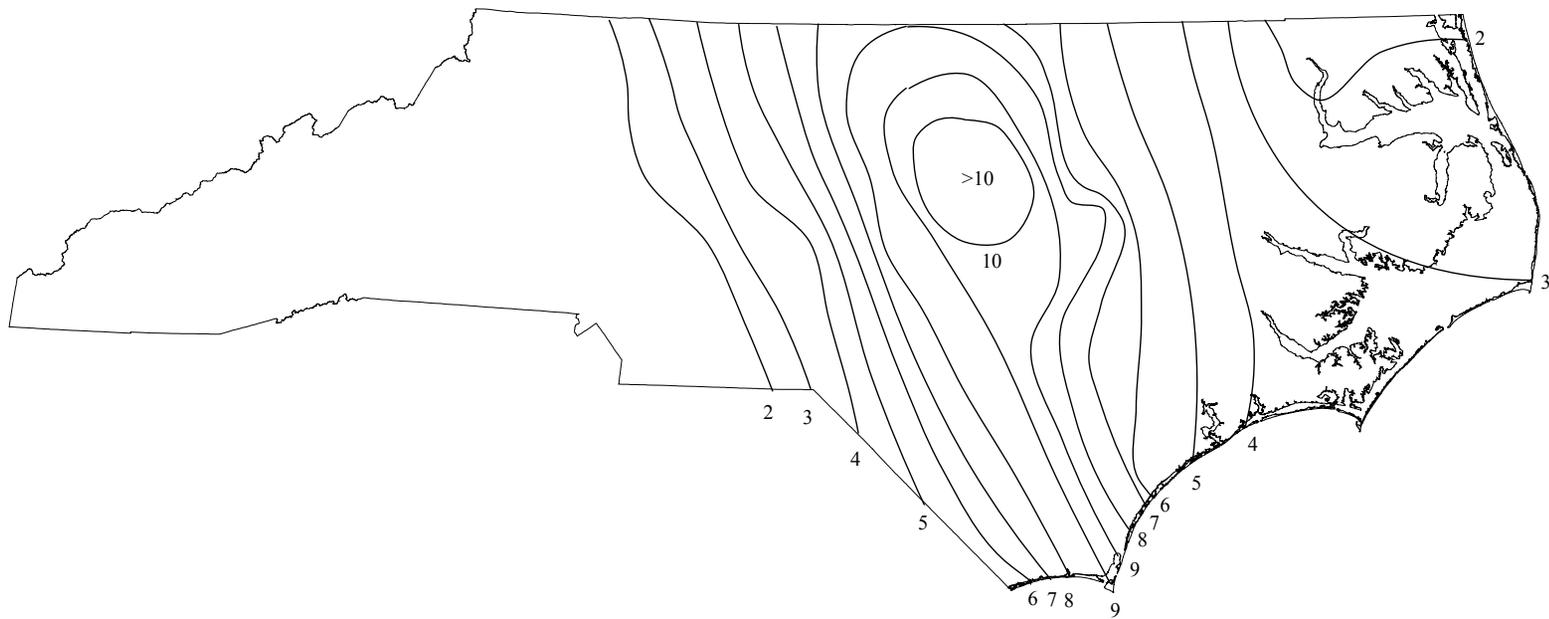
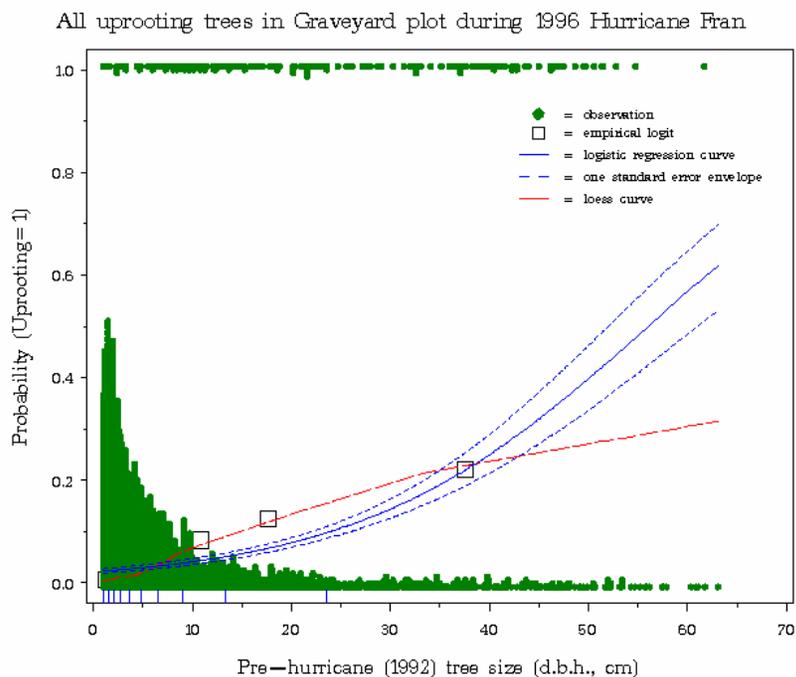
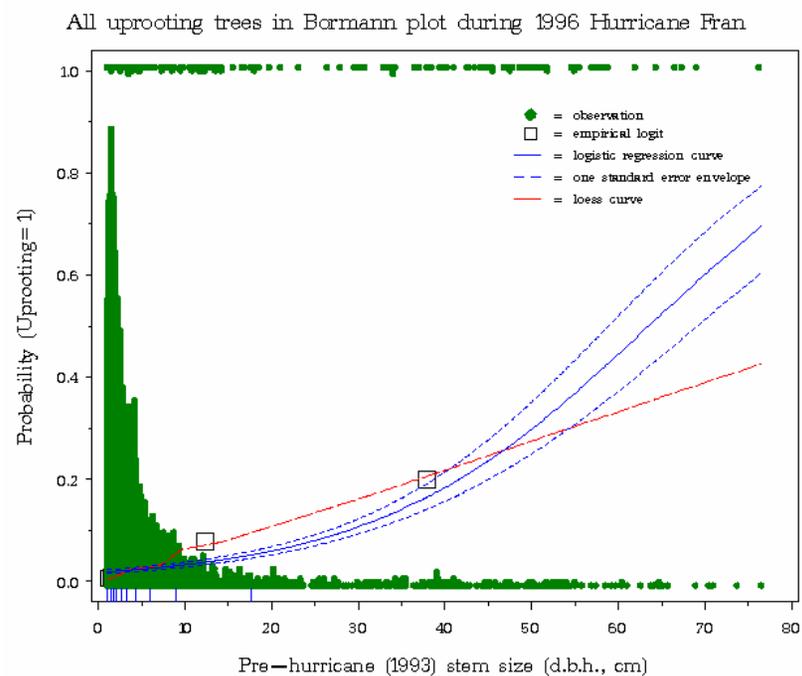


Figure 3.3. Map of precipitation across North Carolina during the 1996 Hurricane Fran. Precipitation data are from Joel Cline in the National Weather Service (1996). Isobars indicated precipitation intervals of inches.



(a) Graveyard Plot



(b) Bormann plot

Figure 3.4. The possibility of a tree uprooting increased with increases in tree size in (a) the Graveyard plot and (b) the Bormann plot. Empirical log odds and the probability plot for uprooting as a function of pre-hurricane tree size. The observed response are plotted as stacked points at the top (i.e., uprooting) and bottom of the figure (i.e. no such type damage). The squares show the empirical sample logits and the analogous adjusted sample probability. The curves on these plots show predicted probabilities and 95% confidence bands.

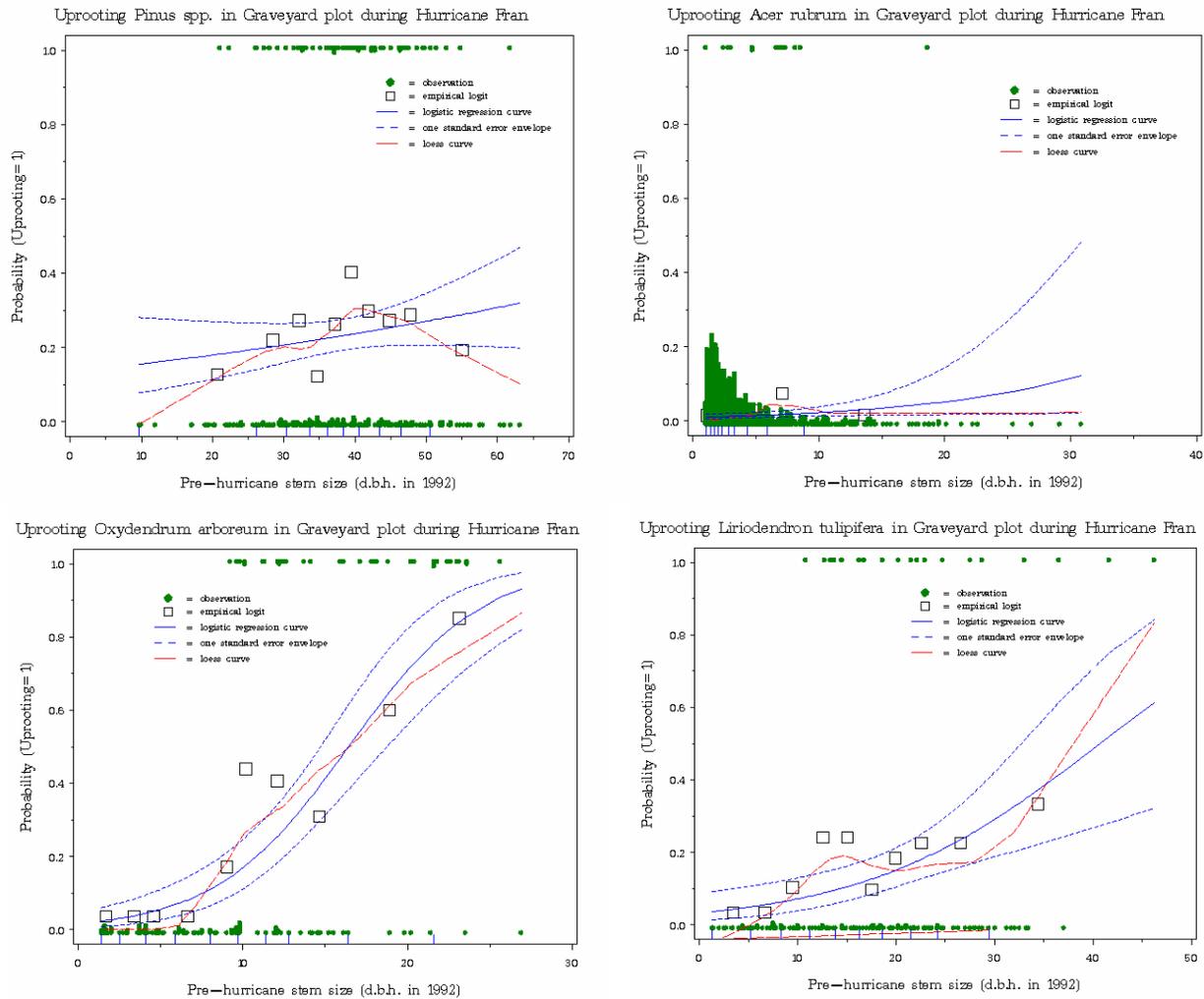


Figure 3.5. The probability of uprooting during the 1996 Hurricane Fran in Gravetayd plot of the Duke Forest increased with increases in tree size (d.b.h.). Interactions between diameter and species showed that rate of increase with diameter varies among species.

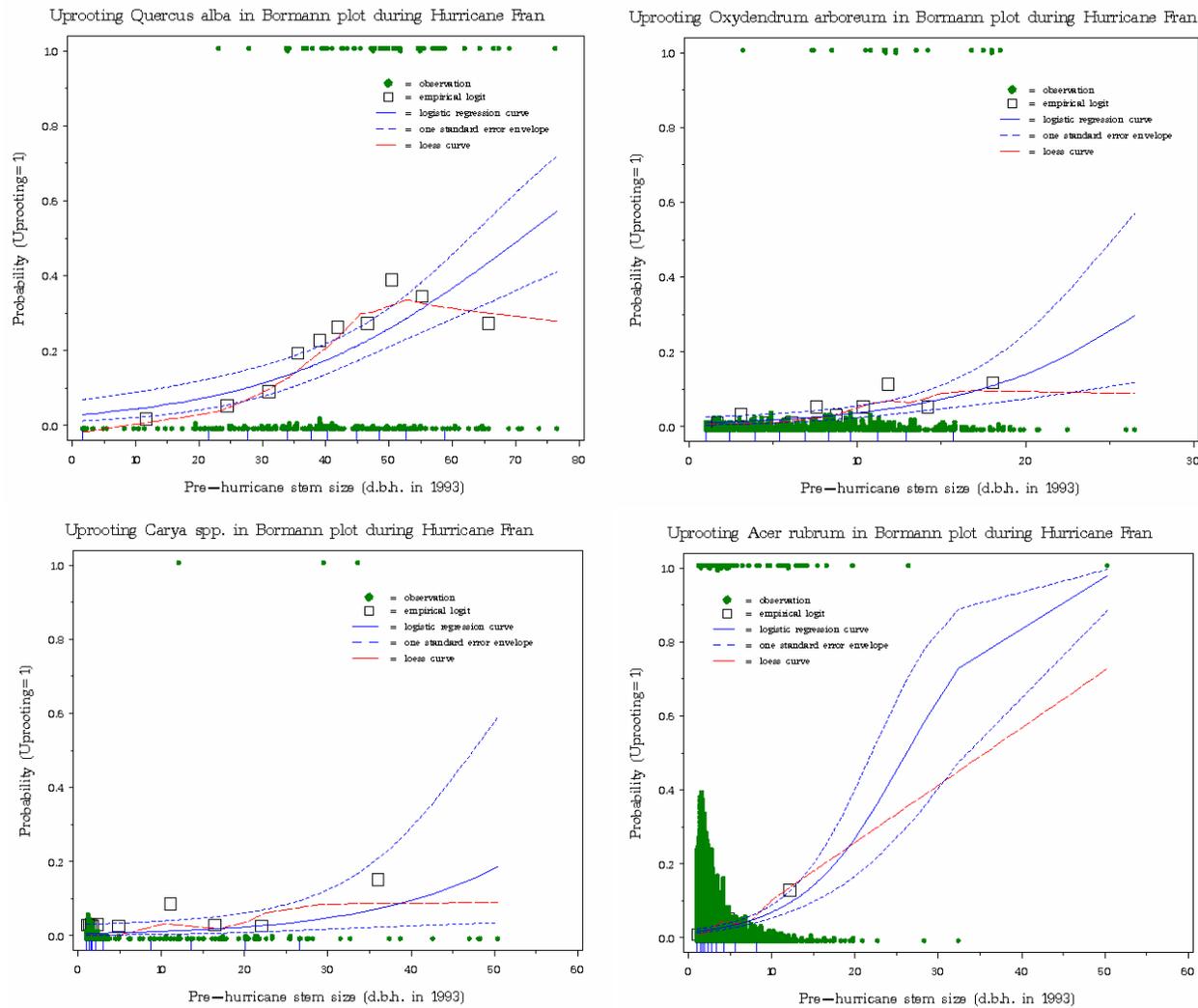


Figure 3.6. The possibility of uprooting tree during the 1996 Hurricane Fran increased with increases in tree size (d.b.h.) for four major species in Bormann plot, Duke Forest, North Carolina, USA.

CHAPTER 4

THE IMPACT OF HURRICANE FRAN ON WOODY SEEDLING AND SAPLING DYNAMICS AND DIVERSITY IN NORTH CAROLINA PIEDMONT FORESTS

Abstract. In 1996 Hurricane Fran significantly damaged the forest canopy above many long-term seedling and sapling census plots in the Duke Forest of Piedmont North Carolina providing a rare opportunity to examine detailed times-series data spanning a major wind disturbance event. I analyzed population dynamics of woody seedlings and saplings and changes in diversity and composition during an interval lasting from 5 years before the 1996 Hurricane Fran to 5 years post-hurricane through use of seedling and sapling transects where individual seedling and sapling stems have been censused annually or nearly annually 1978-2001. I hypothesized that canopy disturbance by large, infrequent hurricanes enhances recruitment and establishment of light-demanding species, and increases growth rates of established seedlings and saplings. I tested the hypothesis by comparing damage and mortality of seedlings and saplings caused by the hurricane and exploring changes in understory composition, diversity and growth rates, and population dynamics before and after the hurricane event.

This study supports the hypothesis that large canopy disturbances can promote local tree species diversity in the understory of Piedmont forests. Most seedling transects experienced an immediate drop in stem density in the first year after the disturbance, followed by a rebound of stem density in second year and a gradual recovery and enhancement in tree species richness and diversity by the end of the survey period. Changes in sapling density

were less dramatic relative to the understory seedlings, and most transects experienced decreases in stem density. Species diversity of saplings remained relatively stable or decreased slightly due to the hurricane-induced damage. Large tree gaps created by the hurricane resulted in release of established shade-intolerant or mid-tolerant seedlings and saplings. Large windstorm disturbances appear to be responsible for temporal and spatial variations in understory regeneration, which contribute to a diverse but temporally relatively stable canopy layer. In addition, comparison of responses across the multiple forest stands showed that the hurricane-induced species diversity changes varied greatly among forest stands, suggested that the post-hurricane changes must be viewed in the context of pre-disturbance species composition that in turn reflects differences in habitat and stand history.

Key words: species diversity; hurricane impact; forest dynamics, seedling recruitment, advanced growth, forest dynamics, canopy disturbance, Piedmont forests, heterogeneity, light, micro-topography, spatial patterns.

INTRODUCTION

The role of small-scale tree gap disturbances in temperate forests has long been recognized and in recent decades increasingly understood (e.g., Watt 1947, Canham and Marks 1985, Beckage et al. 2000). In intact temperate forests without large-scale canopy disturbance, much of the tree seedling recruitment occurs within or around tree gaps resulting from the natural death of individual canopy trees. Thus, small and localized gaps generally have positive effects on forest understory regeneration and species diversity maintenance (Watt 1947, Bormann and Likens 1979, Runkle 1982, Pickett and White 1985). In addition, these tree gaps release both seedlings and saplings that were previously experiencing high mortality and slow growth. Consequently, small-tree gaps create openings for colonization

by new individuals, reduce dominance of a site by established individuals, and enhance advanced growth of pre-existing individuals in forest understory (Canham and Marks 1985). However, the effects of large-scale canopy disturbances such as major hurricanes on understory population dynamics and species diversity are little known (Everham and Brokaw 1996, Whitmore 1996, Turner et al 1999, Webb 1999).

The importance of windthrows in the temperate forest regeneration has been emphasized by several previous studies (e.g., Loretta et al. 1999, McNab et al. 2004), and intensive wind damage has been hypothesized to influence species composition, tree diversity and population dynamics through enhanced understory recruitment, establishment, and growth (Peet and Christensen 1981, Beckage et al. 2000, see review by Webb 1999). Nonetheless, to date few studies have explicitly investigated understory response to major canopy disturbance events as r plant ecologists and foresters have rarely had available the combination of long-term pre- and post-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 tree seedling and sapling census plots in the Duke Forest of Piedmont North Carolina. Seedlings in this study are defined as any woody stems of a tree species up to 50 cm in height, whereas saplings are defined as any tree stems or shrubs 50-137 cm in height. 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 trees and seedling dynamics were available. I here analyze changes in the composition and diversity of woody seedlings and saplings over an interval lasting from 5 years prior to Hurricane Fran until 5 years after Fran.

In Piedmont forests of the southeastern United States, tree seedling recruitment of canopy dominant species such as oaks (*Quercus spp.*) and hickories (*Carya spp.*) has been observed to be limited, while other, perhaps more shade-intolerant species such as red maple (*Acer rubrum*) have exhibited a continuous supply of recruits and thus increased dominance (McDonald et al. 2002). McDonald et al. have observed that the understory seedling composition of Piedmont forests differs substantially from canopy composition, and that the difference has been increasing over the past several decades. Although oaks and hickories still remain the dominant canopy species, there has been a steady decline in dominance of these genera. This trend appears widespread in the eastern United States and the mechanisms are still under investigation. Clearly, alteration of trends in understory species composition will have important consequences for post-hurricane forest dynamics. Glitzensten et al. (1986) suggested the relatively shade-intolerant canopy species are adapted to rapid growth following major canopy disturbance, such as these associates with hurricanes. What has been unclear is whether occasional catastrophic disturbances, such as caused by large, infrequent hurricanes, would allow enhanced regeneration of the canopy dominants to maintain continued dominance of the oaks and hickories, or whether the rate of increase in the understory red maple and beech populations would be amplified.

The first goal of this paper is to examine whether large canopy disturbances increase understory woody seedling and sapling diversity and alter their population structure and dynamics. My general hypothesis is that major canopy disturbance enhances seedling recruitment of the more light-demanding species due to increased resource availability. The second goal is to examine the impacts of large-scale hurricanes on tree seedling and sapling growth patterns. I hypothesized that large tree gaps created by Hurricane Fran would result in

the release of established shade-intolerant or mid-tolerant seedlings and saplings and that large-scale hurricanes create conditions that allow increased growth rates of the existing seedlings and saplings in the damaged forests. Previous seedling demographic work in the Duke Forest had shown a negative correlation between growth rates in sequential years (Philippi et al. 1992, 1993). As the older, established seedlings and saplings have large root systems, they can be expected to have an ample supply of soil resource and should be able to thrive in the open gap conditions, thereby may reverse the negative correlation observed between relative growth in successive years.

The overall objective of this study was to examine the effects of a large hurricane disturbance on understory woody seedling and sapling composition, diversity, and dynamics in both even-aged pine stands and mixed-aged hardwood forests. By taking advantage of the fortuitous availability of detailed long-term pre- and post hurricane seedling and sapling demographic data, I am able to provide insights on the extent of increased growth and the degree of difference among species in response to hurricane-induced large canopy openings. In this chapter, I focus on the following questions. (1) How do understory seedling and sapling stem density, mortality, and recruitment change after a major canopy disturbance? (2) Do large hurricanes enhance seedling and sapling species richness and species diversity? (3) Do growth rates of tree seedlings and saplings increase after major canopy disturbance? (4) To what extent do the large canopy disturbances influence seedling and sapling species differently? Which trees species/or group have increased understory seedling and sapling density, and how are the rates of establishment modified? (5) Will understory tree seedlings and saplings become more divergence in tree species composition after the large hurricane disturbance?

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 m to 250 m above sea level. The annual average temperature is around 15°C. Precipitation averages about 1,120 mm annually and is well distributed across the year. Varied topography, moderate climate and a complex disturbance history support vegetation composed of a diversity of plant species and forest types. Over 100 species of trees have been identified in the Duke Forest (Palmer 1990). The natural vegetation in this region belongs to the Oak-Hickory-Pine forest group (Braun 1950, Martin et al. 1993). 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 this region. The hardwoods are mostly uneven-aged, secondary forests significantly influenced by soil type and past disturbance. The dominant hardwood species include red oak (*Quercus rubra*), white oak (*Q. alba*), mockernut hickory (*Carya tomentosa*), 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., Oosting 1942, Peet et al. 1987, Peet and Christensen 1987, 1988, Peet 1992, McDonald et al. 2002, Taverna et al. 2005).

Data

Long-term seedling and sapling transects were established throughout the Duke Forest by Robert Peet and Norman Christensen in late 1970s (seedlings) and 1980s (saplings) as part of a long-term forest dynamics project. The transects cross the normal range of spatial variation in forest composition in the Duke Forest, and include several 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. These times-series data of woody seedling and saplings spanning the 1996 Hurricane Fran and representing a diversity of sites and stand ages allows examination of both long-term and immediate changes in seedling and sapling dynamics in stands that vary in site conditions and stage of successional development.

From the complete dataset, I extracted a total of 13 intensively mapped seedling and 13 sapling transects from four mapped forest plots in the Duke Forest (Table 4.1). These transects include annually measured records for 5 years pre-Fran (1990-1994) and 5 years post-Fran (1997-2001). The four selected mapped forest plots were substantially damaged by Hurricane Fran in 1996 and are representative of severely damaged areas in the Duke Forest. Specifically, the Graveyard plot and the Land's end plot represent the transition phase of older (ca. 80 to 100 years old) but even-aged pine forest stands with a hardwood understory, whereas the Bormann plot and the Rocky plot represent the steady-state phase's mixed-aged, upland deciduous hardwood forest in North Carolina Piedmont forests. From each of the four forest stands, I selected three seedling transects (four in Graveyard plot) from the available six (seven in Graveyard plot) seedling transects along with corresponding sapling transects. Overall, the selected 13 intensive mapped seedling transects and 13 sapling transects which are nearly evenly distributed in each of the four large mapped forest stands are largely

representative of the whole dataset. The two reasons for using a half of the total transects in my following analysis are: 1) the selected transects were all annually surveyed (except in 1995 and 1996 when no surveys were conducted) whereas the other transects were not surveyed in 1997 owing to time limitations; 2) the selected transects were surveyed for understory light conditions thereby allowing examination of the relationships among seedling and sapling recruitment, diversity, growth, and light variation.

The seedling censuses was generally conducted between middle May and the end of July of each survey year. All the seedling transects are 50 m long and 1 m wide (50 m² in size). Within each seedling transect, all seedling stems of potentially arborescent species, with the exception of flowering dogwood (*Cornus florida*), were identified, mapped (with x, y coordinates) and measured for height, age, and leaf number for living stems. Botanical nomenclature follows USDA Plants v 4.0. Taxa were generally identified to the species level except for pines (*Pinus*), which were always identified to genus. Height of each seedling individual was measured from the base of the plant at soil surface level to the terminal bud. Seedling age of individual stems, including ingrowth (new seedlings and those that had apparently been overlooked in previous years), was estimated by the number of terminal bud scars on the stem. New woody seedlings have an age of zero, and early in the season can be distinguished by the presence of cotyledons. The purpose of this age variable is to determine whether the seedling is making its first appearance (Age= 0) or if it was perhaps overlooked in the past. Stems 5 years old or older are recorded as Age= 5. A condition code was assigned to each seedling individual: 1= alive and reasonable normal, 2= dead, 3= missing, 4= significant loss in height, 5= severe damaged by insects or diseases, or in some cases,

accidentally pulled out by the field crew. In 2001, a total of 5731 seedlings existed in the selected 13 tree seedlings transects (Table 4.2).

A set of 4 m wide woody sapling transects parallel to the seedling transects was established in 1989, on top of the one-meter-wide woody seedling transects. Unlike in the woody seedling survey, the sapling species include flowering dogwood and shrub species (e.g., *Viburnum spp.*, and *Vaccinium spp.*). For each sapling in each survey, natural sapling height and stem d.b.h. were recorded. Natural standing height referred to the distance between the terminal bud and the ground directly below it. 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 stem damage codes. The stem damage codes used were uprooting, breakage, leaning, and leaned on (i.e., bent or leaning, pinned by their large neighbor trees).

The sapling census was also generally conducted between middle May and the end of July of each survey year. For each year, the census contents also included sprouts, ingrowths and sapling loss (i.e., stems of dead, missing, or growing out of the size range). Sprouts were not mapped unless they were actually rooted in the soil. Where multiple sprouts have 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 has the largest stem > 1 cm in d.b.h., then new individuals from this clump were not recorded for ingrowth. All condition codes previously used for seedlings were also used for saplings, and in addition, a code 8 was used for referring to a living stem > 1 cm d.b.h. and which has thus grown out of the sampling category. New saplings, those that are newly above 50 cm were

recorded as ingrowth. In 2001, there were in total 1, 785 saplings in the 13 selected sapling transects (Table 4.2).

Quantifying forest canopy disturbance

The degree of canopy openness (percentage of open sky seen beneath the canopy) was determined for each of the 13 seedling transects and the 13 sapling transects by using a series of hemispherical photographs taken along transect at 2 m intervals for seedlings and 4 m intervals for saplings. 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 height of 1 m for seedlings and of 1.8 m for saplings in the summers of 2001 and 2002. 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 specifically designed 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 (Frazer et al. 1999). These data were then used with available seedling and sapling population data to examine the effect of forest canopy disturbance intensities on understory diversity and growth.

Statistical analyses

The censused seedling and sapling data were used to calculate species richness, species diversity, annual rates of mortality and recruitment. The seedling and sapling species richness was defined as the number of woody species present per transect (i.e., in 50 m² for seedling

and 200 m² for saplings, respectively). The Shannon-Wiener diversity index (H'), a widely used diversity index which devised to determine the amount of information in a code, was used in this study. The Shannon-Wiener index (H') is defined as:

$$H' = - \sum p_i \log_e p_i$$

where p_i = the proportion of the individuals in the i^{th} species.

Two common parameters of annual growth rates were calculated for woody seedlings and saplings. Annual growth increment (GI) was calculated as the change in height between two consecutive years' censuses (year i and year $i+1$) following formula: $GI = (H_{i+1} - H_i)$, whereas relative growth rate (RGR) was calculated as the height increment between two consecutive years' censuses (year i and year $i+1$) rescaled by initial height following formula: $RGR = (H_{i+1} - H_i) / H_i$. While GI represents absolute annual growth increment of a seedling or sapling, RGR for this analysis is used for removing the effect of plant size and thereby to expose the effects of other major factors on stem growth (e.g., light). To allow stratification by size in comparisons of seedling growth, I used 5 size-classes defined with cut-point intervals of 10 cm (<10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm).

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

I also examined the effects of canopy disturbance intensity, which is defined as canopy openness (CO), on seedling and sapling recruitment and growth. The value of percentage of CO of each sub-block (in 1*2 m for seedlings and 4*4 for saplings) was used to represent the

canopy disturbance intensity. CO ranges from 0 (complete obstruction) to 100 % (open sky). 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 9.0, SAS Inc. 2003).

Compositional patterns and trends were assessed with Nonmetric Multidimensional Scaling (NMDS, PC-Ord 4). All seedling and sapling data (i.e., all 13 seedling and 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 (Woods 2000, McCune et al. 2002, Taverna et al. 2005).

RESULTS

Hurricane-induced understory seedling and sapling damage and mortality

The impact of canopy damage by Hurricane Fran resulted in a significant amount of secondary mechanical damage on the understory saplings. The damage of sapling stems appeared mainly to be caused by their large upper canopy layer neighbors. As Figure 4.1 shows, 44-70% of damaged sapling stems were pinned by their large neighbor trees, suggesting that hurricane damage on understory was largely secondary damage.

Understory saplings experienced significantly higher mortality rates following the hurricane as compared to their pre-hurricane background mortality (Figure 4.12). The average mortality rate of saplings (5-year average for all sapling transects) nearly doubled, increasing from (mean \pm 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 \pm 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.

Delayed sapling mortality was also sustained following Hurricane Fran. In all four forest stands I surveyed, saplings mortality was elevated over background not just immediately following the hurricane, but also for the five-year monitoring period following the storm event. The year-to-year change of hurricane-induced sapling mortality was also different between forest types. In the pine forests, sapling mortality was peaked in 1998 or 1999 and then gradually decreased (Figure 4.12), whereas in mixed hardwood forest, there was relative high sapling mortality in 1998 or 1999, but less consistency in the decline in mortality.

Hurricane Fran had significant effects on understory seedling abundance (Figure 4.2). Overall, Fran significantly decreased seedling density in both even-aged pine stands and mixed-aged hardwood plots ($p < 0.05$). There was an abrupt drop in seedling density across all the tree seedling plots in the Duke Forest following Fran due to direct mortality and limited recruitment in the first growing season. The two loblolly pine stands (Graveyard and Land's end) had a reduction in seedling density of about 48%, whereas the two mixed hardwood stands (Bormann and Rocky) had reductions in seedling density of about 42% across the whole 5-year period.

Whereas sapling mortality increased following Hurricane, seedling mortality decreased. The overall seedling mortality was low in the second year after hurricane, perhaps due to the substantial reduction in existing seedlings the previous year. The hurricane tended to lower seedling density in the seedling transects. Particularly, Hurricane Fran had significant effects on stem density in the first growth season. The lowest seedling densities during the 10 years all occurred (but Land's end plot) in 1997, the first growth season after the hurricane. There

appeared a significant seedling population rebound in the second year due to high ingrowth ($p < 0.05$). Note 1994 was a drought summer so seedling density was at its lowest of the pre-Fran period. This was followed by a gradual recovery in stem density. Nonetheless, the overall seedling density post Fran was lower than the pre-disturbance level.

Change in understory tree seedling and sapling richness and diversity

Although Hurricane Fran greatly changed understory stem density, it had only a modest impact on species richness and diversity (Figures 4.3 and 4.4). Seedling species richness and diversity dropped slightly in the first two years after Hurricane Fran, and subsequently gradually rebounded to the pre-disturbance baseline level, and in some cases reached levels higher than pre-hurricane (Figure 4.4).

Across the seven seedling transects that represent seedling dynamics of pine stands, species richness and diversity increased slightly over the 5-year interval following Fran. Species richness of seedlings decreased slightly in the first years after the hurricane damage and then increased slightly in following years. All the seedling transects ($n = 7$) in the two pine stands showed this pattern. Species diversity indices increased in 1997, one year after Hurricane Fran, dropped the next year, and increased following three years.

Change in seedling richness and diversity in the mixed hardwood forest appears more complex than that in the pine stands. As in the pine stands, the Shannon indices increased in 1997 and dropped slightly in 1998. Although similar in the different transects in hardwood forest types, the seedling patterns varied after a clear drop in the species diversity. Species diversity across the entire seedling transect dataset increased to some extent, but with a slight dip in 2000.

The response of sapling richness and diversity to the hurricane was relatively stable compared to the seedling patterns, varying from decreasing to about constant (Figures 4.10 and 4.11). The sapling species richness in two of the forest stands (Graveyard, Bormann) slightly increased over time, whereas other two plots (Land's end, Rocky) lost several species. Sapling species diversity was relative stable over time. 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 woody seedling and sapling recruitment

Post-hurricane sapling recruitment was general higher than pre-hurricane (Figure 4.13), in large part due to enhanced growth of the larger seedlings, 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 folds those 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 surprisingly high level of sapling recruitment. In the two hardwood plots, increases in sapling recruitment were significant with high year-to-year variance. However, I 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 significantly increased sapling stem density after the hurricane, while the other three other stands decreased in sapling stem density (Figure 4.9).

I found little evidence of a significant increase in seedling recruitment after the hurricane, either in the pine forest stands or in the mixed hardwood forests. Post-hurricane seedling influx showed that seedling ingrowth was limited. Overall, recruitment of the seedlings was low after Hurricane Fran when compared to the pre-hurricane recruitment baselines, although in some years they were higher than pre-hurricane levels. Moreover, I noticed some shade-intolerant species, such as tuliptree, sweetgum and elm increased their recruitment. My results showed that several early successional, light-demanding species such as tuliptree and sweetgum, increased their recruitment in the first or second years after the hurricane, but the fate of these species remains unclear. In addition, I found a few cases of “mast seedling years” for white oak and redbud where seedling density was surprisingly high in a given year, which led to a less unpredictable pattern in the understory seedling layer.

Effects of Hurricane Fran on understory seedling and sapling growth

I found significant but varied seedling and sapling releases across the damaged understories after the hurricane. Relative growth rates of both seedlings and saplings increased significantly (Figure 4.7 and Figure 4.14). In contrast to pre-hurricane growth patterns, large rooted stems had higher relative growth rates than small stems. The 5-year average growth comparison showed that post-hurricane large seedlings and saplings experienced significantly higher vertical growth (about double growth) than prior to the hurricane.

Post-hurricane sapling growth was higher than its pre-hurricane level. Prior to Hurricane Fran, saplings grew at very slow rates. 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 first or second year, suggesting small-scale multiple release.

The hurricane resulted in an increased rate of relative height growth for seedlings. On average, the seedling growth rates in the pine stands increased about 12%, and about 30% in the hardwood forests. The largest height increase was generally in 1998, the second growing season after the hurricane. Both forest types have shown evidence of seedling release. However, increased growth rates were not sustained, and they tended to decline within four or five years, presumably due to the transient nature of availability of resources. As tree biomass is reestablished at a site, the relative availability resources (water, soil nutrient and particularly light) declines.

One major effect of the canopy disturbance by Hurricane Fran was that it altered the negative correlation between growth in sequential years previously observed in the undamaged seedling transects. Previous work by Philippi et al. (1992, 1993) showed that prior to the hurricane, the established tree seedlings exhibited low relative growth forests and that there was a negative correlation reflecting the inability of a seedling to be one of the better performers in sequential years. However after the hurricane, the large established seedlings, because they had well-established roots and benefited from increased light and nutrient availability, grow faster than the small seedlings. The yearly variation in growth increased after the hurricane and there was a gradual decrease after the peaks at the second years (Figures 4.7 and 4.14).

I found a mixed relationship between light intensity and seedling growth rates after the hurricane at the sub-transect scale (i.e., 4*4 m sub-plot for saplings and 1*2 m sub-plot for seedlings, see Figure 4.8). The growth rates were weakly correlated with light intensity, but the relationship was not significant. The relationship between seedling growth and canopy

openness was negative in the two loblolly pine stands whereas it was positive in one of the hardwood stands.

Hurricane influence on understory tree species composition

Figures 4.15 and 4.16 show the successional trajectory in composition of saplings and seedlings over the 10-year observation period in ordination space (i.e., 5 years prior to Hurricane Fran and 5 years after). For the saplings, NMDS indicated that composition of saplings in the forest stands was changing greatly among the forest types and sites. There was no clear division of forest types. For understory seedlings, the NMDS analysis showed that although post-Fran changes were often conspicuous, each of the understories in four forest stands had a distinctive tree species composition prior to the hurricane, and the composition of seedlings remained distinctive after the hurricane.

The hurricane temporally increased the relative abundance of light-demanding pioneer species in the forest understory. However, eventually these species may be lost from the stand through competition. Some light-demanding tree species (e.g., tuliptree, sweetgum) show increased ingrowth. However, some recruits appeared to be a temporary phenomenon. Hurricane Fran led to an increase in shade intolerant species. These 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 five 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.

As mention above, the seedling data did not include flowering dogwood (*Cornus florida*) due to difficulty in distinguishing individual dogwood seedlings. Dogwood was one of the species most damaged during the hurricane, but its long-term fate remains unclear.

DISCUSSION

The effects of canopy disturbance on mortality of seedlings and saplings

The data presented here show that understory damage and mortality were variable among forest types. Moreover, in the heavily disturbed forests 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 seedling and sapling mortality in disturbed forests (e.g., Walker 2000, Battaglia et al. 2000), canopy damage by winds increased mortality of both seedling and saplings in the first two years after the hurricane. In the Duke Forest, mortality of saplings of many species remained high five years after the canopy disturbance, but so did relative growth rate, perhaps more than compensating and leading to an over increase in potential contribution to future canopy composition. I conclude 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 can potentially affect the future structure and dynamics of the damaged forests.

Canopy damage-induced change in understory diversity

Results from this study partially support observations from other hurricane damage studies showing that major canopy damage can increase understory tree species diversity. The census seedling and sapling plots experienced an immediate drop in seedling density and

species richness due to high mortality in established seedlings and limited recruitment in the first post-disturbance growing season. This was followed by a rapid rebound in stem density and more gradual recovery and enhancement in species richness and diversity. While major canopy disturbance resulted in reduced seedling density and species richness immediately after disturbance, this was reversed by subsequent enhanced recruitment of tree seedlings and sprouting from existing damaged but living trees. Other biotic and environmental factors, such as masting events and drought stress could also greatly alter seedling mortality and recruitment, although the various effects were difficult to separate.

Effects of hurricane damage on seedling and sapling recruitment

In this study, Hurricane Fran decreased overall recruitment of seedlings of the predominant species in my survey plots but increased sapling recruitment. Heavy-seeded, late successional species such as *Quercus spp.* and *Carya spp.* experienced both a low recruitment rate, and lower mortality in response to the windstorm damage, but in total were little affected by the windstorm. In contrast, widespread light-seed tree species such as *Acer rubrum*, *Cercis canadensis*, *Fraxinus spp.*, *Liriodendron tulipifera* and *Ulmus spp.* were more negatively impacted.

Effects of hurricane damage on seedling and sapling growth rates

It has long been recognized that growth rates of understory plants may increase after disturbance due to increased resource availability. However, subtle year-to-year variation in growth has received little attention. In this study, I found large gaps created by Hurricane Fran resulted in release of both established seedlings and saplings with higher growth of large-size seedlings and sapling of plants. I also noted possible multiple releases in several seedling transects where seedlings exhibited multiple growth peaks. Canopy damage

increased the overall understory growth rate by a factor of 2, and the increased rates tended to consistently decrease toward baseline levels over time. I failed to find a clear relationship between annual growth and light intensity, perhaps because soil resources tend to be more limiting than light in Piedmont forests.

The regenerative capacity of Piedmont forests as represented by the Duke Forest is limited. This study of recently 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, despite reduced seedling density in the first year.

Importance of understory dynamics in Piedmont forests

The understory plants a major part in Piedmont forest response to canopy disturbance by windstorms. The success of hurricane-induced tree seedlings establishment and growth into understory layer, and then growth from the sapling layer into the midstory layer following major canopy disturbances, is crucial for forest regeneration, especially when natural seedling regeneration is limited. In some cases the shade-intolerant seedlings and 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. Establishment of new tree seedlings is particularly important for forest structure and dynamics. In addition, the growth response of established seedling following disturbance can be a critical factor contributing to forest dynamics.

There is an increasing body of literature that supports the hypothesis that wind damage contributes significantly to tree species diversity (e.g. Peet and Christensen 1987,

Beckage et al. 2001). 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., Battaglia et al. 2000, Dalling 2002). However, I did not find significant evidence to support the Connell's intermediate hypothesis in that I failed to find a consistent relation across the entire seedling and sapling transect dataset. Instead, this study suggested that a major canopy disturbance may not necessarily lead to an increase in species diversity. Thus, the understory changes must be viewed in the context of variation in species composition resulting from differences in habitat and stand history. The hypothesis that large canopy disturbances increase species diversity was generally supported by my study of the understory seedling layer. 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.

By providing a pool of species and functioning as the selective filter on establishment of canopy trees, the understory seedling layer has a profound influence on the composition, diversity, and dynamics the forests (Swaine 1996). Changes in seedling dynamics and diversity following a large disturbance provide an indication of the direction that forest succession will take and the potential importance of wind disturbance for the regeneration of potential canopy species (DeCoster 1996). Responses of seedlings (both mortality and

recruitment) to major canopy disturbances were loosely species-specific. Overall, the detailed combination of pre- and post-hurricane understory data has provided an exceptional opportunity to understand the establishment and growth patterns, and for understanding dynamics of forest recovery of temperate forests.

CONCLUSIONS

Seedling and sapling regeneration following large canopy disturbance provides an indication as to the direction that forest succession will take and the potential importance of wind disturbance for the regeneration of canopy species (DeCoster 1996). Analyses of long-term understory seedling and sapling data from mapped permanent plots across an interval lasting from 5 years prior to Hurricane Fran to 5 years after the hurricane clarifies some aspects of such disturbance effects.

The study shows that understory seedling and 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 subtle and 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 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 seedling density and diversity. Consequently, the mortality of understory saplings after the storm was generally higher,

while the mortality of seedlings was not necessarily higher than pre-hurricane due to high background seedling mortality.

Change in seedling density and richness over time is highly variable and therefore is less predictable. Previous studies on seedling regeneration have shown fluctuations in seedling density over time without large-scale disturbances. My research on hurricane damage and forest dynamics in Piedmont forests, like similar research elsewhere (Veblen et al. 1997, Putz and Sharitz 1991), suggests that early successional pine trees are characterized by high mortality and low recruitment, even in significantly damaged stands, suggesting a trend toward accelerated loss of pines.

In the small tree gaps of Piedmont forests, seedling recruitment is limited and thus the large canopy disturbances may be critical for the maintenance of early successional and more shade-intolerant species. My results of post-disturbance patterns of seedlings varied among forest types, but even under large-scale canopy disturbances seedling recruitment is low. Nonetheless, the hurricane helped, in some heavily damaged stands to maintain species diversity, but the role is more limited than anticipated.

In addition to theoretical implications for forest regeneration and dynamics, the findings from this study may have implications for post-hurricane, even-aged pine and mixed-aged hardwood forest management and species diversity conservation. Moreover, even after a large hurricane disturbance like Fran, seedling regeneration of oaks and hickories is still limited. Therefore, forestry practices are needed in the Piedmont for the purpose of conservation of traditional late successional oak-hickory forests.

LITERATURE CITED

- Abe, S., T. Masaki, and T. Nakashizuka. 1995. Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. *Vegetatio* 120:21-31.
- Aguilera, M. O. and W. K. Lauenroth. 1993. Seedling establishment in adult neighborhoods: intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. *Journal of Ecology* 81:253-261.
- Aguilera, M. O. and W. K. Lauenroth. 1995. Influence of gap disturbances and types of microsites on seedling establishment in *Bouteloua-gracilis*. *Journal of Ecology* 83:87-97.
- Ashton, P. M. S., C. V. S. Gunatilleke, and I. Gunatilleke. 1995. Seedling survival and growth of 4 *Shorea* species in a Sri-Lankan rain-forest. *Journal of Tropical Ecology* 11:263-279.
- Bassow, S. L., K. D. M. McConnaughay, and F. A. Bazzaz. 1994. The response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecological applications* 4:593-603.
- Battaglia, L. L., S. A. Fore, and R. R. Sharitz. 2000. Seedling emergence, survival and size in relation to light and water availability in two bottomland hardwood species. *Journal of Ecology* 88:1041-1050.
- Battaglia, L. L., R. R. Sharitz, and P. R. Minchin. 1999. Patterns of seedling and overstory composition along a gradient of hurricane disturbance in an old-growth bottomland hardwood community. *Canadian Journal of Forest Research* 29:144-156.
- Beckage, B. and J. S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* 84:1849-1861.
- Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research* 30:1617-1631.
- Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1995. Competition vs facilitation of tree seedling growth and survival in early successional communities. *Ecology* 76:1156-1168.
- Bourdeau, P. F. 1954. Oak seedling ecology determining segregation of species in piedmont oak-hickory forest. *Ecological Monographs* 24:297-320.
- Bourdeau, P. F. 1954. Oak seedling ecology determining segregation of species in piedmont oak-hickory forests. *Ecological Monographs* 24:297-320.
- Burton, P. J. and F. A. Bazzaz. 1991. Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. *American Journal of*

- Botany **78**:131-149.
- Cain, M. D. and J. P. Barnett. 1996. An 8-year field comparison of naturally seeded to planted container *Pinus taeda*, with and without release. Canadian Journal of Forest Research **26**:1237-1247.
- Canham, C. D., A. R. Berkowitz, V. R. Kelly, G. M. Lovett, S. V. Ollinger, and J. Schnurr. 1996. Biomass allocation and multiple resource limitation in tree seedlings. Canadian Journal of Forest Research **26**:1521-1530.
- Canham, C. D., J. B. Mcaninch, and D. M. Wood. 1994. Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. Canadian Journal of Forest Research **24**:817-825.
- Catovsky, S. and F. A. Bazzaz. 2000. The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. Journal of Ecology **88**:100-112.
- Catovsky, S. and F. A. Bazzaz. 2002. Feedbacks between canopy composition and seedling regeneration in mixed conifer broad-leaved forests. Oikos **98**:403-420.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. Hillerislambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology **80**:1475-1494.
- Connell, J. H. and P. T. Green. 2000. Seedling dynamics over thirty-two years in a tropical rain forest tree. Ecology **81**:568-584.
- Dalling, J. W. and S. P. Hubbell. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. Journal of Ecology **90**:557-568.
- Dalling, J. W., S. P. Hubbell, and K. Silvera. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. Journal of Ecology **86**:674-689.
- Dalling, J. W., C. E. Lovelock, and S. P. Hubbell. 1999. Growth responses of seedlings of two neotropical pioneer species to simulated forest gap environments. Journal of Tropical Ecology **15**:827-839.
- Desteven, D. 1988. Light gaps and long-term seedling performance of a neotropical canopy tree (*Dipteryx panamensis*, Leguminosae). Journal of Tropical Ecology **4**:407-411.
- Desteven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession - seedling emergence. Ecology **72**:1066-1075.
- Desteven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession - seedling survival and growth. Ecology **72**:1076-1088.
- Desteven, D. 1994. Tropical tree seedling dynamics - recruitment patterns and their

- population consequences for 3 canopy species in Panama. *Journal of Tropical Ecology* **10**:369-383.
- Ellison, A. M., J. S. Denslow, B. A. Loiselle, and M. D. Brenes. 1993. Seed and seedling ecology of Neotropical Melastomataceae. *Ecology* **74**:1733-1749.
- Ellison, A. M. and E. J. Farnsworth. 1993. Seedling survivorship, growth, and response to disturbance in Belizean mangal. *American Journal of Botany* **80**:1137-1145.
- Fetcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of 2 species of tropical trees. *Oecologia* **58**:314-319.
- Finzi, A. C. and C. D. Canham. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. *Forest Ecology and Management* **131**:153-165.
- George, L. O. and F. A. Bazzaz. 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* **80**:833-845.
- George, L. O. and F. A. Bazzaz. 1999. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology* **80**:846-856.
- Gray, A. N. and T. A. Spies. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *Journal of Ecology* **84**:635-645.
- Guariguata, M. R. 1998. Response of forest tree saplings to experimental mechanical damage in lowland Panama. *Forest Ecology and Management* **102**:103-111.
- Gunatilleke, C. V. S., I. Gunatilleke, P. M. S. Ashton, and P. S. Ashton. 1998. Seedling growth of *Shorea* (Dipterocarpaceae) across an elevation range in southwest Sri Lanka. *Journal of Tropical Ecology* **14**:231-245.
- Gunatilleke, I. A., P. M. S. Ashton, C. V. S. Gunatilleke, and P. S. Ashton. 1996. An overview of seed and seedling ecology of *Shorea* (section *Doona*) Dipterocarpaceae. Page 81-102 in I. M. Turner, C. H. Diong, S. S. L. Lim, and P. K. L. Ng, editors. *Biodiversity and the Dynamics of Ecosystems*, Kyoto, Japan.
- Guzman-Grajales, S. M. and L. R. Walker. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23**:407-413.
- Harmon, M. E. and J. F. Franklin. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* **70**:48-59.
- Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493-495.

- Horn, J. C. 1985. Responses of understory tree seedlings to trenching. *American Midland Naturalist* **114**:252-258.
- Huenneke, L. F. and R. R. Sharitz. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. *American Midland Naturalist* **115**:328-335.
- Jones, R. H., B. P. Allen, and R. R. Sharitz. 1997. Why do early-emerging tree seedlings have survival advantages? a test using *Acer rubrum* (Aceraceae). *American Journal of Botany* **84**:1714-1718.
- Jones, R. H. and R. R. Sharitz. 1998. Survival and growth of woody plant seedlings in the understorey of floodplain forests in South Carolina. *Journal of Ecology* **86**:574-587.
- Jones, R. H., R. R. Sharitz, and K. W. McLeod. 1989. Effects of flooding and root competition on growth of shaded bottomland hardwood seedlings. *American Midland Naturalist* **121**:165-175.
- Kitajima, K. and D. Tilman. 1996. Seed banks and seedling establishment on an experimental productivity gradient. *Oikos* **76**:381-391.
- Kneeshaw, D. D. and Y. Bergeron. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. *Ecoscience* **6**:214-222.
- Lambers, J. H. R. and J. S. Clark. 2003. Effects of dispersal, shrubs, and density dependent mortality on seed and seedling distributions in temperate forests. *Canadian Journal of Forest Research* **33**:783-795.
- Lavine, M., B. Beckage, and J. S. Clark. 2002. Statistical modeling of seedling mortality. *Journal of agricultural Biological and Environmental Statistics* **7**:21-41.
- Lorimer, C. G., J. W. Chapman, and W. D. Lambert. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* **82**:227-237.
- McDonald, R.I., R.K. Peet, and D.L. Urban. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea* **67**:84-95.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2003. Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a piedmont forest. *Journal of Vegetation Science* **14**:441-450.
- Meiners, S. J., S. T. A. Pickett, and S. N. Handel. 2002. Probability of tree seedling establishment changes across a forest-old field edge gradient. *American Journal of Botany* **89**:466-471.
- Oosting, H. J., P. J. Kramer, and C. F. Korstian. 1952. Survival of pine and hardwood

- seedlings in forest and open. *Ecology* **33**:427-430.
- Pacala, S. W., C. D. Canham, J. A. Silander, and R. K. Kobe. 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* **24**:2172-2183.
- Palik, B. J., R. J. Mitchell, G. Houseal, and N. Pederson. 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. *Canadian Journal of Forest Research* **27**:1458-1464.
- Peroni, P. A. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. *American Journal of Botany* **81**:1428-1434.
- Peroni, P. A. 1995. Field and laboratory investigations of seed dormancy in red maple (*Acer rubrum*) from the North Carolina piedmont. *Forest Science* **41**:378-386.
- Philippi, T. E., R. K. Peet, and N. L. Christensen. 1992. Survivorship and growth of *Acer rubrum* seedlings in stands representing different successional stages from old-field *Pinus taeda* to mature mixed hardwoods. *Bulletin of the Ecological Society of America* **73(Suppl.)**:304-305.
- Philippi, T. E., R. K. Peet, and N. L. Christensen. 1993. Tree seedling demography in old-field *Pinus taeda* and mature mixed hardwoods stands in a piedmont forest. *Bulletin of the Ecological Society of America* **74(Suppl.)**:393.
- Pickett, S. T. A. and M. J. McDonnell. 1987. Seed bank dynamics in temperate deciduous forest. *American Journal of Botany* **74**:637-638.
- Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* **64**:1069-1074.
- Runkle, J. R., G. H. Stewart, and T. T. Veblen. 1995. Sapling diameter growth in gaps for two *Nothofagus* species in New Zealand. *Ecology* **76**:2107-2117.
- Setterfield, S. A. 2002. Seedling establishment in an Australian tropical savanna: effects of seed supply, soil disturbance and fire. *Journal of applied Ecology* **39**:949-959.
- Shelton, M. G. and M. D. Cain. 1996. Distinguishing features of loblolly and shortleaf pine seeds: implications for monitoring seed production in mixed stands. *Canadian Journal of Forest Research* **26**:2056-2059.
- Shelton, M. G. and M. D. Cain. 2002. Recovery of 1-year-old loblolly pine seedlings from simulated browse damage. *Canadian Journal of Forest Research* **32**:373-377.
- Shibata, M. and T. Nakashizuka. 1995. Seed and seedling demography of 4 co-occurring *Carpinus* species in a temperate deciduous forest. *Ecology* **76**:1099-1108.

- Silvertown, J. and J. M. Bullock. 2003. Do seedlings in gaps interact? A field test of assumptions in ESS seed size models. *Oikos* **101**:499-504.
- Streng, D. R., J. S. Glitzenstein, and P. A. Harcombe. 1989. Woody seedling dynamics in an east Texas floodplain forest. *Ecological Monographs* **59**:177-204.
- Taverna, K., R.K. Peet and L. Phillips. 2005. Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. *Journal of Ecology* **93**:202-213.
- Valverde, T. and J. Silvertown. 1995. Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment. *Functional Ecology* **9**:942-950.
- Walker, L. R. 2000. Seedling and sapling dynamics of treefall pits in Puerto Rico. *Biotropica* **32**:262-275.
- Walker, L. R. and L. E. Neris. 1993. Posthurricane seed rain dynamics in Puerto Rico. *Biotropica* **25**:408-418.
- Webb, C. O. and D. R. Peart. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* **88**:464-478.
- Welden, C. W., S. W. Hewett, S. P. Hubbell, and R. B. Foster. 1991. Sapling survival, growth, and recruitment - relationship to canopy height in a neotropical forest. *Ecology* **72**:35-50.
- Whitmore, T. C. 1998. Potential impact of climatic change on tropical rain forest seedlings and forest regeneration. *Climatic Change* **39**:429-438.
- Wright, E. F., C. D. Canham, and K. D. Coates. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Canadian Journal of Forest Research* **30**:1571-1580

Table 4.1. The characteristics of the 13 selected seedling and 13 sapling transects in the Duke Forest, North Carolina, USA. The number in the first column is for seedlings, and the second column (parenthesis) is for the sapling's information.

Forest type	Stand name	Number of transects	Transect size	Survey period
<u>Loblolly pine stands</u>				
	Graveyard plot	4 (4)	50*1 m (50*4 m)	1978-2001 (1989-2001)
	Land's end plot	3 (3)	50*1 m (50*4 m)	1978-2001 (1989-2001)
<u>Mixed-aged hardwoods</u>				
	Bormann plot	3 (3)	50*1 m (50*4 m)	1978-2001 (1989-2001)
	Rocky plot	3 (3)	50*1 m (50*4 m)	1978-2001 (1989-2001)
Total		13 (13)	650 m ² (2600 m ²)	

Table 4.2. Seedling and sapling sampling size for 13 selected major taxa in the two loblolly pine plots (Graveyard and Land' send) and the two mixed-aged hardwood stands (Bormann and Rocky) in the Duke Forest, North Carolina, USA. The number in the first column is for seedlings, and the second column (parenthesis) is for the sapling's information. The total sample area in the Graveyard plot is 200 m² for seedlings and 800 m² for saplings. And total sample area in other three plots (Land' end, Bormann, and Rocky) is 150 m² for seedlings and 600 m² for saplings.

Species	Code	Family	Seedling (sapling) sampling sizes in 2001			
			Graveyard	Land' end	Bormann	Rocky
<i>Acer rubrum</i>	ACRU	Aceraceae	1579(97)	450(41)	442(101)	72(24)
<i>Carpinus caroliniana</i>	CACR	Betulaceae	89(42)	2(0)	0(0)	2(0)
<i>Carya spp.</i>	CARY	Juglandaceae	68(17)	65(40)	61(26)	104(68)
<i>Cercis canadensis</i>	CECA	Fabaceae	10(1)	370(27)	0(0)	205(13)
<i>Fraxinus spp.</i>	FRAX	Oleaceae	4(2)	27(21)	2(1)	47(46)
<i>Liquidambar styraciflua</i>	LIST	Hamamelidaceae	27(5)	0(2)	0(1)	0(0)
<i>Liriodendron tulipifera</i>	LITU	Magnoliaceae	9(0)	21(0)	4(7)	0(0)
<i>Nyssa sylvatica</i>	NYSY	Nyssaceae	1(0)	3(2)	5(3)	2(1)
<i>Ostrya virginiana</i>	OSVI	Betulaceae	198(132)	98(67)	0(0)	2(1)
<i>Pinus spp.</i>	PINU	Pinaceae	936(1)	7(0)	0(0)	2(0)
<i>Prunus serotina</i>	PRSE	Rosaceae	57(19)	12(12)	19(4)	18(14)
<i>Quercus alba</i>	QUAL	Fagaceae	13(6)	5(10)	265(0)	23(7)
<i>Quercus red group</i>	QURG	Fagaceae	22(3)	33(0)	40(4)	13(6)
<i>Ulmus spp</i>	ULMU	Ulmaceae	23(1)	32(4)	0(1)	7(1)
Others			73(266)	57(375)	45(123)	42(140)
Total			3127(592)	1182(601)	883(271)	539(321)

Table 4.3. Changes in seedling population of major species over 11 years in a loblolly pine stand (Graveyard plot) in the Duke Forest, North Carolina, USA. The density values used are the means of four seedling transects of the forest stand. Note no data available for 1995 and 1996.

Species	STC*	Stems/50m ²									
		1990	1991	1992	1993	1994	1997	1998	1999	2000	2001
<i>Acer rubrum</i>	II	424.0	489.3	461.3	726.8	397.3	174.5	455.5	369.0	335.8	399.3
<i>Carpinus caroliniana</i>	I	39.5	26.8	19.8	45.5	24.3	20.3	18.5	17.5	18.3	22.3
<i>Carya spp.</i>	III	11.3	12.5	13.8	13.8	13.5	9.8	16.0	15.0	14.0	17.0
<i>Cercis canadensis</i>	II	3.8	5.0	4.0	5.3	5.3	1.5	3.0	4.3	4.3	2.5
<i>Liquidambar styraciflua</i>	IV	1.0	1.3	1.3	1.3	1.3	1.0	1.8	4.5	7.3	6.8
<i>Liriodendron tulipifera</i>	IV	1.0	1.0	1.0	1.0	0.8	2.3	5.0	1.8	1.3	2.3
<i>Ostrya virginiana</i>	II	80.0	73.3	64.8	169.5	104.0	59.3	72.5	57.3	57.8	49.5
<i>Pinus spp.</i>	IV	67.5	2.0	301.8	107.3	35.0	5.0	10.0	3.0	15.8	234.0
<i>Prunus serotina</i>	IV	17.0	17.8	14.5	14.8	13.0	11.0	13.5	14.3	12.3	14.3
<i>Quercus alba</i>	III	2.5	2.5	2.5	2.5	2.5	2.3	2.5	3.3	3.0	3.3
<i>Quercus red group</i>	III	10.3	9.8	9.5	9.3	8.3	6.3	6.0	6.0	6.0	5.5
<i>Ulmus spp.</i>	II	3.5	3.5	3.8	4.8	4.8	4.3	5.0	8.0	7.0	5.8
All species		673.8	650.5	902.5	1118.8	620.3	304.3	621.8	518.5	500.8	781.8

* Shade Tolerant Class: I-Very Tolerant; II-Tolerant; III-Intermediate; IV-Intolerant.

Table 4.4. Changes in seedling population of major species over 11 years in a loblolly pine plot (Land's end plot) in the Duke Forest, North Carolina, USA. The density values used are the means of three seedling transects of the forest stand. Note no data available for 1995 and 1996.

Species	STC*	Stems/50m ²										
		1990	1991	1992	1993	1994	1997	1998	1999	2000	2001	
<i>Acer rubrum</i>	II	408.3	573.3	307.7	444.3	132.0	108.3	297.0	146.0	129.7	150.0	
<i>Carpinus caroliniana</i>	I	10.3	2.7	1.0	0.7	0.7	1.7	1.3	1.3	1.0	0.7	
<i>Carya spp.</i>	III	12.7	12.7	16.7	16.3	16.0	17.0	16.3	16.0	19.3	21.7	
<i>Cercis canadensis</i>	II	274.7	232.3	278.0	196.3	93.0	83.3	261.7	207.3	173.0	123.3	
<i>Fraxinus spp.</i>	IV	7.0	6.0	9.7	10.0	8.7	8.0	7.7	7.3	10.0	9.0	
<i>Liriodendron tulipifera</i>	IV	10.3	5.0	3.3	8.3	1.7	7.3	34.3	6.0	5.0	7.0	
<i>Nyssa sylvatica</i>	IV	1.7	2.7	2.7	2.0	1.3	1.0	1.0	0.7	0.7	1.0	
<i>Ostrya virginiana</i>	II	69.0	38.3	31.7	109.0	38.7	80.7	83.7	45.0	29.0	32.7	
<i>Pinus spp.</i>	II	16.0	1.0	16.0	0.3	0.0	0.7	1.3	0.3	1.7	2.3	
<i>Prunus serotina</i>	IV	3.7	3.0	3.3	3.3	3.0	5.0	3.7	2.7	2.7	4.0	
<i>Quercus alba</i>	IV	1.3	1.7	1.7	1.3	1.7	1.7	1.7	1.7	1.7	1.7	
<i>Quercus red group</i>	III	11.7	11.7	11.7	10.7	10.3	8.7	9.3	9.0	9.7	11.0	
<i>Ulmus spp.</i>	III	7.3	6.0	6.0	7.0	6.0	19.0	14.3	11.0	9.7	10.7	
All species		851.3	914.0	691.7	821.3	323.0	349.3	743.3	470.0	418.0	394.0	

* Shade Tolerant Class: I-Very Tolerant; II-Tolerant; III-Intermediate; IV-Intolerant

Table 4.5. Changes in seedling population of major species over 11 years in a white oak plot (Bormann plot) in the Duke Forest, North Carolina, USA. The density values used are the mean of three seedling transects of the forest stand. Note no data available for 1995 and 1996.

Species	STC*	Stems/50m ²										
		1990	1991	1992	1993	1994	1997	1998	1999	2000	2001	
<i>Acer rubrum</i>	II	146.3	165.7	139.7	250.0	134.0	81.0	126.3	109.0	123.0	147.3	
<i>Carya spp.</i>	III	18.7	19.0	18.0	17.3	16.7	16.7	19.3	19.0	20.0	20.3	
<i>Fraxinus spp.</i>	IV	0.7	0.7	0.7	0.7	0.7	0.7	0.3	0.3	0.3	0.7	
<i>Liriodendron tulipifera</i>	IV	2.0	1.0	1.0	0.7	0.7	5.7	5.3	1.7	2.3	1.3	
<i>Nyssa sylvatica</i>	II	4.0	6.3	3.7	2.7	2.7	1.7	2.0	2.0	2.3	1.7	
<i>Ostrya virginiana</i>	II	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	
<i>Pinus spp.</i>	IV	0.7	0.7	0.7	1.0	0.7	0.0	0.0	0.0	0.3	0.0	
<i>Prunus serotina</i>	IV	8.3	8.3	7.3	8.7	8.7	6.3	7.7	6.7	7.0	6.3	
<i>Quercus alba</i>	III	265.0	200.3	154.3	127.7	91.3	73.3	112.3	104.3	96.0	88.3	
<i>Quercus red group</i>	III	20.3	19.3	16.0	17.0	15.7	16.0	17.0	16.3	15.0	13.3	
All species		472.7	428.7	348.7	432.7	277.7	208.3	298.3	270.7	276.7	294.3	

* Shade Tolerant Class: I-Very Tolerant; II-Tolerant; III-Intermediate; IV-Intolerant

Table 4.6. Seedling composition and population change of major species over 11 years in hardwood stand (Rocky plot) in the Duke Forest, North Carolina, USA. The density values used are the mean of three seedling transects of the forest stand. Note no data available for 1995 and 1996.

Species	STC*	Stems/50m ²										
		1990	1991	1992	1993	1994	1997	1998	1999	2000	2001	
<i>Acer rubrum</i>	II	19.0	22.7	18.3	53.3	24.0	9.7	20.3	15.7	14.7	24.0	
<i>Carpinus caroliniana</i>	I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.7	
<i>Carya spp.</i>	III	36.7	34.7	34.7	34.3	30.3	23.0	25.7	25.7	28.3	34.7	
<i>Cercis canadensis</i>	II	156.7	141.0	140.7	143.7	47.0	30.3	203.3	74.0	90.0	68.3	
<i>Fraxinus spp.</i>	IV	23.3	20.3	19.7	18.3	18.7	12.0	13.0	15.7	18.3	15.7	
<i>Liriodendron tulipifera</i>	IV	1.0	0.0	0.0	0.0	0.0	5.7	10.3	0.0	0.0	0.0	
<i>Nyssa sylvatica</i>	IV	3.0	1.0	1.3	1.3	1.0	0.3	0.7	0.0	0.3	0.7	
<i>Ostrya virginiana</i>	II	0.0	0.0	1.0	0.3	0.0	1.0	0.3	0.7	0.0	0.7	
<i>Pinus spp.</i>	II	1.3	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.3	0.7	
<i>Prunus serotina</i>	IV	6.0	7.0	4.0	3.3	3.0	2.7	1.7	2.0	2.3	6.0	
<i>Quercus alba</i>	IV	17.0	17.0	13.3	14.0	11.3	8.7	8.7	8.0	9.3	7.7	
<i>Quercus red group</i>	III	10.3	9.0	7.3	6.7	4.3	5.3	5.0	4.7	5.0	4.3	
<i>Ulmus spp.</i>	III	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.7	0.0	2.3	
All species		295.7	270.7	264.3	297.0	162.3	112.7	308.0	164.3	183.3	179.7	

* Shade Tolerant Class: I-Very Tolerant; II-Tolerant; III-Intermediate; IV-Intolerant

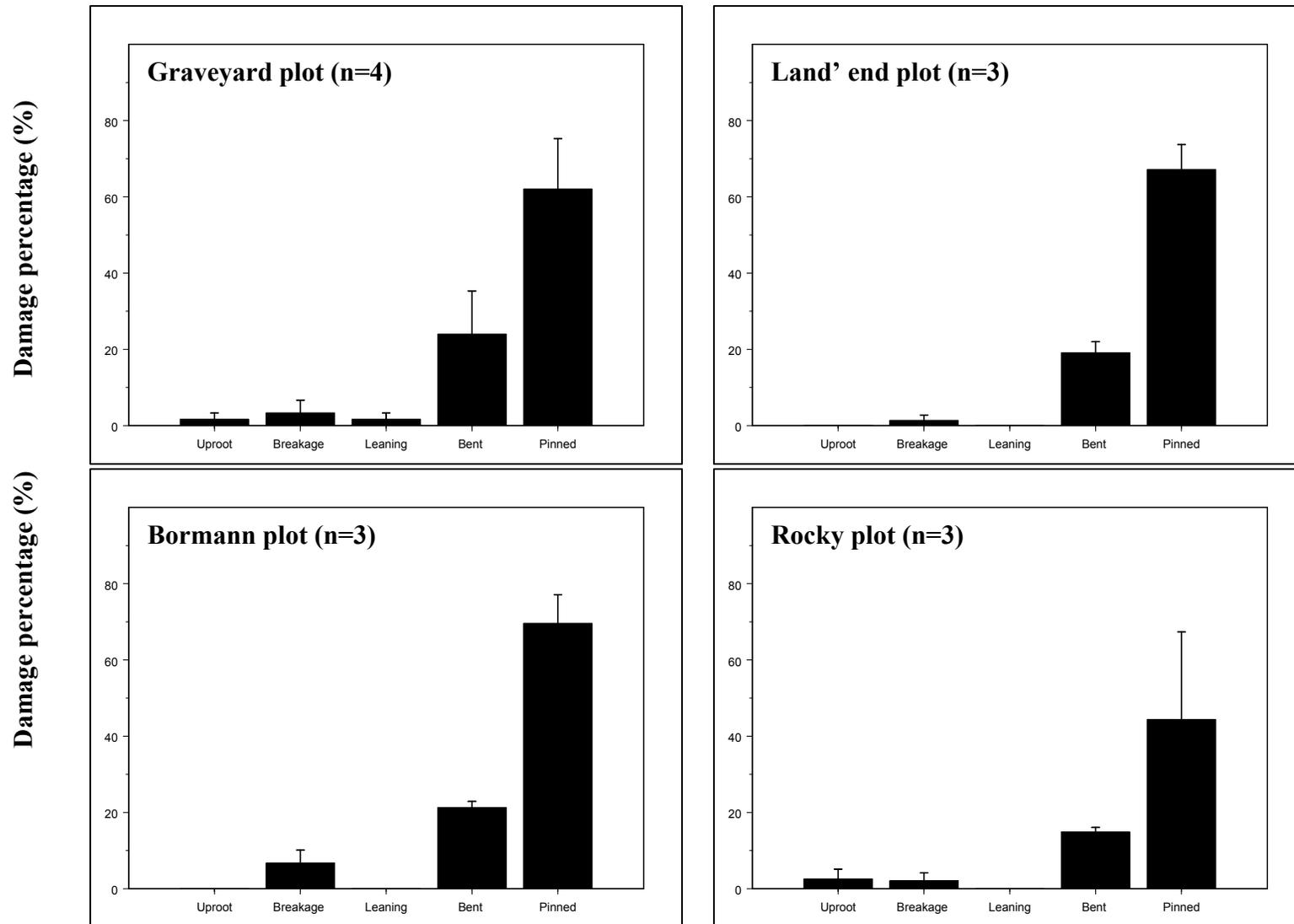


Figure 4.1. Damage types of the saplings in the four forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot ($n=4$), (b) Land's end plot ($n=3$), (c) Bormann plot ($n=3$), and (d) Rocky plot ($n=3$). The error bars are standard errors. n is the number of transects in a forest stand. Damage percentage refers the proportion of a damage type in all damaged stems.

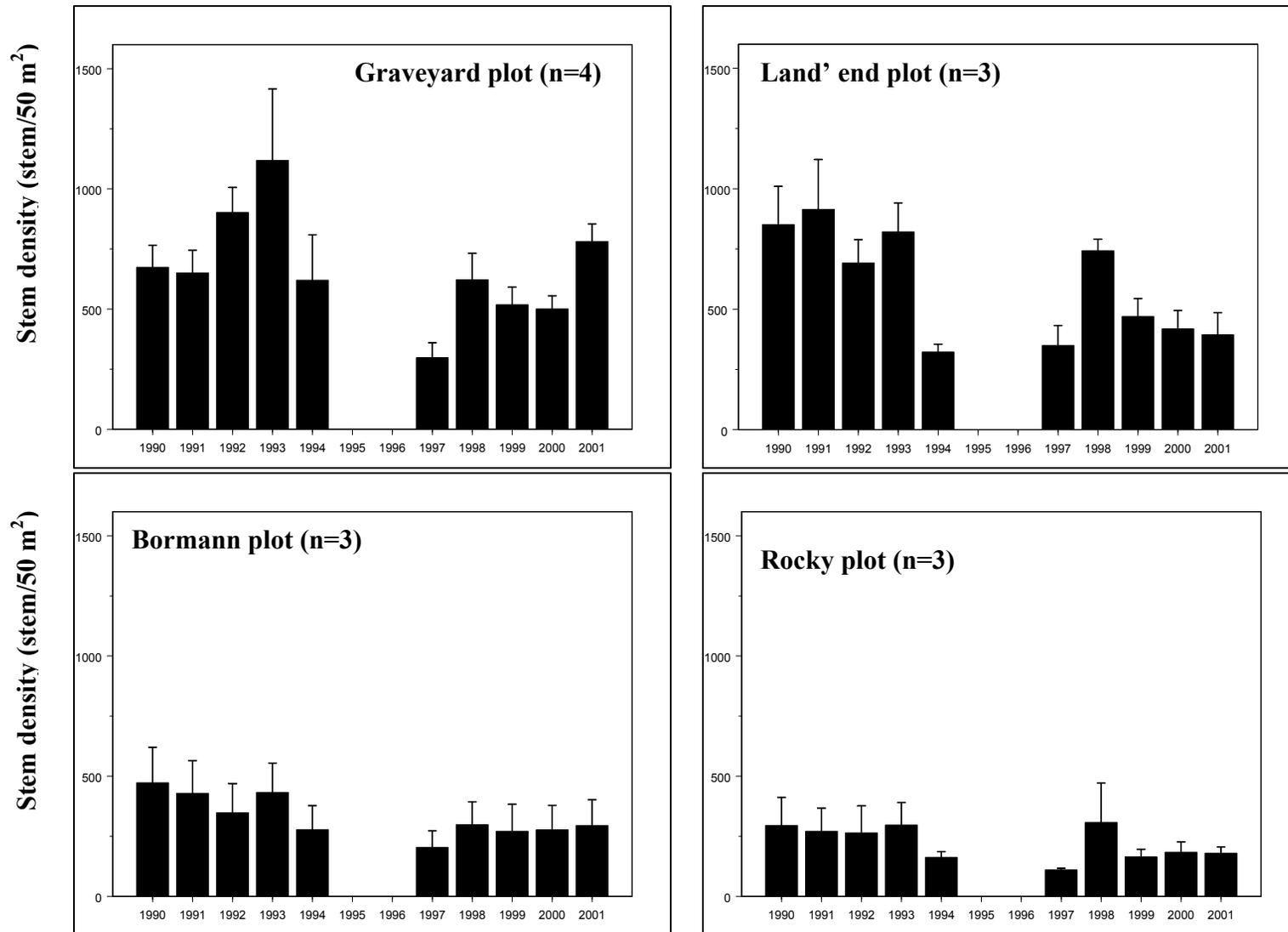


Figure 4.2. The stem density of seedlings in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. *n* is the number of transects in a forest stand.

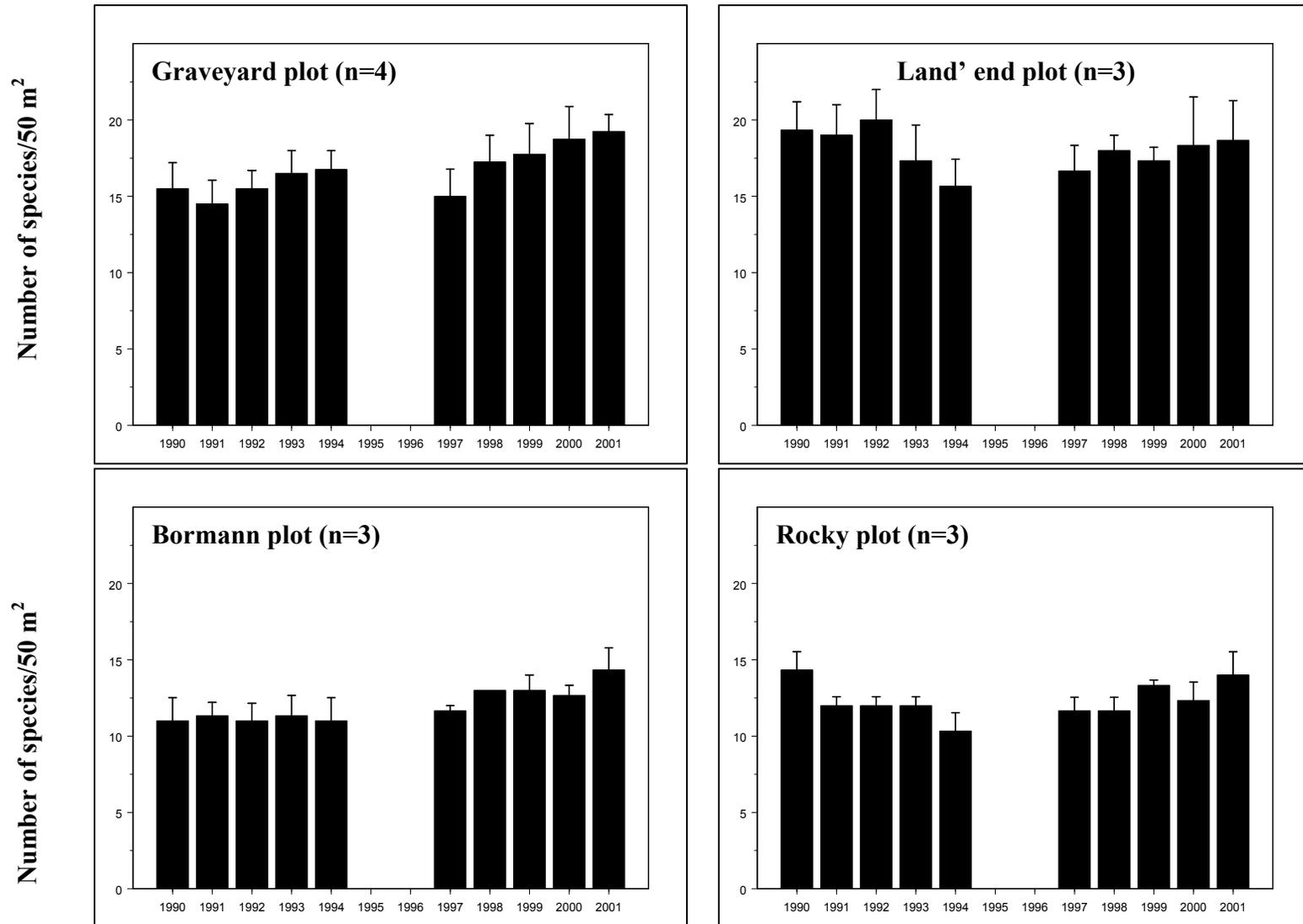


Figure 4.3. The species richness of seedlings in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. *n* is the number of transects in a forest stand.

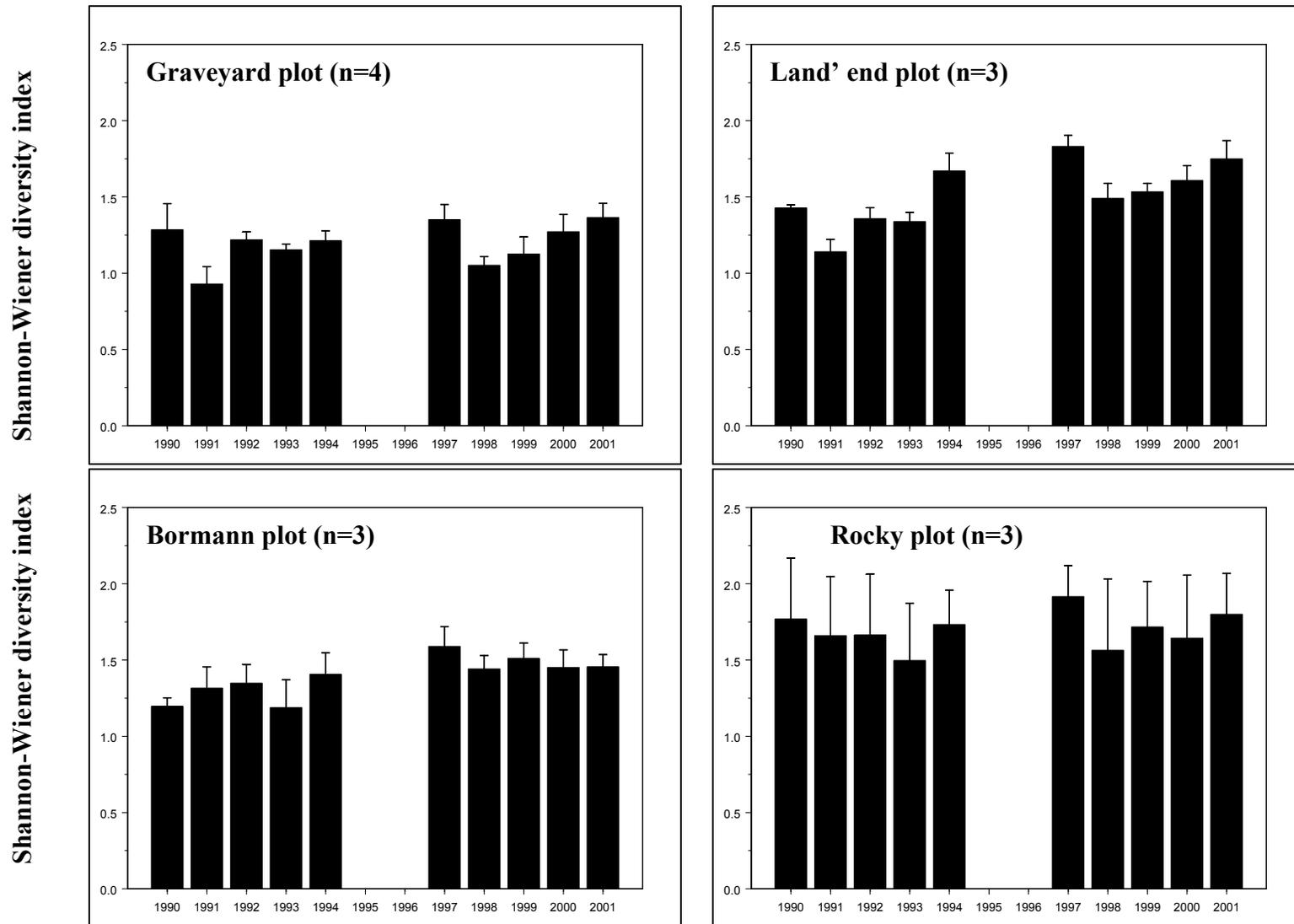


Figure 4.4. The species diversity of seedlings in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot ($n=4$), (b) Land's end plot ($n=3$), (c) Bormann plot ($n=3$), and (d) Rocky plot ($n=3$). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. n is the number of transects in a forest stand.

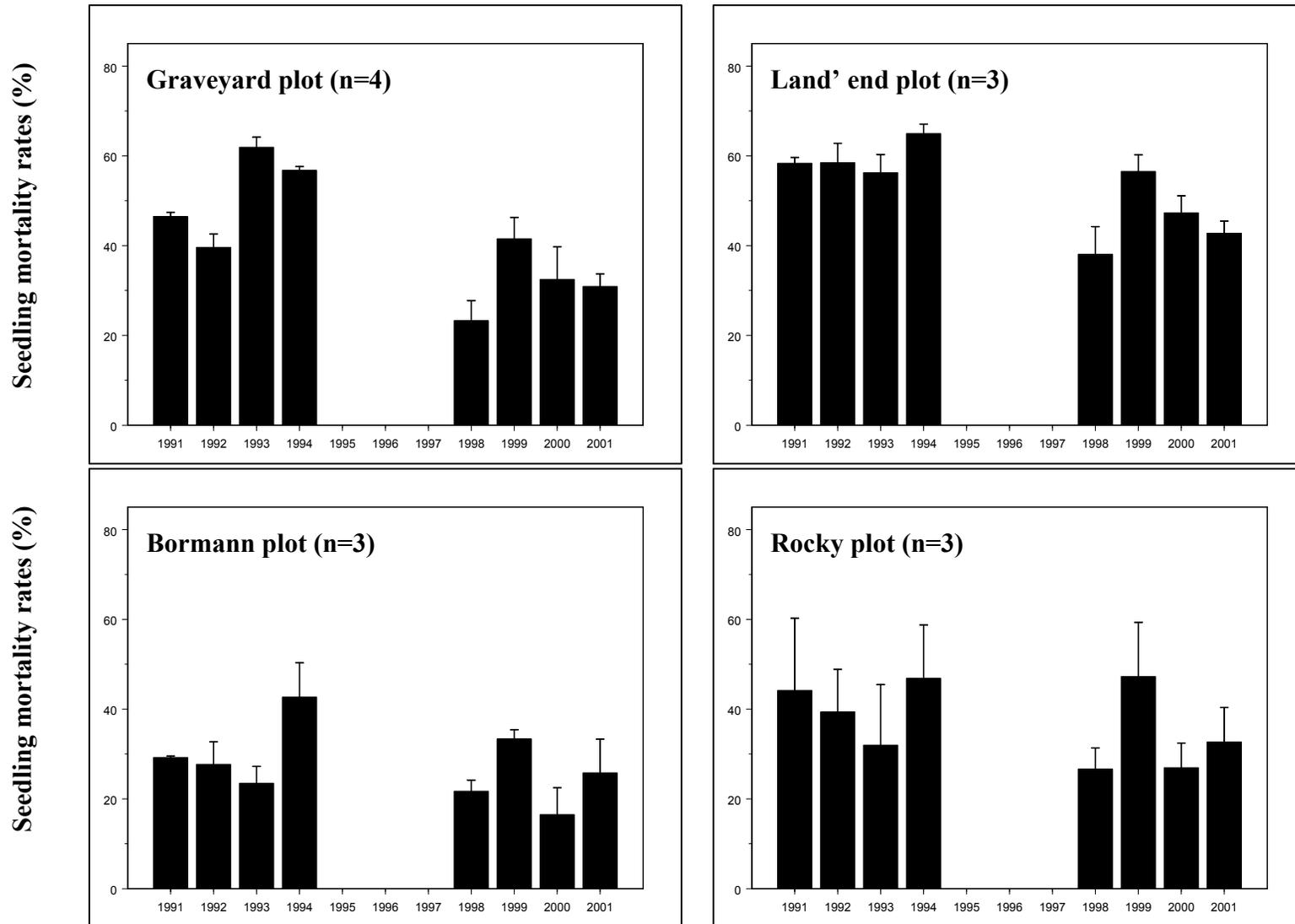


Figure 4.5. Seedling mortality rates (%) for four stands in the 4 forest stands in the Duke Forest, North Carolina, USA . (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. n is the number of transects in a forest stand.

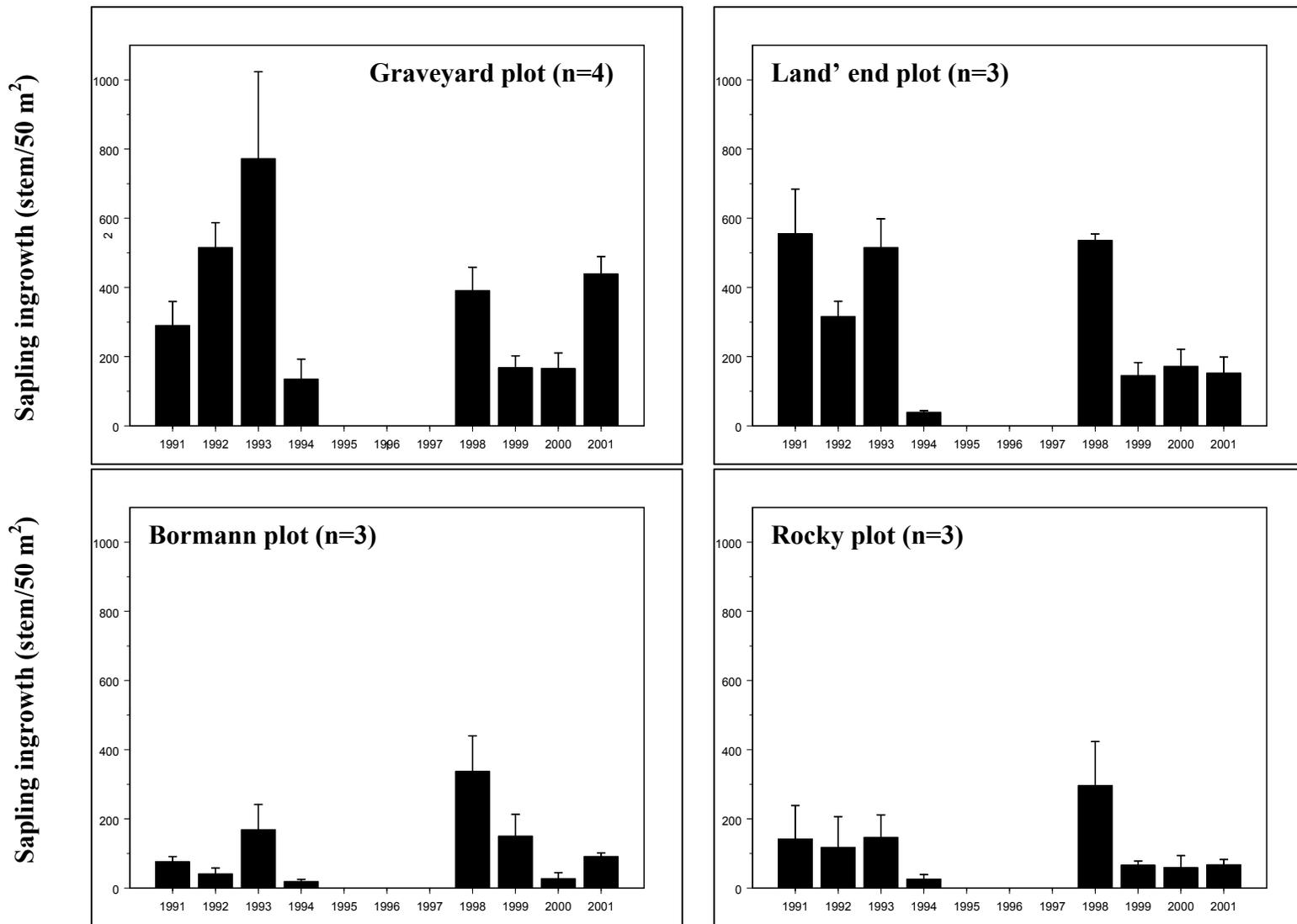


Figure 4.6. Seedling ingrowths for four stands in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. *n* is the number of transects in a forest stand.

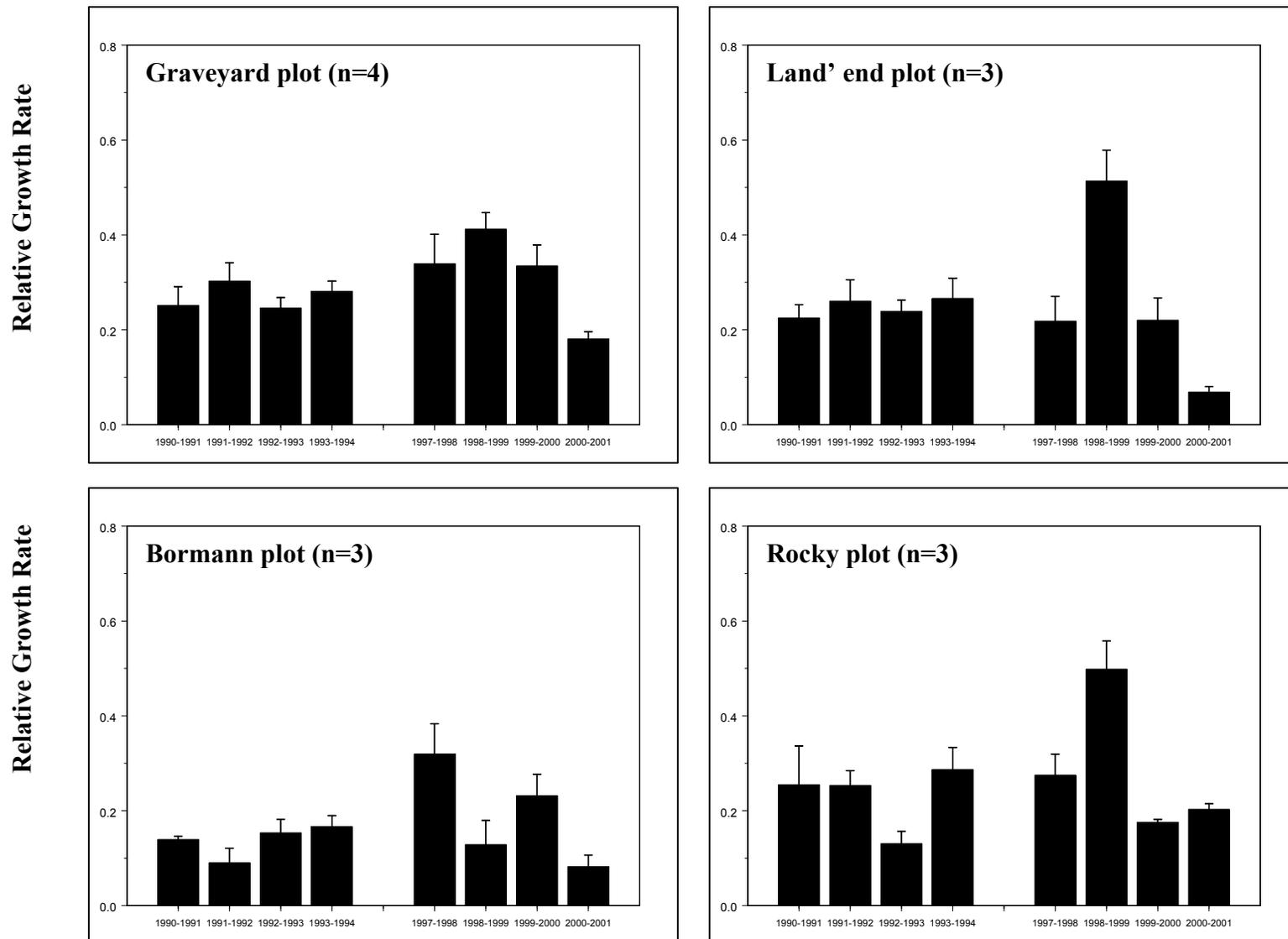
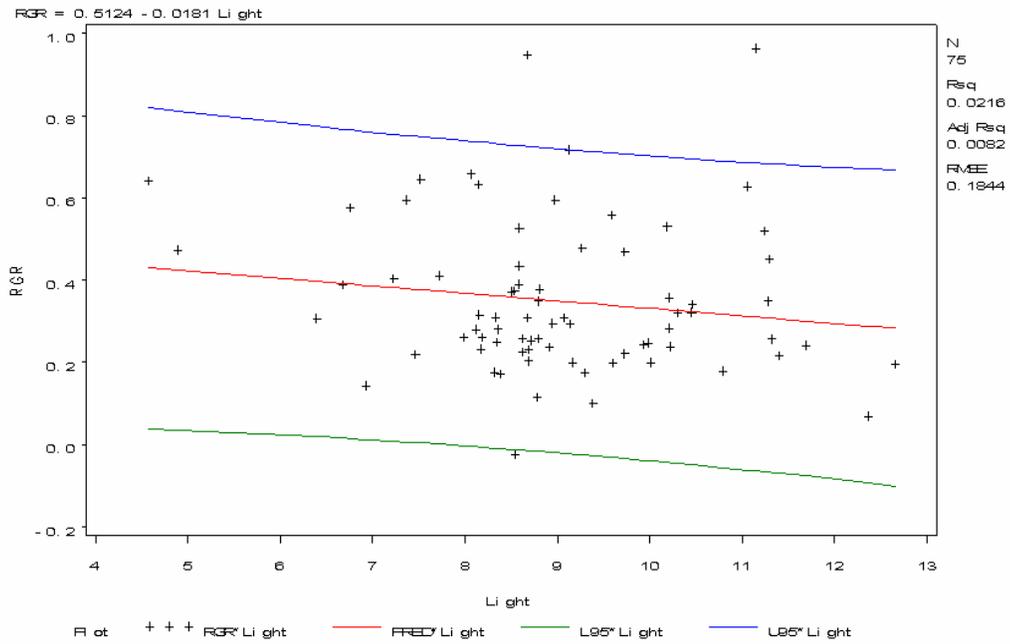
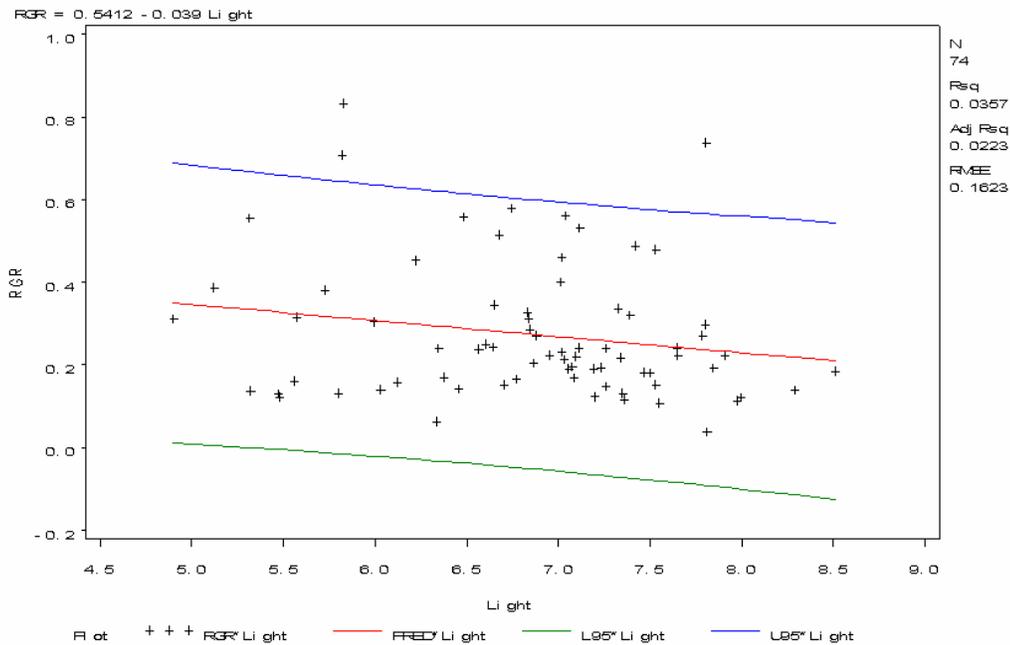


Figure 4.7. Seedling relative growth rates for four stands in the 4 forest stand in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. *n* is the number of transects in a forest stand.

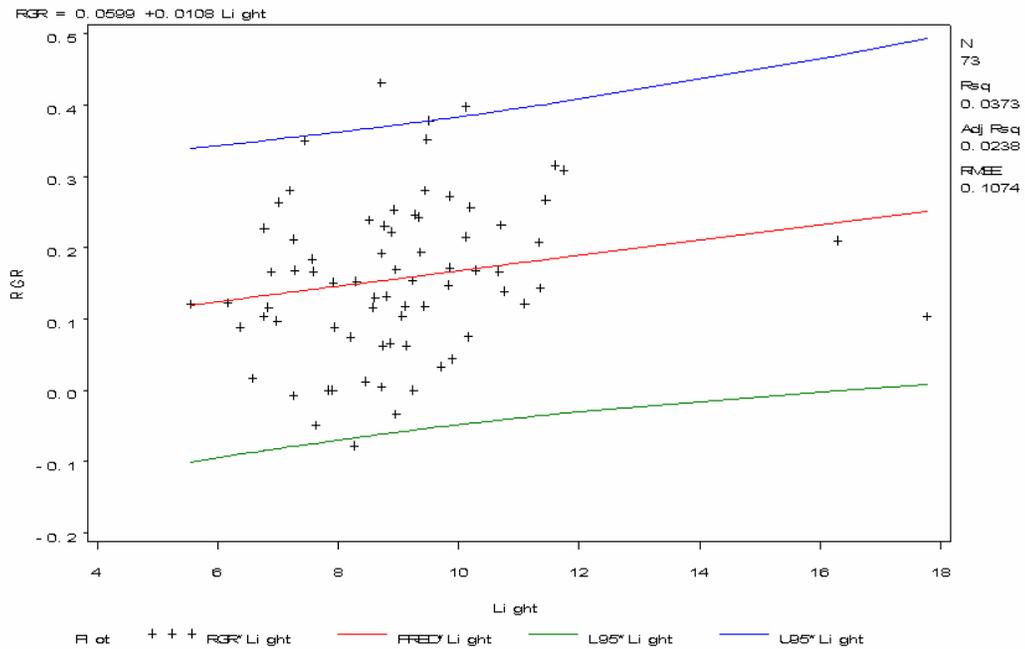


(a) Graveyard plot

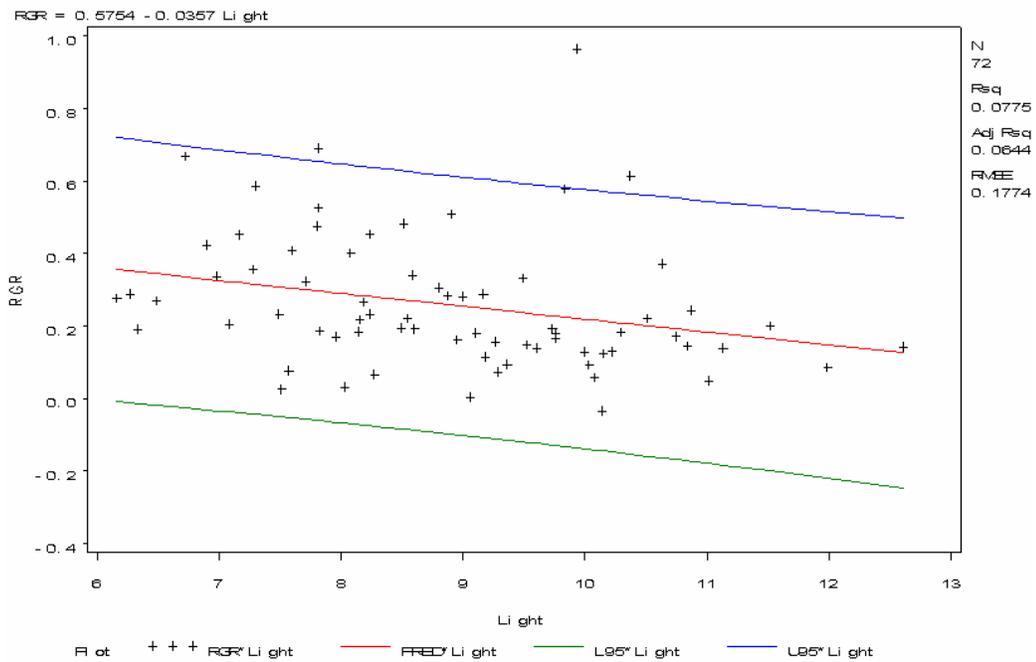


(b) Land' end plot (n=3)

Figure 4.8. Relationship between seedling growth and canopy openness in the four forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard, (b) Land's end. The X axis is the canopy openness (%) and the Y axis is the Relative Growth Rate (RGR) of seedlings. The upper and lower lines are 95% prediction intervals. R-squared is 0.0216 for (a) and 0.0357 for (b).



(c) Bormann plot



(d) Rocky plot (n=3)

Figure 4.8. (Continued) Relationship between seedling growth and canopy openness in the four forest stands in the Duke Forest, North Carolina, USA. (c) Bormann, (d) Rocky. The X axis is the canopy openness (%) and the Y axis is the Relative Growth Rate (RGR) of seedlings. The upper and lower lines are 95% prediction intervals. R-squared is 0.0373 for (c) and 0.0775 for (d).

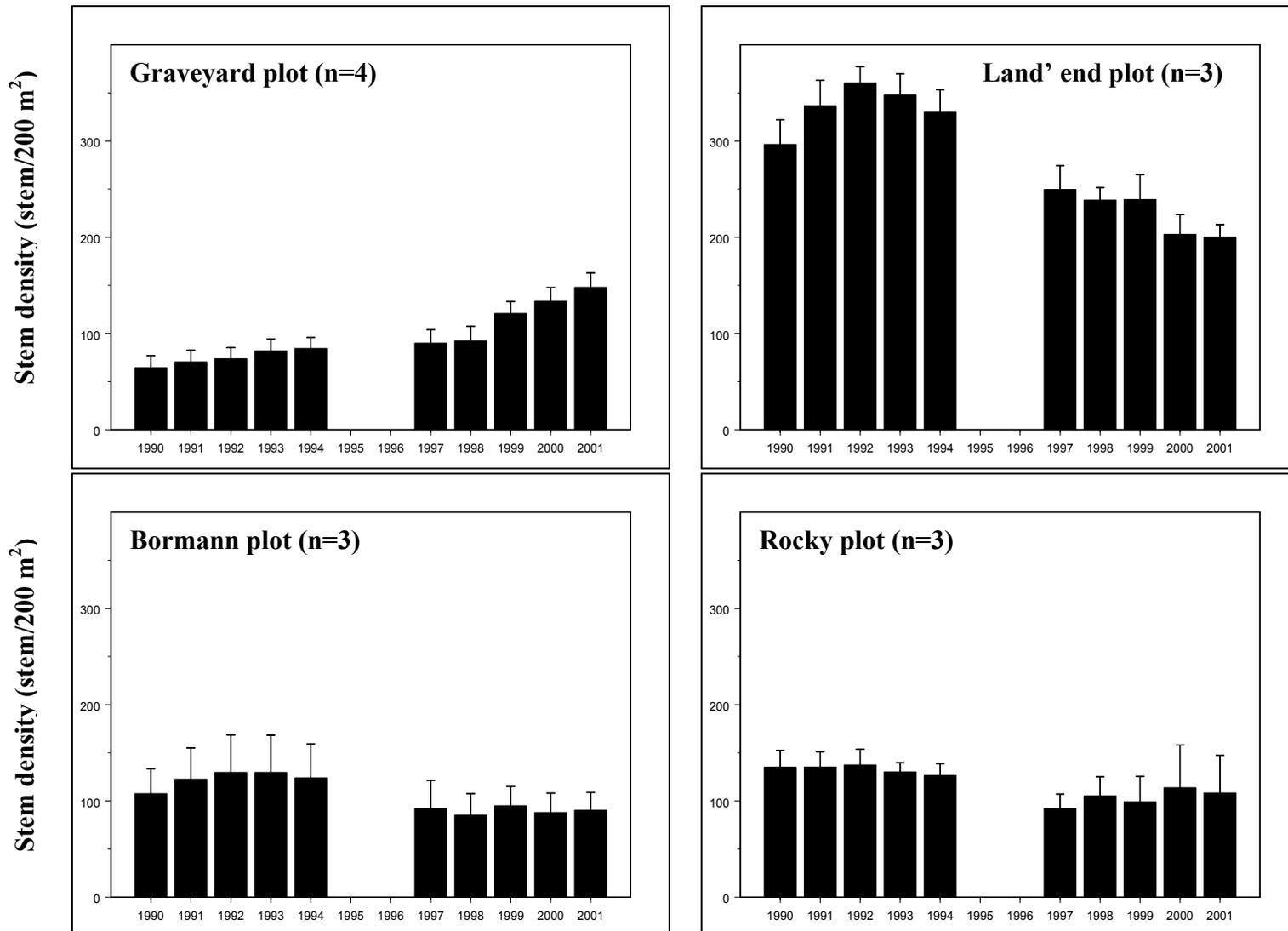


Figure 4.9. The stem density of saplings in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. *n* is the number of transects in a forest stand.

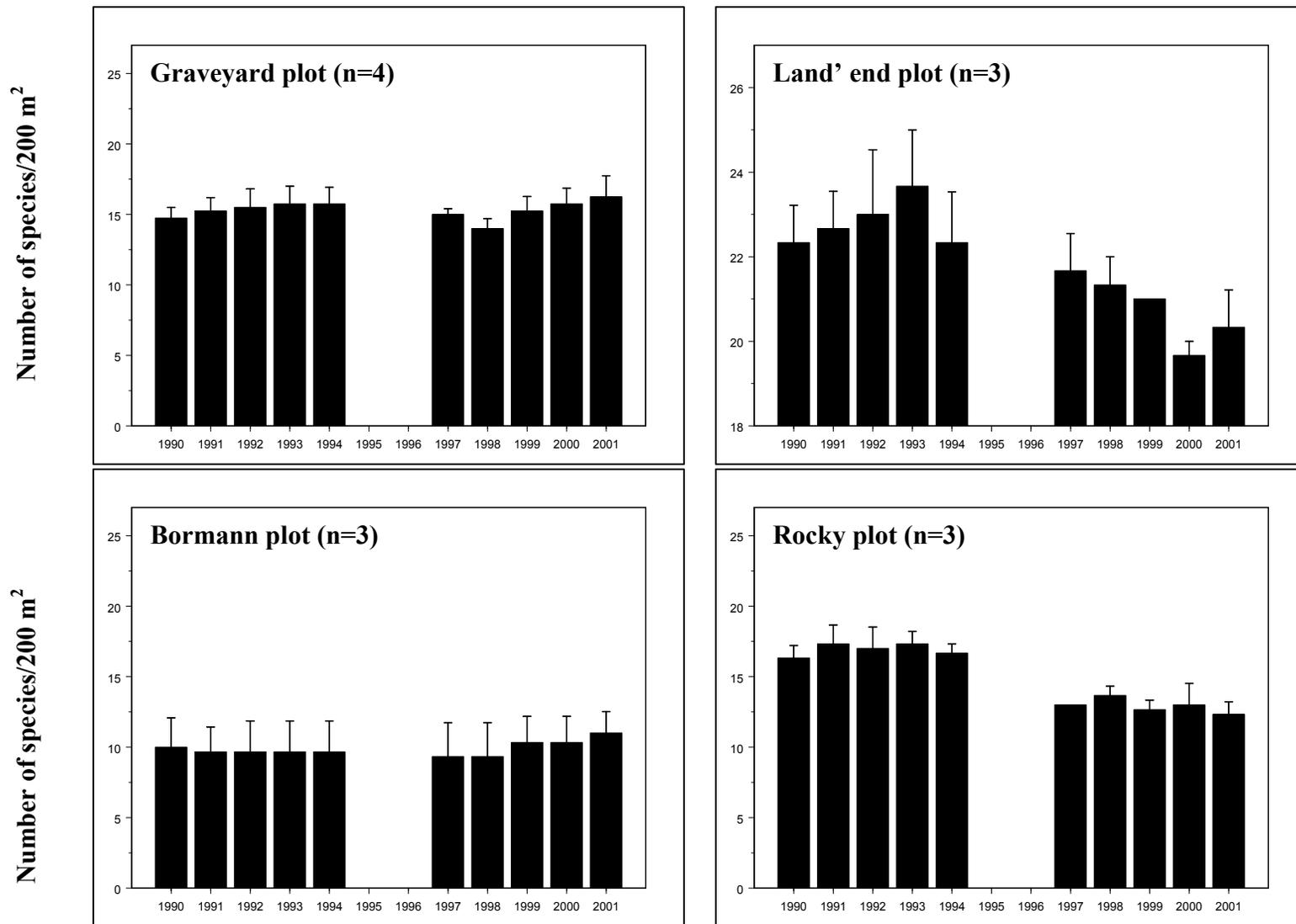


Figure 4.10. The species richness of saplings in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. *n* is the number of transects in a forest stand.

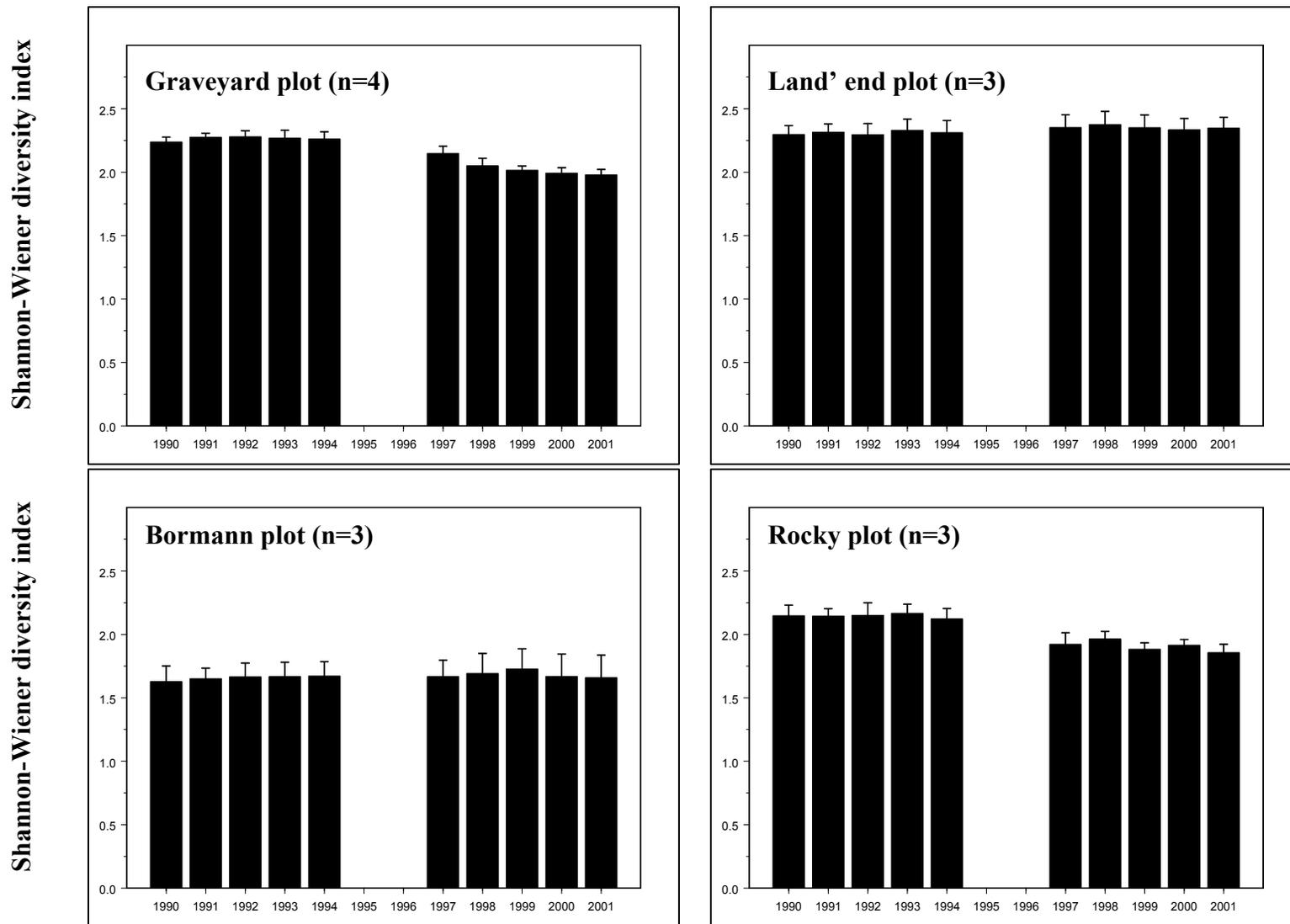


Figure 4.11. The species diversity of saplings in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot ($n=4$), (b) Land's end plot ($n=3$), (c) Bormann plot ($n=3$), and (d) Rocky plot ($n=3$). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. n is the number of transects in a forest stand.

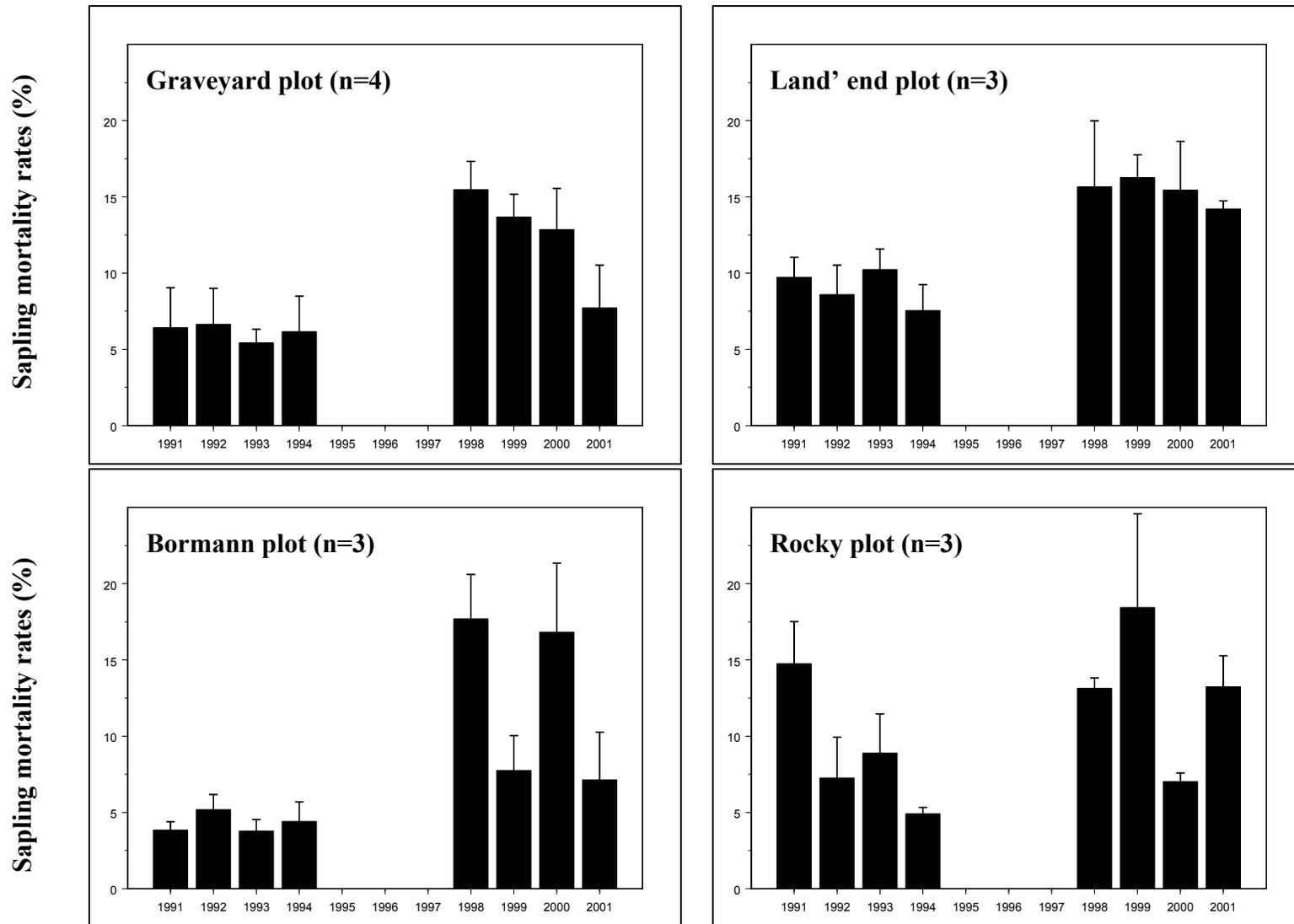


Figure 4.12. Sapling mortality rates (%) for four stands in the 4 forest stands in the Duke Forest, North Carolina. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. n is the number of transects in a forest stand.

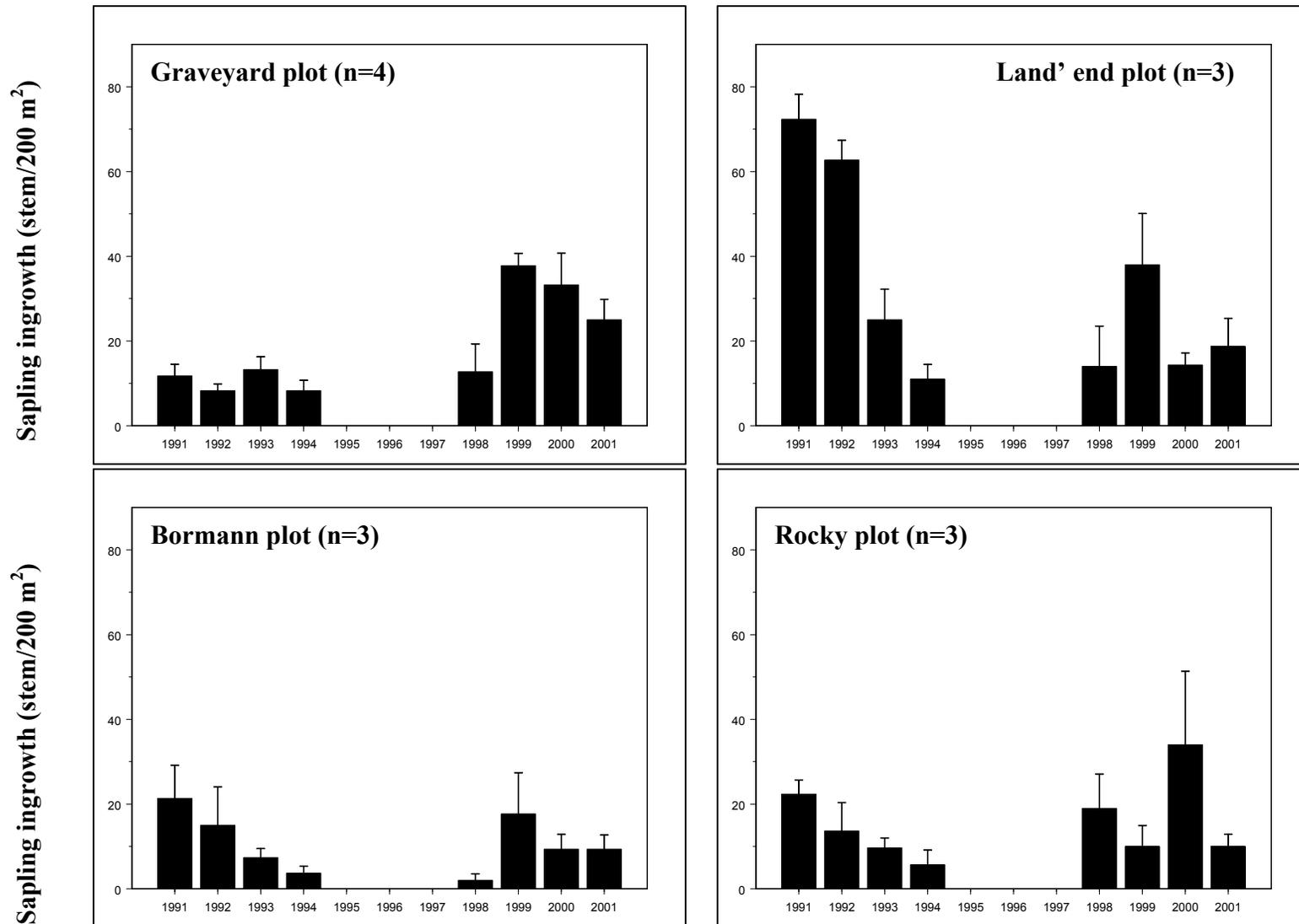


Figure 4.13. Sapling ingrowths for four stands in the 4 forest stands in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. *n* is the number of transects in a forest stand.

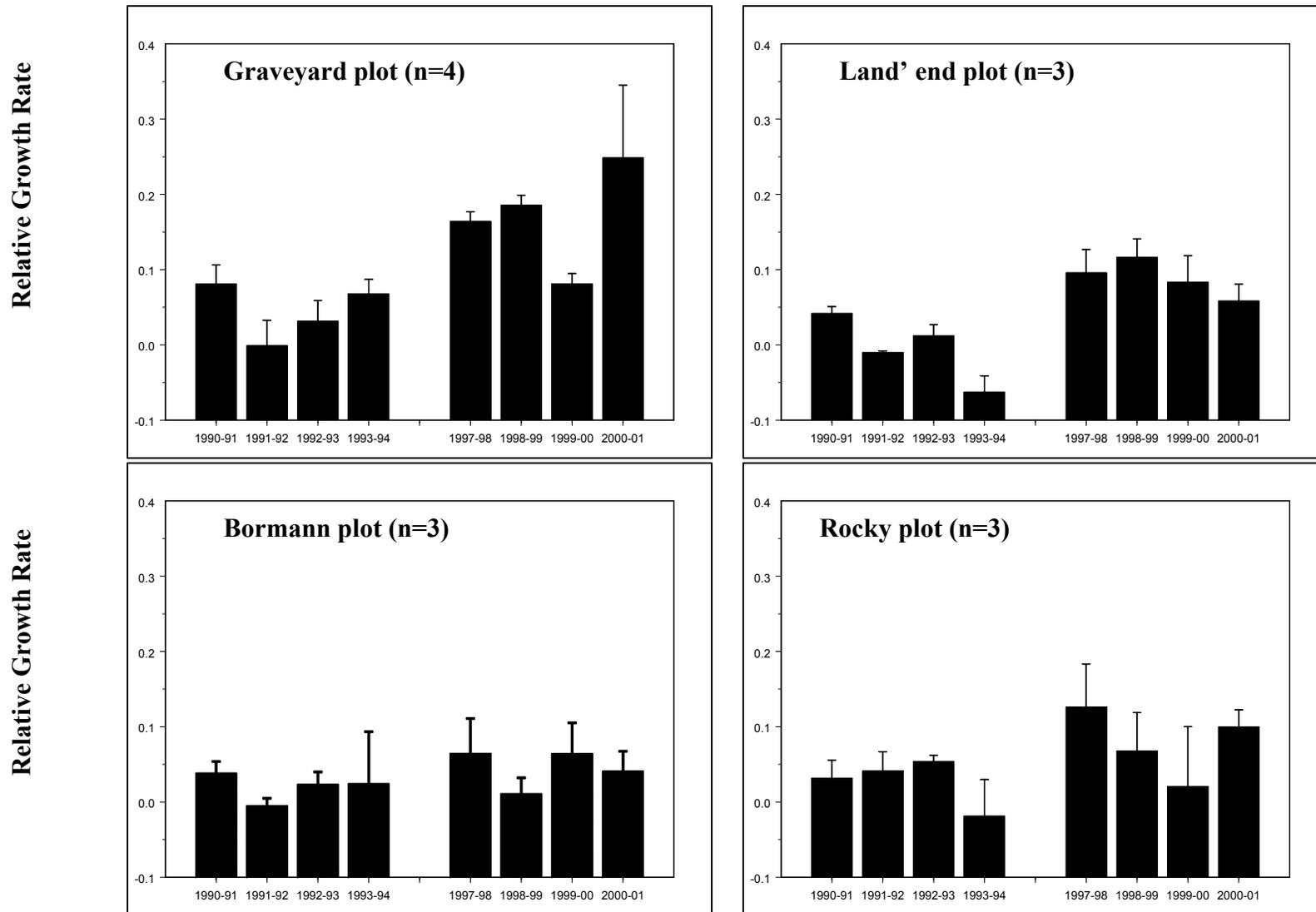


Figure 4.14. Sapling relative growth rates for four stands in the 4 forest stand in the Duke Forest, North Carolina, USA. (a) Graveyard plot (n=4), (b) Land's end plot (n=3), (c) Bormann plot (n=3), and (d) Rocky plot (n=3). The error bars are standard errors. Hurricane Fran occurred on September 5-6 1996. Note no data on 1995 and 1996. n is the number of transects in a forest stand.

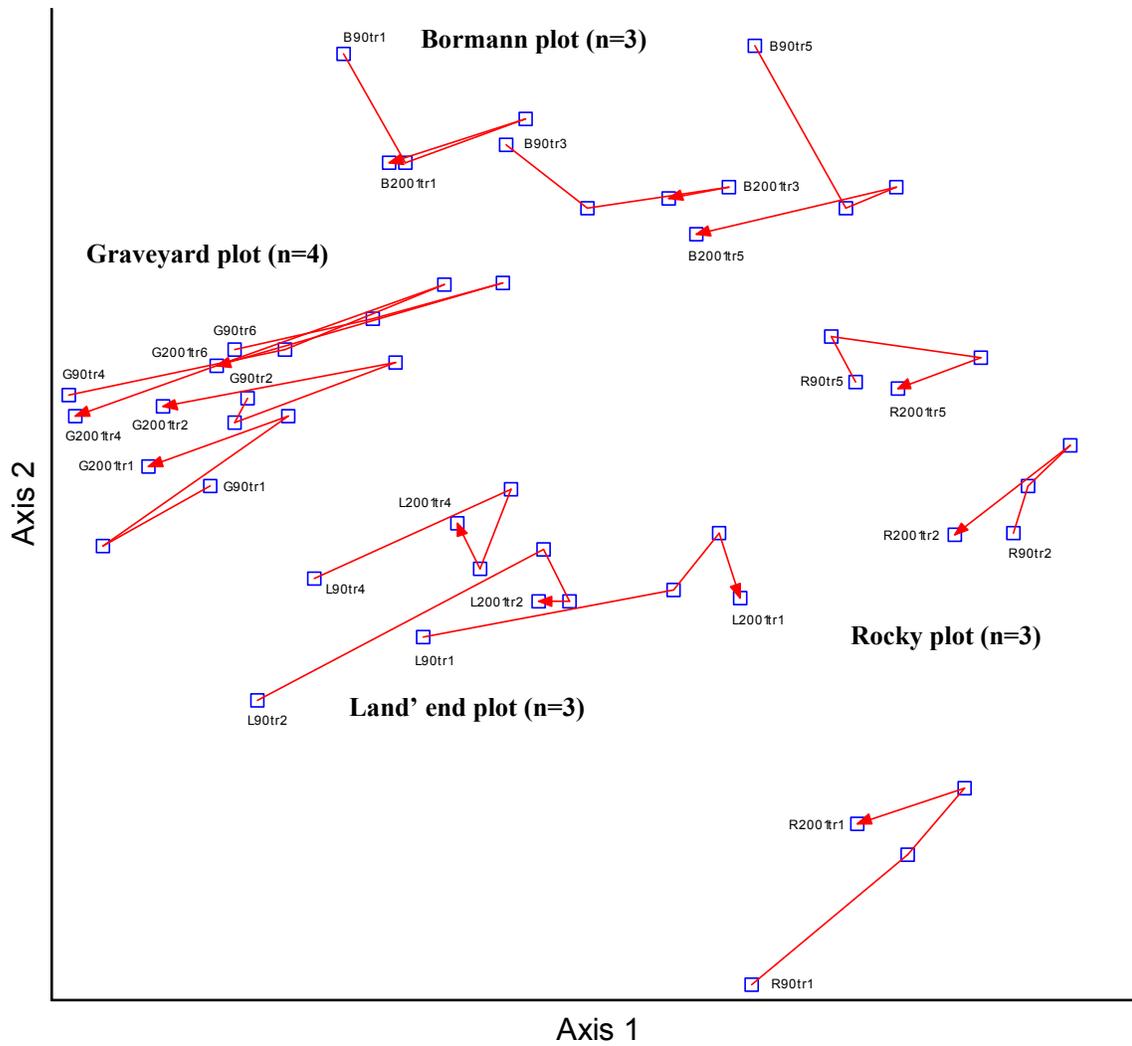


Figure 4.15. Non-metric Multidimensional Scaling (NMDS) ordination of 7 even-aged pine sapling transects and 6 mixed-aged sapling transects in the Duke Forest measured pre-Hurricane Fran (1990 and 1994) and post-Hurricane Fran (1997 and 2001). Empty squares are the transect locations on first and second axes of NMDS ordination. *n* is the number of transects in a forest stand.

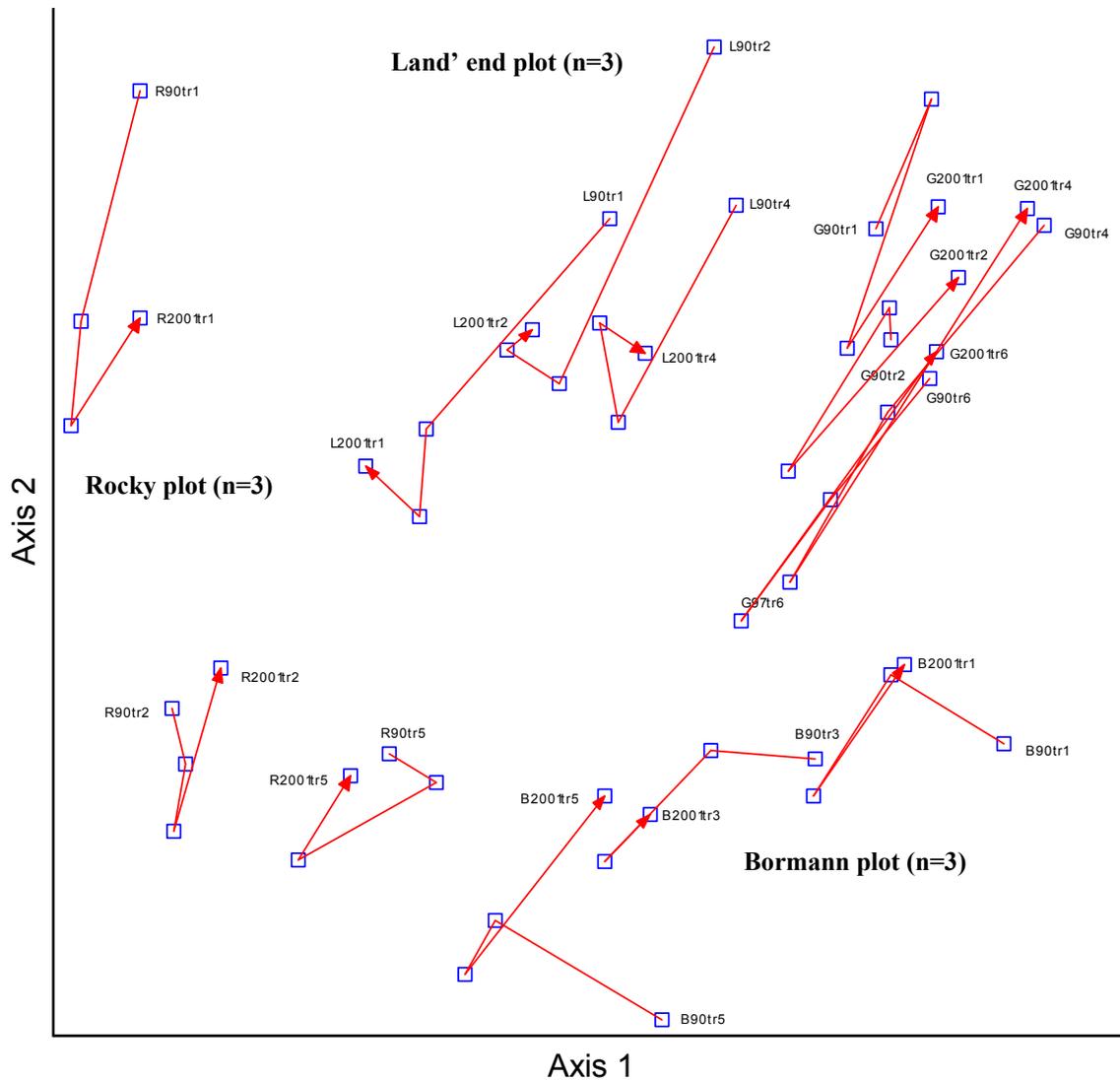


Figure 4.16. Non-metric Multidimensional Scaling (NMDS) ordination of 7 even-aged pine seedling transects and 6 mixed-aged seedling transects in the Duke Forest measured pre-Hurricane Fran (1990 and 1994) and post-Hurricane Fran (1997 and 2001). Empty squares are the transect locations on first and second axes of NMDS ordination. *n* is the number of transects in a forest stand.

CHAPTER 5

HURRICANE DISTURBANCES, TREE DIVERSITY, AND SUCCESSION IN NORTH CAROLINA PIEDMONT FORESTS

Abstract. Windthrow has been hypothesized to play a critical role in maintaining species diversity in temperate deciduous forests. Recent work by Beckage and Clark has shown that large canopy gaps maintain tree diversity in southern Appalachian forests. However, few long-term data are available for assessing the overall importance or generality of disturbance-maintained tree species coexistence. In this chapter I use nearly 70 years of tree demographic data (stems >1.25 cm d.b.h.) to assess the effects of Hurricanes Hazel (1954) and Fran (1996) on tree species diversity and tree replacement in North Carolina Piedmont forests. My results support the hypothesis that large wind disturbances help to maintain local tree species diversity. Although there is often an immediate drop in diversity following a hurricane event, species diversity of saplings quickly increases to levels that exceed those prior to the disturbance. This typically leads to an increase in tree species diversity (sometimes by as much as a factor of two) in stands that were substantially damaged. Nonetheless, time-series analysis shows that hurricanes significantly decrease the dominance of shade-intolerant canopy species such as oaks and hickories owing to lack of advanced regeneration in the understory, while increasing the dominance of pre-established, more shade-tolerant species such as red maple. Pre-hurricane successional phases of forests can influence strongly both forest damage severity and subsequent responses. Late-successional, mixed-aged hardwood forests respond to hurricane damage strongly as

compared with the early successional phase pines. I conclude that large, infrequent wind disturbances help to maintain local tree diversity, but also accelerate the increase in dominance of understory species such as red maple and beach. This pattern may widely apply in the Piedmont region and adjacent temperate forests regions of the eastern United States.

Key words: wind disturbance, tree species diversity, tree demography, plant succession, disturbance-diversity relationship, Piedmont forests.

INTRODUCTION

Windthrows caused by large hurricanes and other intensive windstorms have been shown to have profound impacts on forest structure (Brokaw 1991, Imbert et al. 1996, Greenberg and McNab 1998, Harcombe et al. 2002), species composition (Spurr 1956, Foster 1986, Putz and Sharitz 1991, Vandermeer et al. 2000), and successional development (Hibbs 1983, Ross et al. 2001) in many forests of the world, and have been hypothesized to play a critical role in maintaining species diversity in temperate forests (Peet and Christensen 1980, Beckage and Clark 2000, also see reviews in Foster and Boose 1995, Everham and Brokaw 1996, Webb 1999, Peterson 2000). What less clear is 1) how the pre-disturbance community characteristics or successional stage influences species diversity, 2) how the juxtaposition of background dynamics and succession influences the post-disturbance trajectory of species diversity, and 3) how long the disturbance effects influence species replacement and successional trajectory. Clarifying these issues is important for understanding forest recovery, species dynamics, and disturbance-diversity relationships.

Intensive windstorms generally result in immediate change in forest structure and altered rates of population processes (e.g. tree mortality, growth rates), but their impacts on

community attributes such as species diversity and long-term forest successional development are more complex. Windstorm disturbances may have positive or negative effects on species diversity and forest succession depending on the intensity and frequency of the windstorms and the characteristics of the pre-disturbance forest communities (Pickett and White 1985, Molino and Sabatier 2001, White and Jentch 2004). When wind intensity is high, windstorms may initiate new successions and thereby exert strong and long-lasting influence on tree growth (Merrens and Peart 1992) and forest successional development (Foster 1988, Hibbs 1991). However, if the intensity is low, windstorms may cause only limited forest damage and have only modest, short-term impacts. Species diversity at any time is the result of a dynamic balance of recruitment and extirpation of species that reflects the combined influence of historical disturbance and population change (White 1979, Pickett and White 1985, Glenn-Lewin, Peet and Veblen 1992, Bazzaz 1996). Thus, to better understand disturbance-mediated species dynamics, it is important to analyze disturbance effects in the context of successional change. Clearly, long-term pre- and post-disturbance data are critical for understanding diversity dynamics as often a significant time lag exists before the impact can be detected.

The proposition that windthrow maintains species diversity, originally developed from observations of temperate forests of the northeastern United States (e.g., Spurr 1956, Canham and Loucks 1984, Boose and Foster 1994 and Peart et al. 1992), has been generally supported and further developed by subsequent studies in the southern Appalachian Mountains (Greenberg and MacNab 1999, Beckage and Clark 2000, Elliott et al. 2002). However, this hypothesis has not been thoroughly tested using detailed, long-term data.

Demographic research in the Duke Forest has shown that although oaks and hickories have long remained the dominant canopy species of mature stands, there has been a steady decline in dominance of these genera over the past 60 years, along with a simultaneous increase in abundance of red maple (*Acer rubrum*) (McDonald et al. 2002) and to a lesser extent beech (*Fagus grandifolia*). The mechanisms for this compositional shift are little understood, though various hypotheses have been proposed. One popular hypothesis is that oaks and hickories are well adapted to the chronic, low-intensity fires that ceased during the late 1800s (see Abrams 1992). However, another hypothesis that has received consistent support is that these relatively shade-intolerant species are adapted to rapid growth following major canopy disturbances such as those associated with hurricanes and tornados (see Glitzenstein et al. 1986). A detailed analysis of post-hurricane recovery trajectory could provide insights that at least partially discriminate between these possibilities.

In this paper, I use nearly 70 years of tree demographic data to assess the effect of two large hurricanes, 1954 Hurricane Hazel and 1996 Hurricane Fran, on tree species diversity, tree replacement, and long-term successional trajectories in North Carolina Piedmont forests. I particularly focus on hurricane-disturbance mediated tree diversity dynamics during secondary succession. I first examine several available control plots that received little to no damage in 1954 Hurricane Hazel to provide a tree species diversity baseline during the old-field succession. I then examine the effects of this historic hurricane on tree diversity by comparing the changes in the hurricane-damaged plots with change in control plots that received only minor damage. To clarify long-term effects of hurricanes on the relative abundance of tree species and species diversity, I compare post-Fran recovery patterns with those following the 1954 Hurricane Hazel and conclude by examining how historical

disturbances may influence long-term forest dynamics. Finally, I compare major tree replacement rates among communities in different successional stages before and after hurricanes to understand how large, infrequent hurricanes can alter forest successional trajectories.

The long-term, pre- and post-hurricane data allow me to compare population dynamics and recovery patterns in two forest types (even-aged pine stands and mixed-aged hardwood forests) and across three successional stages (the thinning phase, the transition phase and the steady-state phase) to address three questions. 1) Do hurricane disturbances increase tree diversity in severely damaged plots? 2) Do hurricane disturbances lead to altered relative abundance of shade-tolerant and shade-intolerant species? 3) Did 1954 Hurricane Hazel and 1996 Hurricane Fran alter the succession trajectory of Piedmont forests they impacted?

METHODS

The study site

The study was conducted in the Duke Forest, located in Orange and Durham Counties, North Carolina, USA (approximately 35° 52' N, 79° 59' W). This experimental forest has served as a model system for ecological studies on forest dynamics since its establishment in early 1930s. Old-field forest succession has been one research focus as documented in numerous classic papers (Billings 1938, Korstian and Coile 1938, Oosting 1942, Kozlowski 1949, Keever 1950, Bormann 1953, Christensen 1977, Christensen and Peet 1981, 1984, Peet and Christensen 1979, 1980, 1987, 1988; see review by Peet 1992). As part of this legacy of prior research, there exists a set of long-term data on tree establishment, growth, and mortality of individual plants in permanently marked research plots. These data, in some cases are over 70 years old, include the combined pre- and post-disturbance records for two

hurricanes (1954 Hurricane Hazel and 1996 Fran), thus providing an exceptional opportunity to address questions regarding the effects of large, infrequent wind disturbances on species diversity dynamics and forest succession.

The major forest types of the Duke Forests are even-aged loblolly pine forest and uneven-aged mixed upland hardwood forest. Most of the current loblolly pine stands are 60 to 100-year-old secondary forests that are the result of reversion of abandoned farmland. These forests are generally in the transition phase of succession as represented by canopy pine trees with a cohort of understory hardwood tree species more tolerant of low resource availability (Peet 1992). The light-demanding loblolly pines dominate the initial post-agriculture forest (i.e., the establishment phase). Pine seedlings and saplings grow rapidly and after 5-15 years form a closed canopy above other seedlings (Peet and Christensen 1987). Once a closed canopy has formed, these young pine stands then enter the thinning phase of forest development. A number of light-demanding and more shade-intolerant hardwood species such as *Liquidambar styraciflua*, *Liriodendron tulipifera* and *Acer rubrum* often invade simultaneously with or slightly after the pines (Peroni 1994). During the thinning phase, stem density steadily declines and establishment is minimal, which can lead to relatively low tree species diversity.

The current uneven-aged, mixed upland hardwood forests are the putative 'climax' forest of the Piedmont region and are in the steady-state terminal phase (a mosaic of patches of various sizes and ages) of succession (Oosting 1942, Christensen and Peet 1981). The younger hardwoods are dominated by hardwood species of varying age and include *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Acer rubrum* and *Ostrya virginiana*. The classical expectation is that the composition of these younger hardwood forest will probably

change gradually for another 200-500 years as these species are replaced by the slow growing *Quercus rubra*, *Q. alba*, *C. glabra*, *C. ovata* and *Fraxinus spp.* (Oosting 1942, Bormann 1953, Peet et al. 1987, Peet and Christensen 1980, 1987 and 1988). However, more recent work suggests a trend toward eventual dominance by more shade-tolerant understory species such as *Acer rubrum* and *Fagus grandifolia* (McDonald et al. 2002, 2003).

Disturbance history

Historically, the Duke Forest and adjacent Piedmont areas were a landscape dominated by oak-hickories forests with some pines on poorer soil habitats. Prior to European colonization (ca. 1650-1750), native Indian tribes lived in the region and practiced farming in the alluvial bottomlands. Fire had been their tool for managing the woodlands. Soon after European colonization, a large portion of the Piedmont forest was converted into cropland. That land too rocky or steep for agriculture was used instead for selective harvest of timber and grazing of domestic stock. During the latter half of the 1800s and early 1900s, much of the farmland was abandoned due to depleted soil conditions and other economic factors. Thereafter, the natural processes again became the dominant factors influencing forest development. Much of the Piedmont forest land today is in some stage of recovery from this abandonment (Oosting 1942, Peet and Christensen 1980).

The disturbance history of the Duke Forest has been well documented subsequent to its establishment as an experimental forest in the early 1930s. After farmland abandonment, the one-time agricultural lands of the Duke Forest largely progressed through old-field succession (Oosting 1942, Peet and Christensen 1980). Overall, there were no major human-caused wild fires and few clear-cuts in the Duke Forest, except the forest did experience various natural disturbance events, mainly variable local windstorms in the summers and ice

storms in the winters. Some forest stands in the Duke Forest have received moderate forest management. Wildfires have been generally prohibited in the Duke Forest since 1930s and the current forests have developed under fire suppression conditions. In addition to hurricanes, natural disturbances include ice storms, gales, and local severe windstorms. Since the late 1990s deer grazing has increasingly inhibited forest understory regeneration.

Among the various disturbances impacting Duke Forest, hurricanes are the most destructive force of nature and affect a particular Piedmont forest on average about once every 50 years. Over the past 100 years, two major wind disturbance events have substantially damaged Duke Forest woodlands and caused widespread windthrow, Hurricanes Hazel and Fran. Hazel occurred in 1954 and at the time was recognized as the greatest natural disaster to ever affect central North Carolina (Banner 2001). Hazel made landfall as a category-4 hurricane near the North Carolina - South Carolina border on October 15, 1954 and subsequent rapid motion took the storm from the coast across eastern North Carolina. Hazel's violent winds toppled countless trees across eastern North Carolina. At the Raleigh-Durham Airport, which is the nearest official weather station to the Duke Forest, wind gusts of 40.23 m/s were recorded (the State Climate Office of North Carolina and the National Hurricane Center). Heavy rains of up to 280 mm occurred far inland and resulted in local flooding. Hazel caused widespread tree mortality and breakage in the Duke Forest.

Hurricane Fran was a category-3 hurricane when it made landfall near Cape Fear on the southeast coast of North Carolina. After making landfall, it moved north-northwest across North Carolina's central plains. On 1996 September 6, Hurricane Fran struck Durham and Orange counties in the central North Carolina Piedmont. Its eye passed about 24 km east of

the Duke Forest. Although its intensity had begun to decrease to tropical storm levels, Fran caused significantly forest damage in and near the Duke Forest. Hurricane Fran was one of the most destructive hurricanes to occur in the North Carolina Piedmont region and the fourth most costly hurricane to occur on the United States mainland during the 20th century (Barnes 2001). The maximum sustained wind speeds at Raleigh-Durham airport were about 26.82 m/s and the maximum wind gusts reached 31.85 m/s.

Hurricane Fran dropped a huge amount of rainfall along its path. The total rainfall at Raleigh-Durham International Airport was 224 mm during the hurricane. The Duke Forest area had received nearly 76 mm of rainfall two days prior to Fran and another 51 mm immediately afterward. Overall, this forest region experienced about 423 mm rainfall during September 1996, the highest in a single month since 1908 (the State Climate Office of North Carolina and the National Hurricane Center). The pre-hurricane heavy rains were particularly significant as they saturated the soil and reduced the ability of canopy trees to withstand high winds.

Vegetation plots and data

I used two sets of long-term demographic data in this study to examine the effects of historical hurricane disturbance events on species diversity change during secondary succession. The first dataset includes 20 long-term permanent sample plots (PSPs) with nearly 70 years of tree records ranging from the early 1930s to 2000. These PSPs contain information on all woody stems greater than 1.25 cm diameter at breast height (d.b.h., at about 1.37 m height), including tree diameter, height, and condition (alive or dead). The sizes of the 20 selected PSPs ranged from 404 to 1440 m² (Table 5.1a). Many of the selected PSPs were originally designed to study the effects of silvicultural thinning treatments on tree

growth and timber yield. Therefore, manipulated plots were generally paired with control stands. The management and disturbance history of these plots was well documented in the Duke Forest archives. For the purpose of examining the effects of historical hurricane disturbance on species diversity dynamics and succession, I further divided these 20 PSPs into three sub-groups.

(1) The first subgroup includes the 14 control PSPs that were subjected to no thinning treatments of any kind and experienced no major hurricane damage during the 1954 Hurricane Hazel. These include 10 loblolly pine PSPs (PSP 12, PSP 14, PSP 15, PSP 17, PSP 19, PSP 21, PSP 23, PSP 26, PSP 28, and PSP 50) that were about 10-20 year-old in early 1930s when the plots were established (Table 5.1a). Among the controls, three plots (PSP 15, PSP 26 and PSP 28) experienced minor tree damage (hurricane-induced plot-level basal area loss 2.5%, 3.9% and 3.5% respectively) during Hazel.

Four mixed-aged hardwood PSP control plots (PSP 10, PSP 35, PSP 36, and PSP 44) were relatively open hardwood stands when the plots were established (perhaps reflecting a history of grazing or low-intensity fire). These stands increased in biomass and canopy tree size over the 60 years of development. My data did not record any hurricane Hazel damage for PSP 10, PSP 35 or PSP 44. PSP 36 experienced only minor damaged and lost about 6.7% of its basal area. In sum, during the 60 years prior to Hurricane Fran, the control plots did not experience major disturbances. However, five of these 14 controls (PSP 14, PSP 19, PSP 50, PSP 10, and PSP 36) experienced a high degree of tree damage and mortality (with basal area loss >10% of previous basal area) in 1996 as a result of Hurricane Fran.

(2) The second subgroup contains controls with significant damage in 1954 from Hurricane Hazel (measured as basal area loss >10% of previous basal area). This group

includes two PSPs which did not receive any thinning treatment from early 1930s to 1960s, but were subjected to significant damage from 1954 Hurricane Hazel. One is a loblolly pine plot (PSP 40) and other is a hardwood plot (i.e., PSP 37). PSP 40 experienced a loss rate of 40 trees/acre and about 14% of the previous basal area during Hazel, while PSP 37 was substantially damaged during Hurricane Hazel and lost over 42% of previous basal area.

(3) The third group contains three pine PSPs (i.e., PSP 20, PSP 22, and PSP 39) and one hardwood PSP (PSP 43) that were subjected to varied degrees of thinning treatments from early 1930 to 1960s and all experienced significantly hurricane damage during 1954 Hurricane Hazel. PSP 20 and PSP 22 lost 40 and 50 trees/acre and 12.3% and 8.1% of previous basal area respectively. They were also significantly damaged by the glaze storm of February of 1947. PSP 39 was heavily thinning from below (removal of 2015 trees/acre and about 47% of the previous basal area) in November 1934, and had extensive Hazel damage (loss of 90 trees /acre and about 36.3% previous basal area). In addition, this plot was also extensively damaged in the glaze storm of February of 1947. PSP 43 is a hardwood plot that experienced thinning at the time of establishment and in addition lost 33.3% of previous basal area during 1954 Hurricane Hazel.

The dataset I used to examine tree diversity dynamics and succession has one significant limitation in that after the first complete inventory, subsequent inventories generally did not include records of ingrowth trees until the late 1970s. These plots had not been designed for study of species composition or tree diversity, but rather the focus was tree growth, so the understory recruitment of saplings and small trees was at the start considered irrelevant. With this consideration in mind I limit, where possible, comparisons of diversity to species counts

based on full stem inventories, and otherwise exercise care to point out this limitation in the data.

The second dataset includes seven large mapped permanent plots (MPPs) from the Duke Forest with over 20 years of tree data (d.b.h.>1 cm) to study spatial pattern and process (Peet and Christensen 1980). The sizes of these seven mapped plots ranged from 0.68 to 6.5 ha (Table 5.1b). Data from these seven mapped plots include the same information as from the PSPs, except that tree height was generally not recorded. Remeasurement of all the mapped plots was carried out at roughly 5-year intervals from 1978 to 2000. Among these seven mapped plots, I focused primarily on two large mapped plots. Graveyard plot is dominated by even-aged loblolly pine and was observed during the interval 1978-2001. Bormann plot is a mixed-aged hardwood stand with tree records from 1950 to 2000. These two MPPs were chosen to represent two major types of forest at two different succession phases: the transition phase and the steady-state phase. Both of these mapped plots experienced significant tree damage and mortality in the 1996 Hurricane Fran.

In four of the five large mapped plots (Graveyard, Land's end, Bormann, Rocky plot) saplings were monitored on nearly an annual basis during 1979-2001 along set of 21 sapling transects. I used these understory sapling (stems > 1m tall and < 1 cm d.b.h.) growth and survival data to project post-hurricane changes in canopy composition. Sapling transects are 200 m² in size (50 x 4 m), arranged paralleled to each other, with typically 5 per plot. For each sapling in each survey, height, d.b.h., coordinates, and condition (live, dead, missing, and significantly damaged with height loss) were recorded. New saplings (newly above 50 cm, or apparently overlooked in previous years) were recorded. Live saplings that grew to

exceed 1 cm d.b.h. were so noted and no longer recorded as a sapling. In 2001, there were approximately 4,300 saplings on 21 sapling transects.

Measurement of species diversity and data analysis

I used two indices, species richness (S) and the Shannon-Weiner's diversity index (H'), to evaluate the change in woody plant diversity as a consequence of hurricane damage. I define species richness (S) as the number of vascular tree species of d.b.h.>1.25 cm per ca 0.04 ha (400 m²) plot when comparing pine PSPs and per ca 0.1 ha (1000 m²) for comparing hardwood PSPs, but stem d.b.h.>1 cm per 0.1 ha (1000 m²) when comparing between the MPPs.

I divided each large mapped plot into several subplots (ca 1000 m²) to examine changes in tree diversity. The plot size of 1000 m² is widely used as a standard sampling size, which facilitates comparison with other Piedmont forest plots (Peet et al. 2001). In this way, I minimized the possible sample effects that would arise from using unequal plot sizes.

The Shannon-Wiener diversity index (H') is widely used in ecology and is defined as $H' = - \sum p_i \log_e p_i$ where p_i = the proportion of the individuals in the i^{th} species. I expressed this form of diversity as $\exp H'$ which gives a value equal to the number of equally common species that would provide the same value of H' as the sample. Thus, $\exp H'$ is a more intuitively meaningful expression than H' (Peet 1974).

Compositional patterns were assessed with Nonmetric Multidimensional Scaling (NMS) with varimax rotation (Kruskal 1964; Mather 1976) as implemented in version 4.39 of PC-ORD (McCune & Mefford 1999). Ordinations of multiple plot measurements over time allowed examination of plot successional trajectories in ordination space and patterns of community change. All control PSPs (except PSP 12) with data from 1933-2000 were used

to assess the range of change of tree species composition. Analyses of 1978-2000 data from the seven MPPs were used for more detailed examination of compositional patterns within upland stands due to the impacts from Hurricane Fran.

RESULTS

Tree diversity dynamics in old-field succession without major disturbances

I examined PSP data from 70-year records to document diversity trends in tree species for both even-aged loblolly pine stands from the thinning phase through the transition phase and relatively mature upland mixed-aged hardwood stands (Table 5.2).

As shown in the 10 loblolly pine control stands, tree richness and diversity in 10-25 year-old loblolly pine stands was generally low. During this thinning phase, these pine stands were mainly comprised of loblolly pine plus a few shade-intolerant hardwoods such as sweetgum and tuliptree. Most of the 10 controls only had 1-3 tree species with an average value of $\exp H'$ of 1.86. Tree richness and diversity had increased by about a factor of 5 ($\exp H'$ 7.01) when these loblolly pine stands reached 60-75 years old and entered the transition phase. Tree diversity continued to increase at a lower rate to 8.29 in 1992, the last overall census prior to Hurricane Fran (Table 5.2). Although there was considerable variation among these loblolly pine stands due to differences in site conditions and stand ages, overall the trend of increasing tree species diversity in pine stands during the 60 years of succession was clear and significant.

There was substantial variation in tree species richness among the pine stands at 10-25 years (Table 5.2). Two of the controls (the 19-year-old pine stand PSP 26, and the 25-year-old pine stand PSP 50) had high tree species richness, perhaps due to unusual edaphic conditions (both plots had a soil-based site index of 85, compared to an average of 79 on the

other sites, Duke Forest Archives). This suggests that rapid post-abandonment tree species recruitment sometimes occurred during the early thinning phase.

In contrast to the loblolly pine stands, tree species diversity and richness in the four undisturbed upland mixed-aged hardwood plots showed an initial increase and then remained relatively stable for most of the 60-year period of record (Table 5.2). However, observed tree species diversity was lower than in the transition-phase 80-year-old pine stands.

Changes in mortality and density in old-field succession

Tree mortality is the dominant population process driving secondary old-field succession (Peet 1980). Long-term changes in tree mortality and density were examined in this study. There has been a relatively constant rate of tree mortality during pine stand development (Figure 5.1), even though initial tree density varied greatly. In each of the matched plots, after critical crowding was reached tree mortality showed a nearly perfect exponential decrease (also see Peet and Christensen 1980). The stem density of pine trees steadily decreased and converged to a rather narrow range of densities during the 60 years of thinning. Tree density strongly influences mortality and species diversity along the succession process.

Tree mortality in the mixed-aged hardwood stands is less easily interpretable during the nearly 70 years of stand records, primary due to the ever-changing age structure of the populations and size dependence of mortality (Peet 1988). However, the mortality pattern also fit a negative exponential model. Species-based differences in mortality can be seen both within and between stands. For instance, flowering dogwood (*Cornus florida*) in PSP 36 has the highest depletion rates of any the common species. In addition, flowering dogwood was

substantially damaged by 1996 Hurricane Fran. Similar patterns can be seen for oak species in PSP 10 due to the damage effects by Hurricane Fran.

Damage effects of Hurricane Hazel on tree diversity in the thinning phase stands

Comparison of change in diversity in PSPs severely damaged by Hurricane Hazel with their controls during the 50-year period following the storm allows evaluation of the impact on forest development and possible long-term effects. In general, Hurricane Hazel had less long-term effect on loblolly pine stands than uneven-aged hardwoods.

To detect whether hurricane damage has long-term effects on tree species composition I compared tree diversity changes in a pair of pine PSPs, one modestly damaged by Hurricane Hazel (PSP 40, lost 14% basal area by Hazel) and the other with minimal damage (PSP 28, lost 3.5% basal area by Hazel). The two PSPs were both 808 m² in size and 15-years-old in 1933. There was only a weak increase in diversity on the damaged plot. Although the species number in PSP 40 is not always significant higher, the species diversity index is weakly higher than in the control plot, probably owing to reduced dominance by loblolly pine.

One damaged young pine stand (PSP 20) lost 9% of previous basal area during Hurricane Hazel plus additional about 9% basal area removed in thinning immediately after 1954 Hazel, while its paired control plot (PSP 21) was subject to no damage in 1954 Hurricane Hazel and received no thinning of any kinds before or after Hurricane Hazel. These plots had reached a similar tree diversity value in 1992, about 50 years after Hazel. Similarly, comparison of PSP 39, a pine stand which lost 36.3% previous basal area with PSP28, a pine control which lost only 3.5% basal area by Hazel showed that the species diversity is slightly higher (but mixed in terms of species richness) in the damaged PSP than

the control. These results suggest that the hurricane damage has relatively little effect on species composition and tree diversity when the impact comes in the thinning phase.

In contrast with the few long-term effects of hurricanes on thinning-phase loblolly pine stands, I found clear evidence of positive effects of hurricanes on hardwood stands in that tree species diversity in a severely damaged oak stand (PSP 37) increased significantly over 50 years following the storm. This severely damaged plot (PSP 37) lost about 42% previous basal area during Hurricane Hazel whereas the control neighbor oak plot (PSP36) had only minor damage and only lost about 6% previous basal area during Hurricane Hazel. The tree species diversity in the severely damaged plot decreased immediately after Hazel and remained low another 5 years, then dramatically increased by a factor of four in late 1980s, and decreased again in 1990s. At 2000, the stand level of tree diversity was still about two-fold higher than the control plot (Table 5.4b). The diversity changes in the two oak hardwood stands with identical community attributes pre-Hazel suggested that hurricane damage severity was the major control factor for this species increase at stand level. This suggested that a loss ca 40% basal area of the stand may be over a threshold value for affecting species composition and diversity.

In summary, the effects of 1954 Hurricane Hazel on species diversity are stronger in later successional hardwood stands than that on the early successional pine stands. As I will show below, the effects of the hurricane were reversed during 1996 Hurricane Fran to largely impact the transition phase pine stands in the Duke Forest.

Effects of 1996 Hurricane Fran on canopy and understory tree species diversity

In September 1996, 42 years after 1954 Hurricane Hazel, the Duke Forest experienced another powerful hurricane damage event, Hurricane Fran. Two large mapped plots

representing a transition-phase pine stand (Graveyard plot) and a mature hardwood stand (Bormann Plot) demonstrate the relatively short-term hurricane effects on tree diversity and forest successional trajectory.

Following Fran, species richness and diversity of small trees increased somewhat in both the loblolly pine and the mixed hardwood stands (Figure 5.3). In addition, the total number of species present in the mapped pine plots increased slightly for tree species (d.b.h. \geq 1 cm) 5 years after the hurricane (Tables 5.5a and 5.5b). In the two mapped pine stands, three light-demanding, fast-growth tree species, and two woody shrubs recruited into the stands after the hurricane.

Wind damage appeared to favor light-demanding species and pioneer species over shade-tolerance tree species. The importance of the dominant species in both pine and hardwood forests decreased substantially due to their high mortality of canopy trees (Figure 5.5), but the overall ranking of dominant tree species did not change. The damage severity (as loss of basal area) varied slightly between the two MPPs. In the two large mapped pine forest plots, pine decreased in importance value from a pre-hurricane level of 34.5% in 1992 to 32.0% in 1997 and continued to decline to 28.3% in 2000. The dominant *Quercus alba* decreased in its importance value from 38.1% (1993) to 36.2 % in 1997 and continued to decline to 34.01% in 2000. The 80-year old loblolly pine stand lost about 20% of previous survey basal area (1993), and the oak forest lost 16% of basal area. Some understory hardwood species, including *Acer rubrum*, *Liriodendron tulipifera* and *Liquidambar styraciflua*, increased significantly in their importance in the both pine and hardwood stands.

Understory tree diversity showed a minor increase in hardwood forest stands (Table 5.4, Figure 5.5). On average, only a few tree species were added; the Bormann plot added 5 as did the Rocky plot.

Relationship between canopy damage and changes of understory diversity

Patchy canopy damage in the large mapped plots provided an opportunity to examine the relationship between wind damage severity and tree diversity dynamics. For this propose, I divided the two large mapped plots (1.3 and 1.96 ha, respectively) into numerous 1000 m² subplots. The damage intensity of the subplots was calculated by their weighed damage index (ranging from 0-3, by definition the maximum value is 3, meaning all stems were severely damaged).

In both the transition-phase loblolly pine stand and the mature, uneven-aged hardwood stand I found a positive relationship between stand damage intensity and the change of tree diversity (defined as the difference of tree diversity $\exp H'$) between 1992 (4 years before Hurricane Fran) and 2001 (5 years after Hurricane Fran) (Figures 5.4a and 5.4b). As there was insufficient time for significant in-growth of new species, this change is primarily a consequence of increased evenness resulting from disproportionate loss of the most abundant canopy species.

Change in abundance of shade-tolerant understory species after 1996 Hurricane Fran

One of the effects of Hurricane Fran was to alter the abundance of shade-tolerant understory species. I group and compare very tolerant, tolerant, intermediate, intolerant, and very intolerant species before and after Fran among samplings and different size classes of trees (Table 5.7).

My results showed that the hurricane significantly increased the dominance of pre-established, more shade-tolerant species, owing to advanced regeneration. Hurricane Fran greatly decreased pine dominance, and substantially increased hardwoods dominance in transition-phase loblolly pine stands. This wind event resulted in a significant increase of dominance of red maple in the oak forest. Some shade-intolerant species such as tuliptree, sweetgum and American hornbeam increased in the stands after Hurricane Fran, but their ability to influence stand tree diversity is still limited after only 5 years of hurricane recovery (Table 5.7).

The effects of hurricanes on forest succession trajectory

The hurricane disturbances had different effects on the dynamics of the pine stands and the hardwood stands. In the loblolly pine stands, the rate of forest succession towards a more mixed pine and hardwood forests was increased due to the selective damage on the large canopy pine trees and increased growth of light-demanding, understory hardwood trees. In the hardwoods, successional status became a diverse mosaic. Deciduous mixed-aged hardwood forests have been described as the mature, steady-state, or natural late successional forest' in Piedmont forests, but in their different stages of maturation the hardwoods experience somewhat different succession or recovery from disturbances. Recovery following disturbance of hardwood forests in the study area is complex since the hardwood forests are mixed with varied size small and large tree gaps and both early and late successional species due to the selective damage on canopy trees and increased growth of understory hardwood trees like red maple.

Ordination of selected control PSPs from 1933-2000 (Figure 5.6) and seven MPPs from 1978-2000 (Figure 5.7) summarizes overall change in species composition. As shown in

Figure 5.6, the 13 PSP controls show significant separation by forest types (pine stands vs. hardwood stands). There is strong evidence of consistency in directions of change across all plots in composition plots based on the orientation of the NMS succession vectors prior to 1997 Hurricane Fran. Three severely damaged PSP controls (PSPs 14, 19 and 50) shifted directions of succession vectors. These results imply that there was a consistent trend among plots in species composition change between 1933 and 1992/3 prior to Hurricane Fran. Hurricane-damaged PSP plots showed a similar direction and extent of compositional change to those no-hurricane-damaged controls (Figure 5.6).

The rate of succession was significantly increased for damaged pine and hardwood forests. NMS ordination clearly separates the seven mapped plots (Figure 5.7). The two pine mapped plots (Graveyard and Land's end) were on the right side of the ordination (the first and two axis of the ordination space) and move toward the upper side the space, and appeared to shift as similar direction and larger extent of compositional change after Hurricane Fran (Figure 5.7 see G 1997 and G 2000, L 1997 and L 2001). The damaged pine forest stands appeared to move at faster rates in the species space, whereas the hardwood forest stands were more stable after the hurricane damage.

DISCUSSION

Tree diversity dynamics during old-field succession

Changes in tree species diversity in the 20 selected pine PSPs in the Duke Forest over a nearly 70-year period are consistent with the four-stage succession model as proposed by Peet and Christensen (1988). The four-stage succession model predicts tree species diversity to increase during the initial establishment phase, decline during the highly competitive thinning phase, and then increase again during the transition phase. During the late

successional phase, species should either decline due to loss of the noncompetitive successional species, or if more isolated from source populations reach a new peak as new climax-specialist species slowly invade (Peet and Christensen 1980, 1988, Peet 1992). My results based on long-term records suggested that all pine forests in the transition phase (50-year after the plot was established) generally remain stable in or slightly increase in numbers of tree species.

Short-term effects of hurricanes on tree mortality and tree species diversity

The immediate effect of a large hurricane on species diversity at the stand-level is those trees most susceptible to wind damage. Consequently, immediately following a hurricane, tree mortality is high and drives changes in tree species composition and diversity. There is often an immediate drop in species number at a stand scale (1000 m²) following hurricane damage due to tree death. The degree of direct effect is controlled by both the actual stand damage level and pre-community attributes. A combination of intensity of windstorms and pre-hurricane community attributes may play a major role determining tree diversity dynamics.

The major biological effect of hurricane damage, as demonstrated in this paper, is to promote and synchronize regeneration and advanced growth. Species diversity of saplings quickly increases to levels that typically exceed those prior to the disturbance. This typically leads to a gradual increase in tree species diversity (sometimes by as much as a factor of two) in substantially damaged stands. This pattern has parallels in reports from other regions (Webb 1996, DeCoster et al. 1993).

Previous work on forest tree population dynamics (Peet and Christensen 1980) and species diversity (Peet and Christensen 1988) during secondary succession in North Carolina

Piedmont forests showed that species diversity is a dynamic process and that windthrow may be necessary for persistence of many species such as tuliptree and sweetgum. This prediction was consistent with change observed following Hurricanes Hazel and Fran, but the response was much more rapid than expected, being clearly evident after only five years.

Long-term effects of hurricanes on tree diversity in the Piedmont forests

Hurricanes often have been suggested to have a long-lasting effect on younger mixed-deciduous hardwood stands by allowing new species to invade owing to reduced competition and by affecting the balance of understory regeneration among species. However, as numerous studies on hurricane damage have pointed out, changes in diversity need to be examined over a long-term period following disturbance. In this study I use nearly 70 years of observation data to document that large, infrequent wind disturbance can increase stand level tree diversity. Duke Forest data show that a basal area loss of over 40% can lead to a significant increase in tree diversity over a 50-year period. Although small tree gaps caused by more frequently but lower intensity windstorms are too small to maintain species diversity (Beckage and Clark, 2000), extremely intense hurricanes, such as 1938 hurricane in New England (70-80% loss of BA), can decrease tree species diversity at local scale and initiate secondary successional.

The influences of historical hurricane disturbances on forest compositional trajectory

From a broad perspective, large-scale farming in 1800s and subsequently farmland abandonment from middle 1800s to early 1900s largely initialized secondary forest succession in the Piedmont region (Oosting 1942, Peet and Christensen 1980). Had large hurricanes not occurred, time and small natural disturbances (treefall gaps, ice storms)

would have slowly removed the over mature pine trees and therefore gradually led to replacement by hardwoods in a predictable manner (Peet and Christensen 1988).

The role of hurricanes on forest succession is varied and complex and depends on the juxtaposition of several biotic and abiotic factors. The hurricane impacts reported in this study were greater on pine forests than hardwood forests because hurricanes reduced pine dominance in stands with very little pine regeneration present in the understory. Past studies have also shown that the effects of catastrophic wind disturbances on forest succession may vary from setting back succession (Spurr 1956), to advancing successional stages, to initiating multiple-stages of succession (Allen and Sharitz 1998, Palmer et al. 2003), depending on wind intensity, frequency, forest type and pre-disturbance successional stage.

Hurricanes Fran and Hazel had varied effects but generally hastened the rate of pine replacement by hardwoods and therefore accelerated the succession process in even-aged loblolly pine. Hurricane Hazel impacted a thinning phase pine stand by removing pine trees, but had little effects on the overall tree composition and diversity; whereas Hurricane Fran also increased pine death but in addition accelerated the increase in dominance of red maple in the somewhat older pine stands owing to the greater advanced regeneration present in the understory.

In the Piedmont forest region, high intensity hurricanes impacts are rare relative to tree longevity, although less damaging hurricanes and other small-scale wind disturbances are more common. Wind intensity and frequency appear to be the two key factors that determine the extent of wind effects on forest dynamics and diversity in the Piedmont. The return interval of large wind events in the Duke Forest area is about 50 years, but the impact of such

events is patchy such that only a modest portion of the forest is actually badly impacted by such an event.

Alteration of succession in pine forests by large-scale hurricanes has been reported elsewhere in temperate forests. For example, the 1938 hurricane in New England heavily damaged *Pinus strobus*, advancing successional turnover to forests of hardwoods that were in some cases already present in the understory (Spurr 1956, Hibbs 1983, Foster 1988, Foster and Boose 1992). Hibbs (1983) reported that the 1938 hurricane, which caused as high as over 30 percent tree mortality (70-80% basal area loss) had long lasting effects on many aspects of these New England forests, including species composition, community structure and forest succession. Palmer et al. reported the same pattern in Minnesotan forests. This pattern may be particularly common in temperate old-field forests because of the high canopy stature and typically weaker wood associated with fast-growing successional species. On the other hand, frequent but moderate disturbance initiated by wind tends to have little long-term effects on forest structure, growth rates, or other ecosystem properties. This study of the relationship between hurricane damage and forest dynamics, like others (Abrams and Scott 1989, Putz and Sharitz 1991), suggests that the hurricane could accelerate forest succession in the temperate pine forests by removing the pioneer tree species in the canopy. This suggested that in many cases when even-aged pine trees are dominants, instantaneous death of even-aged canopy pine trees may tend to advance forest succession to a mixed or hardwood dominant forest (e.g., Arevola et al. 2000).

In summary, the Duke Forest has experienced considerable historical variation in disturbance agents with wind being the most common post 1900. Successional change in composition and diversity, while showing some consistent patterns discernable in long-term

data, is made extremely complex by the continuous overlay of disturbance events. My work has demonstrated the importance of combined long-term detailed tree demographic data and historical disturbance records for understanding forest dynamics. Although the patterns observed in the Duke forest and reported elsewhere still need further testing to assess their generality, they have the potential to apply widely in the temperate forests regions of the eastern United States.

LITERATURE CITED

- Abrams, M. D. and J. A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Canadian Journal of Forest Research* **20**:1864-1870.
- Abrams, M. D. and G. J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bulletin of the Torrey Botanical Club* **119**:19-28.
- Abrams, M. D., D. A. Orwig, and T. E. Demeo. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine mixed-oak forest in the southern Appalachians, USA. *Journal of Ecology* **83**:123-133.
- Abrams, M. D., D. A. Orwig, and T. E. Demeo. 1996. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine mixed-oak forest in the southern Appalachians, USA. *Journal of Ecology* **84**:328-328.
- Abrams, M. D., D. A. Orwig, and M. J. Dockry. 1997. Dendroecology and successional status of two contrasting old-growth oak forests in the Blue Ridge Mountains, USA. *Canadian Journal of Forest Research* **27**:994-1002.
- Abrams, M. D. and M. L. Scott. 1989. Disturbance-mediated accelerated succession in 2 Michigan forest types. *Forest Science* **35**:42-49.
- Abrams, M. D., D. G. Sprugel, and D. I. Dickmann. 1985. Multiple successional pathways on recently disturbed jack pine sites in Michigan. *Forest Ecology and Management* **10**:31-48.
- Armesto, J. J. and S. T. A. Pickett. 1986. Removal experiments to test mechanisms of plant succession in oldfields. *Vegetatio* **66**:85-93.
- Ashton, P. M. S., S. Gamage, I. Gunatilleke, and C. V. S. Gunatilleke. 1997. Restoration of a Sri Lankan rainforest: using Caribbean pine *Pinus caribaea* as a nurse for establishing late-successional tree species. *Journal of applied Ecology* **34**:915-925.
- Asselin, H., M. J. Fortin, and Y. Bergeron. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Quebec boreal forest. *Forest Ecology and Management* **140**:29-37.
- Battaglia, L. L., J. R. Keough, and D. W. Pritchett. 1995. Early secondary succession in a southeastern US alluvial floodplain. *Journal of Vegetation Science* **6**:769-776.
- Bazzaz, F. A. 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. *Ecology* **49**:924-936.
- Bazzaz, F. A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* **56**:485-488.

- Bazzaz, F. A. and S. T. A. Pickett. 1980. Physiological ecology of tropical succession - a comparative review. *Annual Review of Ecology and Systematics* **11**:287-310.
- Bazzaz, F. A. and S. E. Sultan. 1987. Ecological variation and the maintenance of plant diversity. Pages 69-93 *in* K. Urbanska, editor. *Differentiation Patterns in Higher Plants*. Academic Press, Orlando, Florida, USA.
- Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1995. Competition vs facilitation of tree seedling growth and survival in early successional communities. *Ecology* **76**:1156-1168.
- Bormann, F. H. 1953. Factors determining the role of loblolly pine and sweetgum in early old-field succession in the piedmont of North Carolina. *Ecological Monographs* **23**:339-358.
- Boucher, D. H., J. H. Vandermeer, I. G. De La Cerda, M. A. Mallona, I. Perfecto, and N. Zamora. 2001. Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. *Plant Ecology* **156**:131-137.
- Brown, R. L. and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. *Ecology* **84**:32-39.
- Burslem, D. and T. C. Whitmore. 1999. Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *Journal of Vegetation Science* **10**:767-776.
- Busing, R. T. 1995. Disturbance and the population-dynamics of *Liriodendron ulipifera* - simulations with a spatial model of forest succession. *Journal of Ecology* **83**:45-53.
- Busing, R. T. 1998. Composition, structure and diversity of cove forest stands in the Great Smoky Mountains: a patch dynamics perspective. *Journal of Vegetation Science* **9**:881-890.
- Busing, R. T. and P. S. White. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* **78**:562-568.
- Cain, M. D. and M. G. Shelton. 2001. Secondary forest succession following reproduction cutting on the upper coastal plain of southeastern Arkansas, USA. *Forest Ecology and Management* **146**:223-238.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**:426-429.
- Carson, W. P. and G. W. Barrett. 1988. Succession in old-field plant-communities - effects of contrasting types of nutrient enrichment. *Ecology* **69**:984-994.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of*

- Ecology and Systematics **31**:343-366.
- Chesson, P. and M. Pantasticoaldas. 1994. The forest architecture hypothesis for diversity maintenance. *Trends in Ecology & Evolution* **9**:79-80.
- Christensen, N. L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in piedmont, North Carolina. *American Midland Naturalist* **97**:178-188.
- Christensen, N. L. 1988. Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. Page 62-81 *in* J. K. Agee and D. R. Johnson, editors. *Ecosystem Management for Parks and Wilderness*. University of Washington Press, Seattle, Washington, USA.
- Christensen, N. L. and T. Macaller. 1985. Soil mineral nitrogen transformations during succession in the piedmont of North Carolina. *Soil Biology & Biochemistry* **17**:675-681.
- Christensen, N. L. and R. K. Peet. 1981. Secondary forest succession on the North Carolina piedmont. Pages 230-245 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest Succession: concepts and application*. Springer-Verlag, New York, New York, USA.
- Christensen, N. L. and R. K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* **72**:25-36.
- Clark, J. S. and J. S. Mclachlan. 2003. Stability of forest biodiversity. *Nature* **423**:635-638.
- Clebsch, E. E. C. and R. T. Busing. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology* **70**:728-735.
- Cohen, A. L., B. M. P. Singhakumara, and P. M. S. Ashton. 1995. Releasing rain forest succession: a case study in the *Dicranopteris linearis* fernlands of Sri Lanka. *Restoration Ecology* **3**:261-270.
- Coile, T. S. 1933. Soils reaction and forest types in the Duke Forest. *Ecology* **14**:323-333.
- Connell, J. H. and M. D. Lowman. 1989. Low-diversity tropical rain forests - some possible mechanisms for their existence. *American Naturalist* **134**:88-119.
- Connell, J. H., I. R. Noble, and R. O. Slatyer. 1987. On the mechanisms producing successional change. *Oikos* **50**:136-137.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Connell, J. H., J. G. Tracey, and L. J. Webb. 1984. Compensatory recruitment, growth, and

- mortality as factors maintaining rain-forest tree diversity. *Ecological Monographs* **54**:141-164.
- Dale, V. H. and R. H. Gardner. 1987. Assessing regional impacts of growth declines using a forest succession model. *Journal of Environmental Management* **24**:83-93.
- Dale, V. H., M. Hemstrom, and J. F. Franklin. 1986. Modeling the long-term effects of disturbances on forest succession, Olympic Peninsula, Washington. *Canadian Journal of Forest Research* **16**:56-67.
- De Grandpre, L. and Y. Bergeron. 1997. Diversity and stability of understorey communities following disturbance in the southern boreal forest. *Journal of Ecology* **85**:777-784.
- Denouden, J. and P. B. Alaback. 1996. Successional trends and biomass of mosses on windthrow mounds in the temperate rainforests of southeast Alaska. *Vegetatio* **124**:115-128.
- Denslow, J. S. 1980. Patterns of plant-species diversity during succession under different disturbance regimes. *Oecologia* **46**:18-21.
- Denslow, J. S. 1984. Influence of disturbance on species-diversity - reply. *Biotropica* **16**:240.
- Denslow, J. S. 1987. Tropical rain-forest gaps and tree species-diversity. *Annual Review of Ecology and Systematics* **18**:431-451.
- Denslow, J. S. 1995. Disturbance and diversity in tropical rain-forests - the density effect. *Ecological applications* **5**:962-968.
- Desteven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession - seedling emergence. *Ecology* **72**:1066-1075.
- Desteven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession - seedling survival and growth. *Ecology* **72**:1076-1088.
- Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. *Ecology* **54**:57-69.
- Elbayoumi, M. A., H. H. Shugart, and R. W. Wein. 1984. Modeling succession of eastern Canadian mixedwood forest. *Ecological Modelling* **21**:175-198.
- Elliott, K. J., L. R. Boring, and W. T. Swank. 1998. Changes in vegetation structure and diversity after grass-to-forest succession in a southern Appalachian watershed. *American Midland Naturalist* **140**:219-232.
- Elliott, K. J., L. R. Boring, W. T. Swank, and B. R. Haines. 1997. Successional changes in plant species diversity and composition after clearcutting a southern Appalachian watershed. *Forest Ecology and Management* **92**:67-85.

- Elliott, K. J. and D. L. Loftis. 1993. Vegetation diversity after logging in the southern Appalachians. *Conservation Biology* **7**:220-221.
- Elliott, K. J. and W. T. Swank. 1994. Changes in tree species-diversity after successive clearcuts in the southern Appalachians. *Vegetatio* **115**:11-18.
- Foster, B. L. and D. Tilman. 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. *Plant Ecology* **146**:1-10.
- Frelich, L. E. and P. B. Reich. 1995. Neighborhood effects, disturbance, and succession in forests of the western Great-Lakes region. *Ecoscience* **2**:148-158.
- Frelich, L. E. and P. B. Reich. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* **65**:325-346.
- Fukamachi, K., S. Iida, and T. Nakashizuka. 1996. Landscape patterns and plant species diversity of forest reserves in the Kanto region, Japan. *Vegetatio* **124**:107-114.
- Glitzenstein, J. S., P. A. Harcombe, and D. R. Streng. 1986. Disturbance, succession, and maintenance of species-diversity in an east Texas forest. *Ecological Monographs* **56**:243-258.
- Goldberg, D. E. and K. L. Gross. 1988. Disturbance regimes of mid-successional old fields. *Ecology* **69**:1677-1688.
- Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* **69**:1703-1715.
- Halpern, C. B. 1989. Early successional patterns of forest species - interactions of life-history traits and disturbance. *Ecology* **70**:704-720.
- Halpern, C. B., J. A. Antos, M. A. Geyer, and A. M. Olson. 1997. Species replacement during early secondary succession: the abrupt decline of a winter annual. *Ecology* **78**:621-631.
- Halpern, C. B., J. F. Franklin, and A. Mckee. 1992. Changes in plant-species diversity after harvest of Douglas-fir forests. *Northwest Environmental Journal* **8**:205-207.
- Halpern, C. B., P. M. Frenzen, J. E. Means, and J. F. Franklin. 1990. Plant succession in areas of scorched and blown-down forest after the 1980 eruption of Mount St. Helens, Washington. *Journal of Vegetation Science* **1**:181-194.
- Halpern, C. B. and T. A. Spies. 1995. Plant-species diversity in natural and managed forests of the Pacific-northwest. *Ecological applications* **5**:913-934.
- Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493-495.

- Harrod, J. C., M. E. Harmon, and P. S. White. 2000. Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. *Journal of Vegetation Science* **11**:465-472.
- Hartnett, D. C., B. B. Hartnett, and F. A. Bazzaz. 1987. Persistence of *Ambrosia trifida* populations in old fields and responses to successional changes. *American Journal of Botany* **74**:1239-1248.
- Harvey, B. D., A. Leduc, and Y. Bergeron. 1995. Early postharvest succession in relation to site type in the southern boreal forest of Quebec. *Canadian Journal of Forest Research* **25**:1658-1672.
- Hibbs, D. E. 1983. 40 years of forest succession in central New England. *Ecology* **64**:1394-1401.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. De Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**:554-557.
- Imbert, D., A. Rousteau, and P. Labbe. 1998. Hurricanes and biological diversity in tropical forests - the case of Guadeloupe. *Acta Oecologica-International Journal of Ecology* **19**:251-262.
- Inouye, R. S., N. J. Huntly, D. Tilman, J. R. Tester, M. Stillwell, and K. C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. *Ecology* **68**:12-26.
- Jentsch, A., C. Beierkuhnlein, and P. S. White. 2002. Scale, the dynamic stability of forest ecosystems, and the persistence of biodiversity. *Silva Fennica* **36**:393-400.
- Kapustka, L. A. A. K., R.G. 1979. The acceleration of succession of a birch-maple forest due to high wind. *Michigan Botanist* **18**:83-87.
- Keever, K. 1950. Causes of succession on old fields of the piedmont, North Carolina. *Ecological Monographs* **20**:229-250.
- Kirkman, L. K. and R. R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. *Ecological applications* **4**:177-188.
- Kruskal, J. B. (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, 29, 115-129.
- Kupfer, J. A. and J. R. Runkle. 1996. Early gap successional pathways in a *Fagus-Acer* forest preserve: pattern and determinants. *Journal of Vegetation Science* **7**:247-256.
- LaDeau S, Clark JS. 2001. Rising CO₂ and the fecundity of forest trees, *Science* 292:95-98.
- Lambers, J. H. R., J. S. Clark, and B. Beckage. 2002. Density-dependent mortality and the

- latitudinal gradient in species diversity. *Nature* **417**:732-735.
- Leigh, E. G., S. J. Wright, E. A. Herre, and F. E. Putz. 1993. The decline of tree diversity on newly isolated tropical islands - a test of a null hypothesis and some implications. *Evolutionary Ecology* **7**:76-102.
- Levin, S. A. 2000. Multiple scales and the maintenance of biodiversity. *Ecosystems* **3**:498-506.
- Levine, E. R., K. J. Ranson, J. A. Smith, D. L. Williams, R. G. Knox, H. H. Shugart, D. L. Urban, and W. T. Lawrence. 1993. Forest ecosystem dynamics - linking forest succession, soil process and radiation models. *Ecological Modelling* **65**:199-219.
- Liptzin, D. and P. M. S. Ashton. 1999. Early-successional dynamics of single-aged mixed hardwood stands in a southern New England forest, USA. *Forest Ecology and Management* **116**:141-150.
- Maily, D., J. P. Kimmins, and R. T. Busing. 2000. Disturbance and succession in a coniferous forest of northwestern North America: simulations with dryades, spatial gap model. *Ecological Modelling* **127**:183-205.
- Mather, P.M. (1976) *Computational Methods of Multivariate Analysis in Physical Geography*. J.Wiley & Sons, London.
- McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.
- McCune, B. & Mefford, M.J. (1999) *PC-ORD. Multivariate Analysis of Ecological Data, Version 4.24*. MjM Software, Gleneden Beach, Oregon.
- McCook, L. J. 1994. Understanding ecological community succession - causal-models and theories, a review. *Vegetatio* **110**:115-147.
- McCune, B. and G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. *Ecology* **66**:1270-1278.
- McDonald, R.I., R.K. Peet, and D.L. Urban. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea* **67**:84-95.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2003. Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a piedmont forest. *Journal of Vegetation Science* **14**:441-450.
- McLachlan, J. S., D. R. Foster, and F. Menalled. 2000. Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. *Ecology* **81**:717-733.
- McQuillan, N. E. 1940. The natural establishment of pine in abandoned fields in the

- piedmont plateau region. *Ecology* **21**:135-147.
- Mikan, C. J., D. A. Orwig, and M. D. Abrams. 1994. Age structure and successional dynamics of a presettlement-origin chestnut oak forest in the Pennsylvania piedmont. *Bulletin of the Torrey Botanical Club* **121**:13-23.
- Myster, R. W. and S. T. A. Pickett. 1988. Individualistic patterns of annuals and biennials in early successional oldfields. *Vegetatio* **78**:53-60.
- Myster, R. W. and S. T. A. Pickett. 1990. Initial conditions, history and successional pathways in 10 contrasting old fields. *American Midland Naturalist* **124**:231-238.
- Myster, R. W. and S. T. A. Pickett. 1992. Dynamics of associations between plants in 10 old fields during 31 years of succession. *Journal of Ecology* **80**:291-302.
- Myster, R. W. and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology* **75**:387-392.
- Myster, R. W. and L. R. Walker. 1997. Plant successional pathways on Puerto Rican landslides. *Journal of Tropical Ecology* **13**:165-173.
- Nagaike, T., T. Kamitani, and T. Nakashizuka. 1999. The effect of shelterwood logging on the diversity of plant species in a beech (*Fagus crenata*) forest in Japan. *Forest Ecology and Management* **118**:161-171.
- Nagaike, T., T. Kamitani, and T. Nakashizuka. 2003. Plant species diversity in abandoned coppice forests in a temperate deciduous forest area of central Japan. *Plant Ecology* **166**:145-156.
- Nicholson, S. A. and C. D. Monk. 1974. Plant species diversity in old-field succession on the Georgia piedmont. *Ecology* **55**:1075-1085.
- Okuda, T., N. Kachi, S. K. Yap, and N. Manokaran. 1997. Tree distribution pattern and fate of juveniles in a lowland tropical rain forest - implications for regeneration and maintenance of species diversity. *Plant Ecology* **131**:155-171.
- Omacini, M., E. J. Chaneton, R. J. C. Leon, and W. B. Batista. 1995. Old-field successional dynamics on the inland Pampa, Argentina. *Journal of Vegetation Science* **6**:309-316.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of piedmont, North Carolina. *American Midland Naturalist* **28**:1-126.
- Palik, B. J., R. J. Mitchell, and J. K. Hiers. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *Forest Ecology and Management* **155**:347-356.
- Palmer, M. A. 1990. Vascular flora of the Duke Forest, North Carolina. *Castanea* **55**:229-

- Palmer, M. W. 1991. Patterns of species richness among North Carolina hardwood forests - tests of 2 hypotheses. *Journal of Vegetation Science* **2**:361-366.
- Parrish, J. A. D. and F. A. Bazzaz. 1982. Competitive interactions in plant-communities of different successional ages. *Ecology* **63**:314-320.
- Pastor, J., R. H. Gardner, V. H. Dale, and W. M. Post. 1987. Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North-America. *Canadian Journal of Forest Research* **17**:1394-1400.
- Payton, I. J., R. B. Allen, and J. E. Knowlton. 1984. A post-fire succession in the northern Urewera forests North Island, New Zealand. *New Zealand Journal of Botany* **22**:207-222.
- Peet, R. K. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics* **5**:285-307.
- Peet, R. K. 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* **37**:65-78.
- Peet, R. K. 1981. Forest vegetation of the Colorado Front Range - composition and dynamics. *Vegetatio* **45**:3-75.
- Peet, R. K. 1984. 26 years of change in a pinus-strobus, acer-saccharum forest, Lake Itasca, Minnesota. *Bulletin of the Torrey Botanical Club* **111**:61-68.
- Peet, R. K. 1992. Community structure and ecosystem properties. Pages 102-151 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession: theory and prediction*. Chapman and Hall, London.
- Peet, R. K. and N. L. Christensen. 1980. Hardwood forest vegetation of the North Carolina piedmont. Pages 14-39 *in* Veröff. Geobot. Inst. ETH Stiftung Rübel.
- Peet, R. K. and N. L. Christensen. 1980. Succession - a population process. *Vegetatio* **43**:131-140.
- Peet, R. K. and N. L. Christensen. 1987. Competition and tree death. *Bioscience* **37**:586-595.
- Peet, R. K. and N. L. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina piedmont. Pages 233-245 *in* H. J. During, M. J. A. Werger, and J. Willems, editors. *Diversity and pattern in plant communities*. SPB Publishers. The Hague. The Netherlands.
- Peet, R. K., P.A. Harcombe and G.R. Parker. 1991. Rates and patterns of mortality in eastern deciduous forests: a comparative study. *Bulletin of the Ecological Society of America* **72**:217.

- Peroni, P. A. 1994. Invasion of red maple (*Acer rubrum*) during old field succession in the North Carolina piedmont - age structure of red maple in young pine stands. *Bulletin of the Torrey Botanical Club* **121**:357-359.
- Peroni, P. A. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. *American Journal of Botany* **81**:1428-1434.
- Peterson, C. J. and B. L. Haines. 2000. Early successional patterns and potential facilitation of woody plant colonization by rotting logs in premontane Costa Rican pastures. *Restoration Ecology* **8**:361-369.
- Philippi, T. E., R. K. Peet, and N. L. Christensen. 1992. Survivorship and growth of *Acer rubrum* seedlings in stands representing different successional stages from old-field pinus taeda to mature mixed hardwoods. *Bulletin of the Ecological Society of America* **73(Suppl.)**:304-305.
- Pickett, S. T. A. 1982. Population-patterns through 20 years of oldfield succession. *Vegetatio* **49**:45-59.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**:109-114.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. *Botanical Review* **53**:335-371.
- Pickett, S. T. A. and M. J. McDonnell. 1989. Changing perspectives in community dynamics - a theory of successional forces. *Trends in Ecology & Evolution* **4**:241-245.
- Poulson, T. L. and W. J. Platt. 1989. Gap light regimes influence canopy tree diversity. *Ecology* **70**:553-555.
- Prach, K., S. Bartha, C. B. Joyce, P. Pysek, R. Van Diggelen, and G. Wiegand. 2001. The role of spontaneous vegetation succession in ecosystem restoration: a perspective. *Applied Vegetation Science* **4**:111-114.
- Rankin, W. T. and S. T. A. Pickett. 1989. Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. *Bulletin of the Torrey Botanical Club* **116**:182-186.
- Reed, R. A., R. K. Peet, M. W. Palmer, and P. S. White. 1993. Scale dependence of vegetation-environment correlations - a case-study of a North Carolina piedmont woodland. *Journal of Vegetation Science* **4**:329-340.
- Reich, P. B., P. Bakken, D. Carlson, L. E. Frelich, S. K. Friedman, and D. F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. *Ecology* **82**:2731-2748.
- Roberts, M. R. and N. L. Christensen. 1988. Vegetation variation among mesic successional

- forest stands in northern lower Michigan. *Canadian Journal of Botany* **66**:1080-1090.
- Runkle, J. R. 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree species-diversity. *Ecology* **70**:546-547.
- Savage, M., M. Reid, and T. T. Veblen. 1992. Diversity and disturbance in a Colorado sub-alpine forest. *Physical Geography* **13**:240-249.
- Schafale, M. and N. L. Christensen. 1986. Vegetational variation among old fields in piedmont North Carolina. *Bulletin of the Torrey Botanical Club* **113**:413-420.
- Schmitt, S. and R. J. Whittaker. 1998. Disturbance and succession on the Krakatau Islands, Indonesia. Pages 515-548 *in* D. M. Newbery, H. N. T. Prins, and N. D. Brown, editors. *Dynamics of Tropical Communities*, British Ecological Society Symposium Volume. Blackwell Science. Oxford, UK.
- Schnitzer, S. A. and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* **82**:913-919.
- Sheil, D. 1999. Developing tests of successional hypotheses with size-structured populations, and an assessment using long-term data from a Ugandan rain forest. *Plant Ecology* **140**:117-127.
- Sheil, D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecology* **155**:183-199.
- Shugart, H. H. 1984. *A theory of forest dynamics: the ecological implication of forest succession models*. Springer-Verlag. New York, USA.
- Shugart, H. H. and D. C. West. 1980. Forest succession models. *Bioscience* **30**:308-313.
- Smith, G. F., N. S. Nicholas, and S. M. Zedaker. 1997. Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. *Forest Ecology and Management* **95**:275-283.
- Sousa, W. P. 1980. The responses of a community to disturbance - the importance of successional age and species life histories. *Oecologia* **45**:72-81.
- Symstad, A. J., F. S. Chapin, D. H. Wall, K. L. Gross, L. F. Huenneke, G. G. Mittelbach, D. P. C. Peters, and D. Tilman. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience* **53**:89-98.
- Tanner, J. E., T. P. Hughes, and J. H. Connell. 1994. Species coexistence, keystone species, and succession - a sensitivity analysis. *Ecology* **75**:2204-2219.
- Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecological applications* **9**:864-879.

- Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. *Ecology* **67**:555-563.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* **57**:189-214.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350-363.
- Tilman, D. 1997. Distinguishing between the effects of species diversity and species composition. *Oikos* **80**:185.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**:1455-1474.
- Tilman, D. 1999. Ecology - diversity by default. *Science* **283**:495-496.
- Tilman, D. 2000. Causes, consequences and ethics of biodiversity. *Nature* **405**:208-211.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300-1302.
- Tilman, D. and C. Lehman. 2002. Biodiversity, composition, and ecosystem processes: theory and concepts. Page 9-41 *in* a. Kinzig, S. Pacala, and D. Tilman, editors. *Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton University Press, New Jersey, USA.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist* **151**:277-282.
- Tilman, D., S. Naeem, J. Knops, P. Reich, E. Siemann, D. Wedin, M. Ritchie, and J. Lawton. 1997. Biodiversity and ecosystem properties. *Science* **278**:1866-1867.
- Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* **1**:511-523.
- Urban, D. L. and H. H. Shugart. 1992. Individual-based models of forest succession. Pages 249-292 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession: theory and prediction*. Chapman and Hall, London. UK.
- Vandermeer, J., D. Boucher, I. Perfecto, and I. G. Delacerda. 1996. A theory of disturbance and species diversity: evidence from Nicaragua after Hurricane Joan. *Biotropica* **28**:600-613.
- Vandermeer, J., I. G. De La Cerda, D. Boucher, I. Perfecto, and J. Ruiz. 2000. Hurricane disturbance and tropical tree species diversity. *Science* **290**:788-791.

- Vanpelt, R., T. A. Spies, and J. F. Franklin. 1992. Disturbance succession and species interactions around canopy gaps in old-growth Douglas-fir forests. *Northwest Environmental Journal* **8**:210-211.
- Walker, L. R. and F. S. Chapin. 1987. Interactions among processes controlling successional change. *Oikos* **50**:131-135.
- Walker, L. R., D. J. Zarin, N. Fetcher, R. W. Myster, and A. H. Johnson. 1996. Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica* **28**:566-576.
- White, P. S. and J. Harrod. 1997. Disturbance and diversity in a landscape context. Pages 128-159 *in* J. Bissonette, editor. *Wildlife and landscapes*. Springer-Verlag, New York, USA.
- White, P. S. and A. Jentsch. 2004. Disturbance, succession, and community assembly in terrestrial plant communities. Pages 342-366 *in* V. Temperton, R. Hobbs, and S. Halle, editors. *Assembly Rules and Restoration Ecology*. Island Press, California, USA.
- Whitmore, T. C. 1985. Forest succession. *Nature* **315**:692.
- Wilson, E. O. 1992. *The diversity of life*. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- Wimberly, M. C. and T. A. Spies. 2002. Landscape- vs gap-level controls on the abundance of a fire-sensitive, late-successional tree species. *Ecosystems* **5**:232-243.
- Wiser, S. K., R. B. Allen, and K. H. Platt. 1997. Mountain beech forest succession after a fire at Mount Thomas Forest, Canterbury, New Zealand. *New Zealand Journal of Botany* **35**:505-515.
- Zobel, K., M. Zobel, and R. K. Peet. 1993. Change in pattern diversity during secondary succession in Estonian forests. *Journal of Vegetation Science* **4**:489-498.

Table 5.1a. Characteristics of 20 selected permanent sample plots (PSPs) in the Duke Forest, North Carolina, USA. The percentage of basal area change before and after the hurricanes was as a measurement of plot-level damage severity. The time period during which this basal area change occurred for Hurricane Hazel was from 1950 to 1954, and for Fran was from 1993-1997.

Plot number	Size (m ²)	Initial trees	Trees 1992	Stand age in 1992	Size-class density (100 m ²) in 1992				Changes in basal area % [#]	
					1*	2	3	4	1954 Hazel	1996 Fran
<u>Loblolly pine stands</u>										
PSP 23	404	1172	228	71	1.98	4.2	55.56	59.75	-1.07	22.52
PSP 50	900	311	137	90	2.87	5.24	12.25	17.49	7.76	-28.19
PSP 17	404	149	139	71	2.96	6.17	33.09	39.26	2.91	4.78
PSP 21	404	431	144	71	2.96	7.41	31.11	38.52	-3.19	-4.04
PSP 20	404	261	164	71	3.21	7.41	49.88	57.28	-9.71	8.57
PSP 22	404	511	100	71	3.21	5.68	27.4	33.09	4.74	-10.76
PSP 39	808	197	159	77	3.21	8.77	15.06	24.09	7.68	-11.67
PSP 12	404	25	89	71	3.26	7.01	16.63	23.46	11.18	6.81
PSP 26	1012	331	198	81	3.36	8.5	16.5	25	-3.7	5.17
PSP 19	404	236	101	71	3.46	5.19	26.42	31.6	0.89	-17.64
PSP 14	404	51	122	71	3.95	6.67	27.9	34.57	4.77	-37.39
PSP 28	808	464	328	77	3.95	6.54	37.28	44.57	-8.83	5.52
PSP 40	808	475	136	77	4.01	9.63	11.23	21.1	-8.69	-19.52
PSP 15	404	79	140	71	4.2	7.41	30.12	37.53	0.52	10.77
<u>Upland hardwoods</u>										
PSP 36	1365	145	528	mixed	1.03	3.66	30.48	34.14	-6.67	5.4
PSP 37	1440	96	704	mixed	1.25	4.33	37.85	42.15	-42	-2.94
PSP 35	1012	186	402	mixed	1.88	5.73	29.45	35.18	5.2	5.12
PSP 44	1118	237	171	mixed	1.97	4.29	12.25	16.55	N/A	7.98
PSP 10	1025	319	262	mixed	2.47	6.23	19.66	25.89	-0.99	-4.24
PSP 43	1012	230	184	mixed	3.16	5.63	11.66	17.29	-33.25	6.75

* Tree size classes are: 1: d.b.h. >25 cm; 2: 25 cm >= d.b.h. >10 cm; 3: 10 cm >=d.b.h. >1 cm; and 4: 1 cm>= d.b.h.>0 cm.

Table 5.1b. Characteristics of the seven mapped plots (MPPs) in the Duke Forest, North Carolina, USA.

Name	Location	Size (m ²)	Establishment	Habitat	Disturbance history
<u>Loblolly pine stands</u>					
Graveyard	Korstian Division	13,000	1978	Dry upland	Old field, abandoned circa 1916 Some salvage cutting following Hurricane Hazel in 1954
Land's end	Korstian Division	9,900	1978	Dry upland	Old field, abandoned circa 1895
<u>Upland hardwood stands</u>					
Rocky	Korstian Division	20,400	1978	Dry upland	Selective cutting prior to 1930
Wooden Bridge	Korstian Division	5,250	1984	Dry mesic upland	Selective cutting prior to 1930
Bormann	Durham Division	19,600	1952	Dry upland	Selective cutting prior to 1930
Bryan Center	Duke Univ. Campus	19,400	1986	Dry mesic upland	Major damage circa 1780
Oosting	Natural area	65,536	1990	Dry mesic upland	Selective cutting prior to 1900

Table 5.2. Changes in species richness (S) and diversity ($\exp H'$) of 14 selected permanent sampling controls in the Duke Forest, North Carolina, USA. The first number in each column is tree species richness; the second number in each column (parentheses) is the Shannon-Weiner's index of diversity ($\exp H'$).

Plot #	Size (m ²)	Initial age	1933	1978	1984	1988	1992	1997	2000
<u>Loblolly pine stands</u>									
PSP 12	404	8	1 (1.0000)	NA	12 (8.5353)	11 (7.9232)	11 (7.9512)	11 (7.4645)	NA/NA
PSP 14	404	8	1 (1.0000)	NA	16 (6.6154)	17 (7.7886)	16 (8.3904)	16 (9.0680)	19 (11.1141)
PSP 15	404	8	1 (1.0000)	NA	15 (10.000)	16 (10.7262)	16 (11.0076)	16 (11.3203)	14 (11.1901)
PSP 17	404	8	2 (1.1042)	NA	12 (2.9838)	18 (4.5428)	18 (6.1187)	19 (9.5287)	18 (11.1238)
PSP 19	404	8	3 (1.2683)	NA	14 (7.1827)	15 (8.5504)	15 (9.9931)	15 (11.2561)	15 (10.2689)
PSP 21	404	8	2 (1.0542)	NA	14 (4.8443)	15 (5.1785)	16 (6.0311)	16 (7.9726)	17 (10.0368)
PSP 23	404	8	2 (1.0184)	NA	14 (5.792)	16 (7.3026)	17 (8.1625)	17 (8.2203)	16 (7.8364)
PSP 26	1012	19	12(3.7792)	12(7.1515)	13 (7.2123)	10 (6.7559)	9 (6.7393)	8 (6.7004)	8 (6.7475)
PSP 28	808	15	2 (1.1786)	NA	15 (7.2449)	16 (7.1141)	17 (6.9715)	14 (6.4913)	14 (6.3946)
PSP 40	808	15	11(1.5840)	20(10.4373)	18(9.7032)	18(9.2682)	15(8.6748)	13(8.7567)	13(9.4329)
PSP 50	900	25	19(6.2320)	NA	16 (9.6542)	15 (9.6982)	20 (11.5307)	20 (12.3108)	22 (13.5233)
<u>Upland hardwoods</u>									
PSP10	1025	Mixed	17(4.8266)	14(6.9402)	18(9.5627)	19(10.2783)	21(11.0939)	22(11.5937)	19(10.5794)
PSP35	1012	Mixed	11(4.0750)	14(6.5184)	21(9.0400)	21(7.5643)	21(7.2089)	21(7.1473)	22(7.3255)
PSP36	1365	Mixed	10(6.0827)	14(5.5299)	15(7.2835)	13(6.9607)	13(6.9747)	13(6.3098)	12(5.9329)
PSP44	1118	Mixed	24(9.6961)	21(11.3243)	27(15.4568)	24(13.3740)	25(12.8620)	24(12.4261)	25(13.4068)

*(For trees d.b.h.>1.25 cm)

Table 5.3. Changes in species richness (S) and diversity ($\exp H'$) of 6 selected Permanent Sample Plots in the Duke Forest, North Carolina, USA. These plots were damaged by Hurricane Hazel in 1954, and some had a thinning manipulation prior to Hazel. The first number in each column is tree species richness; the second number in each column (parentheses) is the Shannon-Weiner's index of diversity ($\exp H'$).

Plot #	Size (m ²)	Initial age	1933	1978	1984	1988	1992	1997	2001
<u>Control pine plot with Hazel damage</u>									
PSP 40	808	15	11(1.5840)	20(10.4373)	18(9.7032)	18(9.2682)	15(8.6748)	13(8.7567)	13(9.4329)
<u>Control hardwood plot with Hazel damage</u>									
PSP 37	1440	Mixed	9(5.3307)	20(12.1846)	22(10.5120)	23(9.6233)	22(9.1808)	24(8.6587)	23(9.1352)
<u>Thinning pine stands with Hazel damage</u>									
PSP20	400	8	1(1.0000)	NA	11(3.7199)	12(3.9057)	12(4.9227)	12(5.6627)	13(6.0889)
PSP22	400	8	2(1.0473)	NA	14(6.3711)	16(6.1663)	17(6.9051)	17(8.0754)	16(9.2020)
PSP39	808	15	3(1.1191)	16(8.5174)	15(7.2941)	13(7.1808)	14(7.5578)	13(7.5171)	16(8.0189)
<u>Thinning hardwood plus with Hazel damage</u>									
PSP43	1102	Mixed	16(8.9690)	17(9.1396)	20(9.2324)	21(9.5785)	19(9.3301)	22 (10.3146)	20(9.3019)

*(For trees d.b.h.>1.25 cm)

Table 5.4a. Effect of Hurricane Hazel on tree establishment and tree diversity in a moderately damaged upland hardwood forests (PSP 36) in the Duke Forest, North Carolina, USA.

Diameter Class ¹	1934				1949				1977				1984			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Species																
<i>Oxydendrum arboreum</i>	1 ²	7	8	1	0	6	9	1	5	9	10	0	5	17	15	0
<i>Quercus velutina</i>	0	0	2	1	0	0	2	1	0	0	0	2	1	0	0	1
<i>Carya spp.</i>	5	4	19	1	2	2	17	2	3	0	7	7	4	0	5	7
<i>Juniperus virginiana</i>	9	7	1	0	3	5	3	0	1	1	3	0	6	1	3	0
<i>Cornus florida</i>	7	35	10	0	1	24	9	0	44	19	7	0	27	18	6	0
<i>Quercus coccinea</i>	0	1	4	3	0	0	2	4	1	0	0	1	1	0	1	0
<i>Quercus alba</i>	1	1	2	3	0	1	1	4	0	1	1	4	0	0	2	4
<i>Acer rubrum</i>	0	1	1	0	0	1	1	0	4	0	2	0	13	0	2	0
<i>Liriodendron tulipifera</i>	0	0	20	0	0	1	1	2	0	0	0	2	0	0	0	3
<i>Nyssa sylvatica</i>	0	1	2	0	0	1	2	0	4	0	1	0	5	0	2	0
<i>Quercus stellata</i>									1	0	0	0	-	-	-	-
<i>Quercus rubra</i>									1	0	0	0	2	0	0	0
<i>Carpinus carolina</i>									1	0	0	0	1	0	0	0
<i>Ostrya virginiana</i>									0	1	0	0	0	1	0	0
<i>Chionanthus virginianus</i>													1	0	0	0
<i>Quercus falcata</i>													1	0	0	0
Total	23	57	51	9	6	40	47	13	65	30	31	16	67	37	35	15

¹ Diameter classes of trees (d.b.h.) are (1) 2.5-5 cm, (2) 5-10 cm, (3) 10-25 cm, and (4) >25 cm.

² Densities are in stems per 0.1 ha.

Table 5.4b. Effect of Hurricane Hazel on tree establishment and tree diversity in a significantly damaged upland hardwood forests (PSP 37) in the Duke Forest, North Carolina, USA.

Diameter Class ¹	1934				1949				1978				1984			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<i>Carya spp.</i>	2 ²	10	5	0	1	6	2	1	11	1	0	0	30	5	1	0
<i>Cornus florida</i>	3	21	5	0	0	17	5	0	44	19	7	0	10	10	6	0
<i>Quercus alba</i>	0	4	7	17	0	1	5	19	1	1	4	0	3	1	3	15
<i>Juniperus virginiana</i>	3	2	1	0	0	2	1	0	9	5	1	0	19	7	3	0
<i>Oxydendrum arboreum</i>	0	4	4	0	0	2	3	0	5	9	10	0	24	9	7	1
<i>Quercus rubra</i>	0	1	1	0	0	0	2	0	0	0	1	0	1	1	2	0
<i>Acer rubrum</i>	0	1	0	0	0	1	1	0	15	6	0	0	13	0	2	0
<i>Nyssa sylvatica</i>	0	1	0	0	0	1	2	0	3	0	0	0	7	1	0	0
<i>Quercus velutina</i>	0	0	0	1					2	1	0	0	4	3	0	0
<i>Quercus falcata</i>									1	0	0	0	3	1	0	0
<i>Ulmus alata</i>									1	0	0	0	0	1	0	0
<i>Sassafras albidum</i>									7	5	0	0	9	6	0	0
<i>Liriodendron tulipifera</i>									10	9	1	0	7	11	1	0
<i>Pinus virginiana</i>													1	7	5	0
<i>Pinus taeda</i>													1	10	11	1
<i>Fraxinus sp.</i>													1	0	0	0
<i>Prunus serotina</i>													3	2	0	0
<i>Diospyrus virginianus</i>													4	1	0	0
<i>Ostrya virginiana</i>													0	1	0	0
<i>Chionanthus virginianus</i>													1	0	0	0
<i>Ostrya virginiana</i>													0	3	0	0
Total	8	44	23	18	1	30	21	20	109	56	24	0	141	80	41	17

¹ Diameter classes of trees (d.b.h.) are (1) 2.5-5 cm, (2) 5-10 cm, (3) 10-25 cm, and (4) >25 cm. ² Densities are in stems per 0.1 ha.

Table 5.5a. Community composition and population change over 12-year period in a 1.3 ha loblolly pine permanent plot (Graveyard plot) in the Duke Forest, North Carolina, USA.

Species	Density (stems/plot)										
	Live					Dead			Ingrowth		
	1989	1992	1997	2001	2010 ^a	1992	1997	2001	1992	1997	2001
<i>Acer barbatum</i>	6	8	10	31	96	0	0	2	2	2	23
<i>Acer rubrum</i>	927	896	734	792	855	74	150	142	43	0	200
<i>Aesculus sylvatica</i>	9	9	11	8	6	0	1	4	0	3	1
<i>Ailanthus altissima</i>	0	2	0	0	0	0	0	0	0	0	2
<i>Carpinus carolina</i>	191	160	116	148	189	37	44	13	6	0	45
<i>Carya spp.</i>	528	502	387	399	411	37	112	29	11	0	41
<i>Cercis canadensis</i>	10	15	8	11	15	2	7	1	7	0	4
<i>Celtis laevigata</i>	2	2	1	1	1	1	1	0	1	0	0
<i>Celtis occidentalis</i>	2	3	1	1	1	0	2	0	1	0	0
<i>Cornus florida</i>	528	563	426	353	293	59	152	165	94	15	92
<i>Diospyros virginiana</i>	2	0	0	0	0	0	0	0	0	0	0
<i>Fagus grandifolia</i>	9	14	19	63	209	0	3	0	5	8	44
<i>Fraxinus spp.</i>	18	17	16	20	25	2	4	1	1	3	5
<i>Ilex deciduas</i>	1	1	0	0	0	0	1	0	0	0	0
<i>Ilex opaca</i>	1	1	1	2	4	0	0	0	0	0	1
<i>Juglans nigra</i>	9	9	7	6	5	0	2	1	0	0	0
<i>Juniperus virginiana</i>	31	25	13	14	15	8	13	1	2	1	2
<i>Liquidambar styraciflua</i>	364	331	269	313	364	38	60	28	5	0	72
<i>Liriodendron tulipifera</i>	150	141	124	148	177	4	14	14	0	0	38
<i>Morus rubra</i>	1	1	1	2	4	0	1	0	0	1	1
<i>Nyssa sylvatica</i>	34	33	24	23	22	1	9	3	0	0	2
<i>Ostrya virginiana</i>	120	140	147	365	906	10	10	15	30	17	233
<i>Oxydendrum arboreum</i>	136	130	104	124	148	7	28	9	1	2	29
<i>Pinus taeda</i>	277	279	208	176	149	5	67	35	7	0	3
<i>Prunus serotina</i>	3	3	2	11	60	0	2	0	0	1	9
<i>Quercus alba</i>	43	33	21	21	21	9	10	1	0	0	1
<i>Quercus coccinea</i>	3	3	1	1	1	0	2	0	0	0	0
<i>Quercus spp.</i>	1	1	0	1	0	0	1	0	0	0	1
<i>Quercus falcata</i>	6	5	4	2	1	0	1	2	0	0	0
<i>Quercus rubra</i>	24	19	12	15	19	3	6	2	0	0	5
<i>Quercus velutina</i>	60	45	30	21	15	13	14	10	0	0	1
<i>Sassafras albidum</i>	4	4	3	3	3	0	1	1	0	0	1
<i>Ulmus alata</i>	17	19	17	21	26	1	2	2	3	0	6
<i>Ulmus americana</i>	7	6	1	2	4	1	5	1	0	0	2
<i>Ulmus rubra</i>	33	37	35	34	33	2	5	5	6	3	4
Unknown species	0	1	0	0	0	0	0	0	0	0	1
<i>Vaccinium corymbosum</i>	5	2	0	0	0	2	2	0	0	0	0
<i>Viburnum acerifolium</i>	0	1	0	0	0	0	0	0	0	0	1
<i>Viburnum prunifolium</i>	0	1	0	0	0	0	0	0	0	0	1
<i>Viburnum rafinesquianum</i>	2	3	4	5	0	0	2	0	1	3	1
<i>Vitis rubra</i>	0	3	0	0	0	0	0	0	0	0	3
Total	3564	3460	2757	3145	3588	316	734	487	212	31	875

^a Projected community composition in 2010, 9 years after the latest actually measurement, assuming exponential growth with constant intrinsic rate of increase.

Table 5.5b. Community composition and population change over 11-year period on a 1.96 ha white oak permanent plot (Bormann plot) in the Duke Forest, North Carolina, USA.

Species	Density (stems/plot)										
	Live					Dead			Ingrowth		
	1989	1992	1997	2001	2010 ^a	1992	1997	2001	1992	1997	2001
<i>Acer barbatum</i>	1	1	2	2	2	0	0	0	0	1	0
<i>Acer rubrum</i>	1517	1642	1572	2070	3128	111	138	97	236	68	595
<i>Amelanchier arborea</i>	3	3	2	2	2	0	1	0	0	0	0
<i>Carpinus carolina</i>	0	0	1	0	0	0	0	0	0	0	1
<i>Carya spp.</i>	154	174	161	213	324	13	20	17	33	7	69
<i>Celtis occidentalis</i>	1	1	3	0	0	0	0	0	1	0	2
<i>Chionanthus virginicus</i>	10	13	15	15	15	1	1	1	4	3	1
<i>Cornus florida</i>	717	804	651	540	408	99	208	213	186	55	102
<i>Crataegus spp.</i>	2	6	4	5	7	0	2	0	4	0	1
<i>Diospyros virginiana</i>	6	5	5	5	5	1	0	0	0	0	0
<i>Fagus grandifolia</i>	0	0	1	2	6	0	0	0	0	1	1
<i>Fraxinus spp.</i>	9	10	7	15	47	0	2	1	1	0	9
<i>Ilex opaca</i>	0	0	1	1	1	0	0	0	0	1	0
<i>Juglans nigra</i>	0	0	0	1	0	0	0	0	0	0	1
<i>Juniperus virginiana</i>	35	36	37	38	40	1	5	4	2	6	5
<i>Liquidambar styraciflua</i>	1	1	2	4	11	0	0	0	0	1	2
<i>Liriodendron tulipifera</i>	19	21	18	76	659	1	4	1	3	1	59
<i>Morus rubra</i>	6	8	6	7	9	0	1	1	2	0	2
<i>Nyssa sylvatica</i>	192	172	159	158	157	27	20	14	7	7	13
<i>Ostrya virginiana</i>	0	1	1	0	0	0	0	1	0	1	1
<i>Oxydendrum arboreum</i>	494	472	430	467	529	31	48	32	9	6	69
<i>Pinus spp.</i>	4	4	4	4	4	0	0	0	0	0	0
<i>Prunus serotina</i>	38	55	57	137	510	3	6	6	20	8	86
<i>Quercus alba</i>	283	276	228	194	152	12	43	34	5	0	0
<i>Quercus coccinea</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Quercus falcata</i>	4	3	3	4	6	1	0	0	0	0	1
<i>Quercus rubra</i>	52	53	46	47	49	4	6	8	5	0	9
<i>Quercus stellata</i>	13	11	10	8	6	2	1	2	0	0	0
<i>Quercus velutina</i>	40	41	31	53	118	3	8	6	4	0	28
<i>Sassafras albidum</i>	1	1	1	2	6	0	0	0	0	0	1
<i>Styrax grandifolia</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Ulmus alata</i>	3	3	3	3	3	0	0	0	0	0	0
<i>Ulmus rubra</i>	1	1	0	1	0	0	1	0	0	0	1
<i>Unknown species</i>	0	0	0	1	0	0	0	0	0	0	1
<i>Viburnum prunifolium</i>	18	35	36	36	36	0	5	4	17	6	4
<i>Viburnum rafinesquianum</i>	0	21	30	56	143	0	5	10	21	14	36
<i>Vitis rotundifolia</i>	0	0	0	3	0	0	0	0	0	0	3
<i>Vitis rubra</i>	19	27	22	21	20	0	5	4	8	0	3
Total	3642	3900	3546	4196	5401	310	530	456	568	176	1106

^a Projected community composition in 2010, 10 years after the latest actually measurement, assuming exponential growth with constant intrinsic rate of increase.

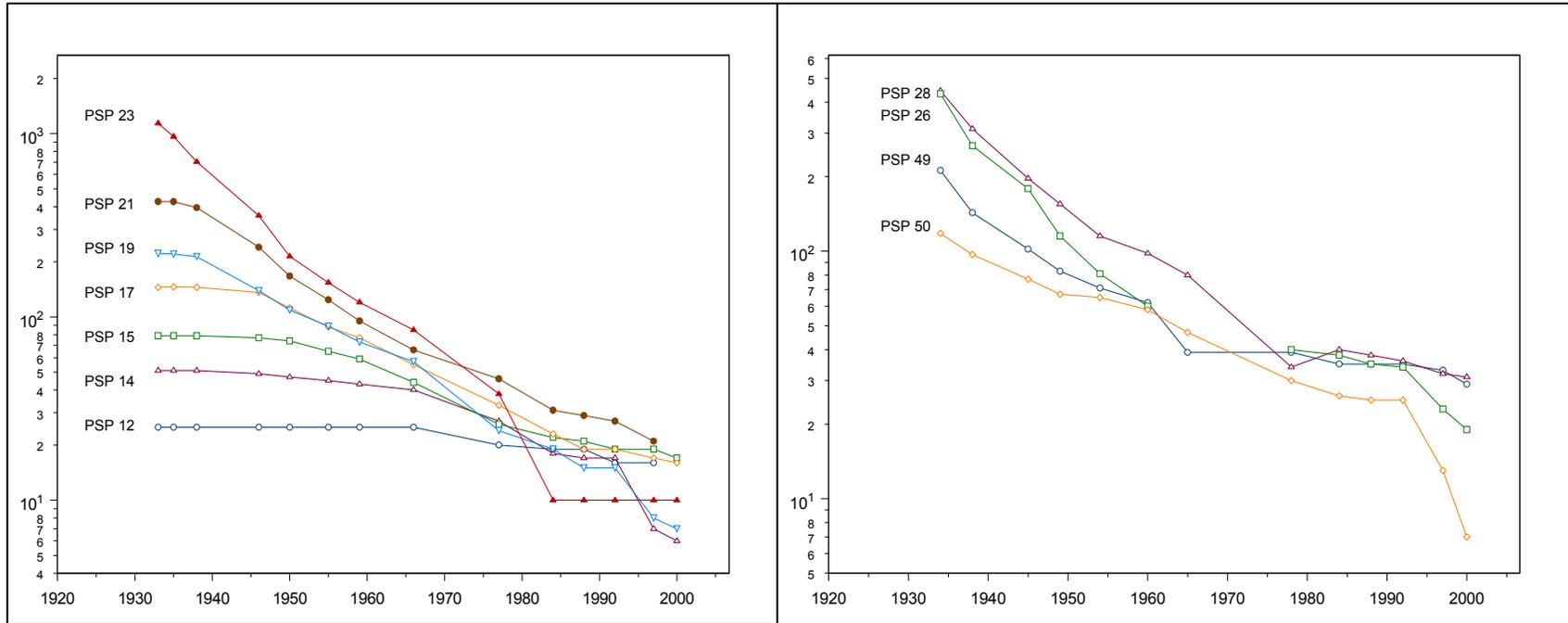
Table 5.6. Annual mean mortality rates (*m*) of tree species in two major forest stands in three periods in the Duke Forest, North Carolina, USA.

	No. of initial stems /dead stems			Annual mean mortality rates		
	1989-93	1993-97	1997-2000	1989-93	1993-97	1997-2000
Pine stands (Graveyard plot)						
All species combined	3435/228	3326/479	2666/328	2.86	3.98	3.60
<i>Acer rubrum</i>	927/46	896/74	734/90	1.7	1.72	4.36
<i>Carya</i> spp.	711/53	658/88	501/22	2.58	2.87	1.5
<i>Cornus florida</i>	528/48	563/123	427/128	3.18	4.93	11.88
<i>Fraxinus</i> spp.	18/2	17/3	16/0	3.93	3.88	0
<i>Juniperus virginiana</i>	31/5	25/9	13/0	5.86	8.93	0
<i>Liquidambar styraciflua</i>	346/35	331/48	269/21	3.55	3.13	2.71
<i>Liriodendron tulipifera</i>	150/4	141/11	125/11	0.9	1.62	3.07
<i>Nyssa sylvatica</i>	34/1	33/3	24/2	1	1.91	2.9
<i>Ostrya virginiana</i>	120/3	140/5	147/2	0.84	0.73	0.46
<i>Oxydendrum arboreum</i>	136/3	130/22	104/8	0.74	3.71	2.67
<i>Pinus</i> spp.	274/5	276/64	208/32	0.61	5.28	5.57
<i>Quercus alba</i>	43/7	33/9	21/0	5.92	6.37	0
<i>Quercus rubra</i>	24/2	19/5	12/2	2.9	6.11	6.08
<i>Quercus velutina</i>	60/3	45/4	30/9	1.28	2.33	8.92
<i>Ulmus rubra</i>	33/1	19/1	35/1	1.03	1.08	0.97
Upland hardwoods (Bormann plot)						
All species combined	3542/178	3747/400	3388/339	1.32	3.21	3.72
<i>Acer rubrum</i>	1517/41	1643/79	1572/54	0.68	1.23	1.17
<i>Carya</i> spp.	154/5	174/16	160/13	0.83	2.41	2.82
<i>Cornus florida</i>	717/72	804/181	650/183	2.65	6.38	11.02
<i>Juniperus virginiana</i>	35/1	36/4	37/3	0.72	2.94	2.82
<i>Liriodendron tulipifera</i>	19/1	21/3	18/0	1.35	3.85	0
<i>Nyssa sylvatica</i>	192/21	172/16	159/8	2.9	2.44	1.72
<i>Oxydendrum arboreum</i>	494/21	472/42	430/29	1.09	2.33	2.33
<i>Prunus serotina</i>	39/1	55/4	57/4	0.65	1.89	2.43
<i>Quercus alba</i>	283/10	276/42	228/33	0.9	4.13	5.21
<i>Quercus rubra</i>	52/3	53/6	46/7	1.49	3	5.5
<i>Quercus velutina</i>	40/2	41/7	31/5	1.28	4.68	5.86

Table 5.7. Change in relative abundance by shade-tolerance class in a 1.3 ha mapped loblolly pine stand and a 1.9 ha oak forest in the Duke Forest after Hurricane Fran.

Tolerant class*	Species	Percentage of IV (%)			
		Pine stand		Oak stand	
		1992	2001	1993	2000
Very tolerant (able to survive in very deep shade)					
	<i>Acer barbatum</i>	0.16	0.57	-	0.02
	<i>Carpinus caroliniana</i>	2.55	2.67	-	0.01
	<i>Fagus grandifolia</i>	0.21	1.03	-	0.02
	<i>Ostrya virginiana</i>	2.28	6.29	-	0.01
Tolerant (able to survive in deep shade)					
	<i>Acer rubrum</i>	14.98	15.63	24.19	29.97
	<i>Cercis canadensis</i>	0.26	0.20	-	-
	<i>Cornus florida</i>	9.36	6.27	11.07	7.17
	<i>Fraxinus americana</i>	0.26	0.34	0.18	0.25
	<i>Oxydendrum arboreum</i>	3.26	3.70	9.19	9.75
	<i>Ulmus rubra</i>	0.71	0.79	0.01	0.01
Intermediate (able to survive in modest shade)					
	<i>Carya alba</i>	7.71	7.64	1.51	1.68
	<i>Carya glabra</i>	1.05	1.03	1.46	1.76
	<i>Carya ovata</i>	0.23	0.19	0.89	0.94
	<i>Juniperus virginiana</i>	0.59	0.45	0.61	0.66
	<i>Nyssa sylvatica</i> var. <i>sylvatica</i>	0.53	0.44	3.01	3.00
	<i>Quercus alba</i>	1.45	1.72	38.10	34.01
	<i>Quercus velutina</i>	1.40	0.65	1.97	1.36
	<i>Ulmus alata</i>	0.43	0.53	0.04	0.04
	<i>Ulmus americana</i>	0.15	0.03	-	-
Intolerant (generally unable to survive very long in deep shade)					
	<i>Liquidambar styraciflua</i>	10.59	12.31	0.01	0.06
	<i>Liriodendron tulipifera</i>	5.63	7.38	0.33	1.07
	<i>Prunus serotina</i>	0.11	0.18	0.74	1.74
	<i>Quercus falcata</i> var. <i>falcata</i>	0.10	0.06	0.25	0.35
	<i>Quercus stellata</i>	-	-	0.95	0.79
Very intolerant (unable to survive very long in very deep shade)					
	<i>Pinus taeda</i>	34.52	28.25	0.50	0.60

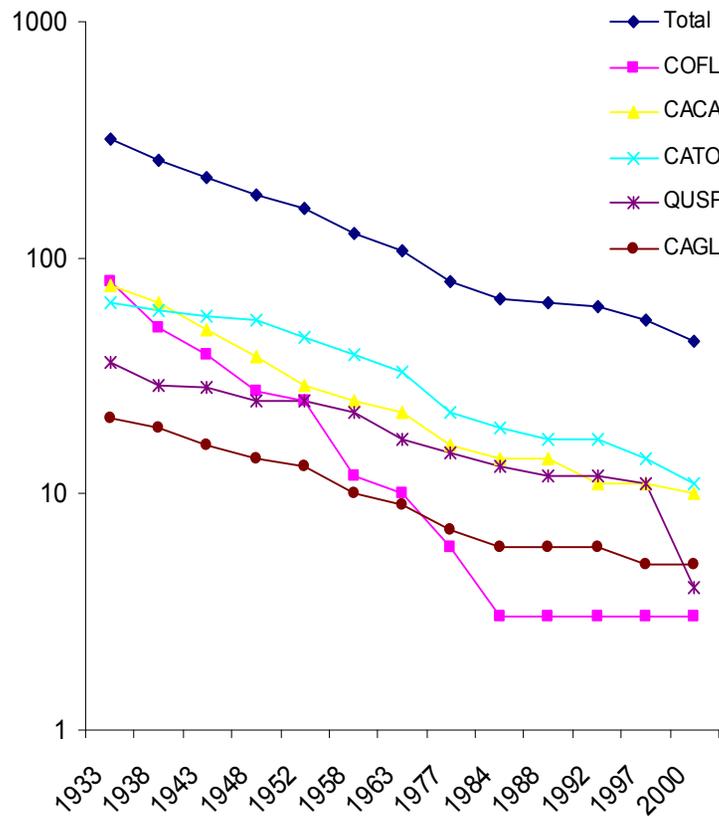
* This shade tolerance classification was compiled mainly based on Burns, Russell M., and Barbara H. Honkala, Tech. Coords. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654.* U.S. Department of Agriculture, Forest Service, Washington, DC. Vol.2, 877 p.. Adjustment of the shade tolerance class has been made for some tree species based on our observations in Piedmont forests.



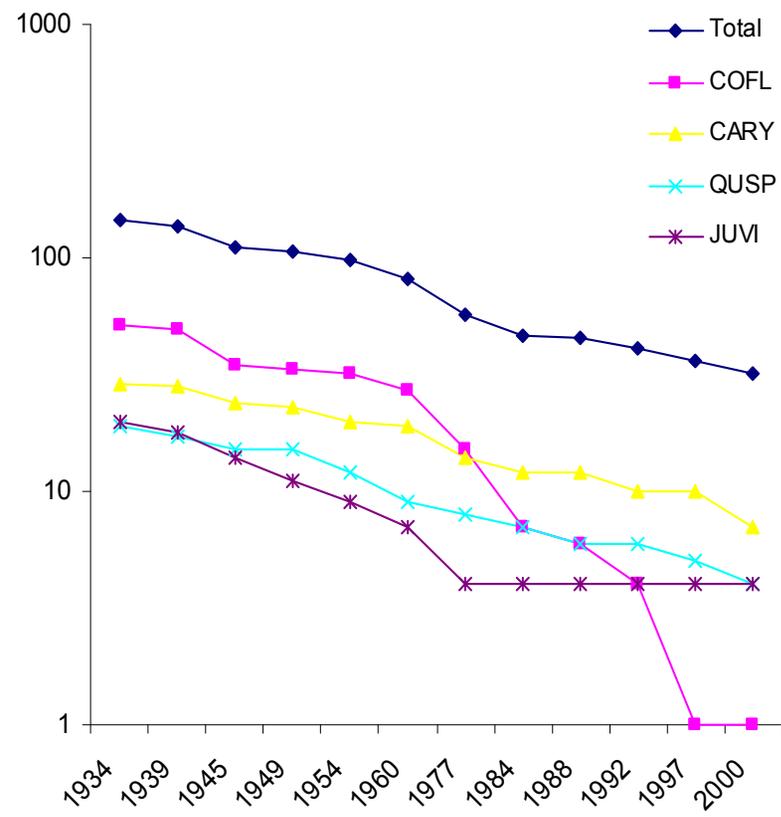
(a) PSP12, 14,15,17,19, 21 and 23

(b) PSP26, 28, 49 and 50

Figure 5.1. Survivorship of *Pinus taeda* (d.b.h.>1.25 cm) in eleven even-aged loblolly pine stands in the Duke Forest. The plot sizes are 404 m² for (a) group and 808 - 1011 m² for (b) group. Despite extreme variation in initial densities, differential mortality has led to convergence in density during 66-year period. Four of the permanent plots (PSP14, 19, 49 and 50) were greatly damaged by 1996 Hurricane Fran, resulted in substantially high mortality and low tree density.



(a) PSP 10



(b) PSP 36

Figure 5.2. Depletion curves illustrating differences in mortality rates of trees from two upland, mixed-aged, mixed-species stands. Species abbreviations: CARY-*Carya* spp.; CACA-*Carya carolinae-septentrionalis*; CATO-*Carya tomentosa*; CAGL-*Carya glabra*; COFL-*Cornus florida*; JUVI- *Juniperus virginiana*; QUSP-*Quercus* spp.. Note that *Quercus* spp. in PSP 10 and *Cornus florida* in PSP 36 greatly decreased in or shortly after Hurricane Fran.

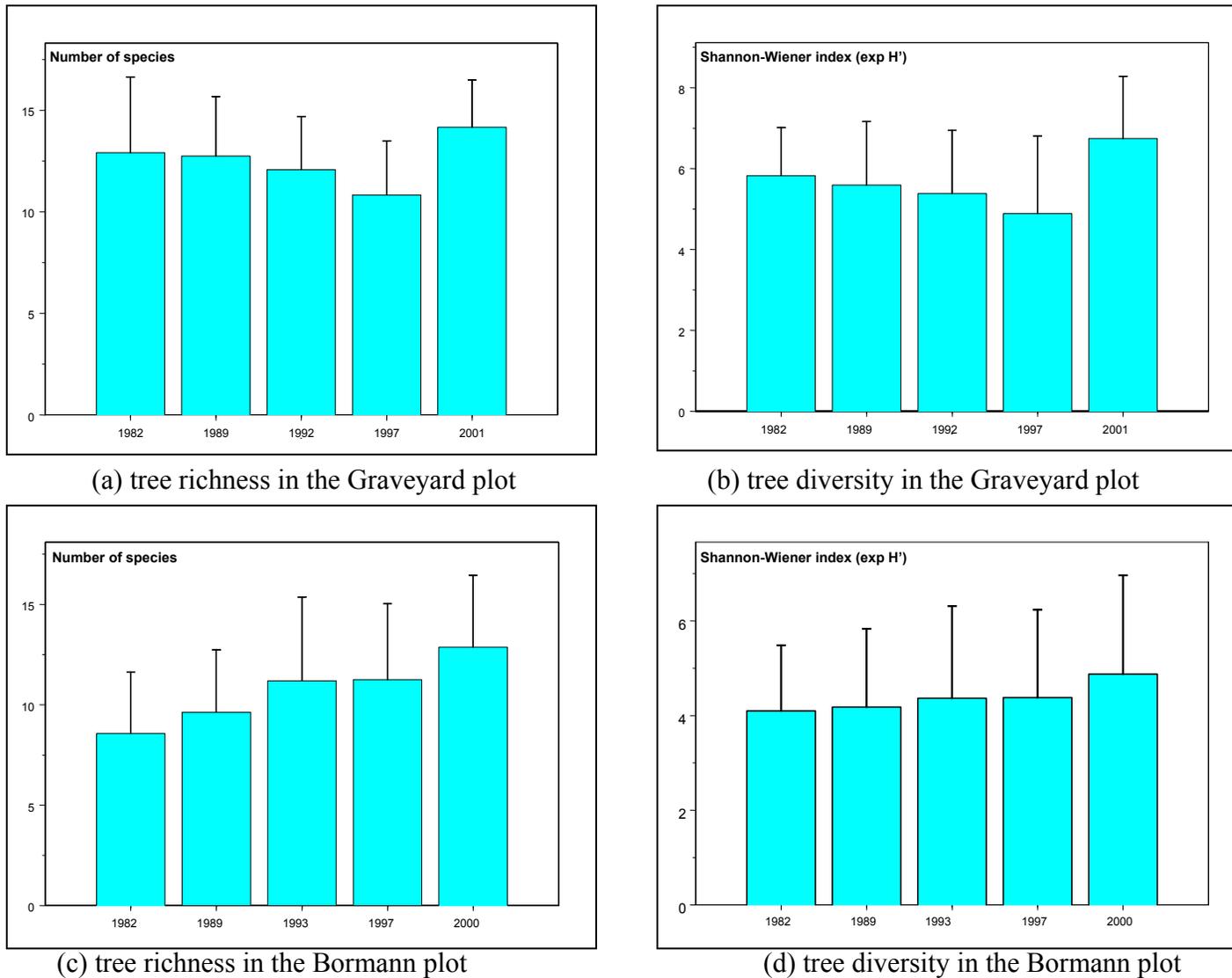
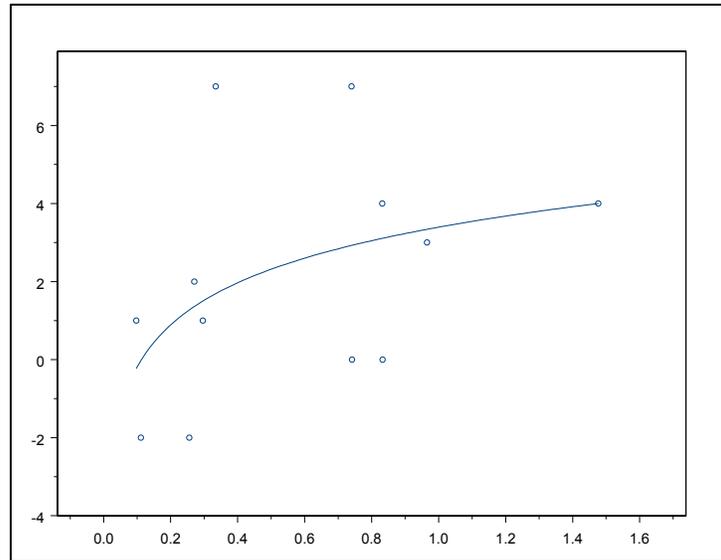


Figure 5.3. Change in understory (stem 1 cm \leq d.b.h. $<$ 5 cm) species richness (number of species per ca.1000 m²) and tree diversity (exp H' per ca.1000m²) in two mapped permanent plots over 18 years in the Duke Forest, North Carolina, USA. (a) tree richness in the Graveyard plot; (b) tree diversity in the Graveyard plot; (c) tree richness in the Bormann plot and (d) tree diversity in the Bormann plot. The error bars on the columns are standard errors.

(a) Graveyard plot



(b) Bormann plot

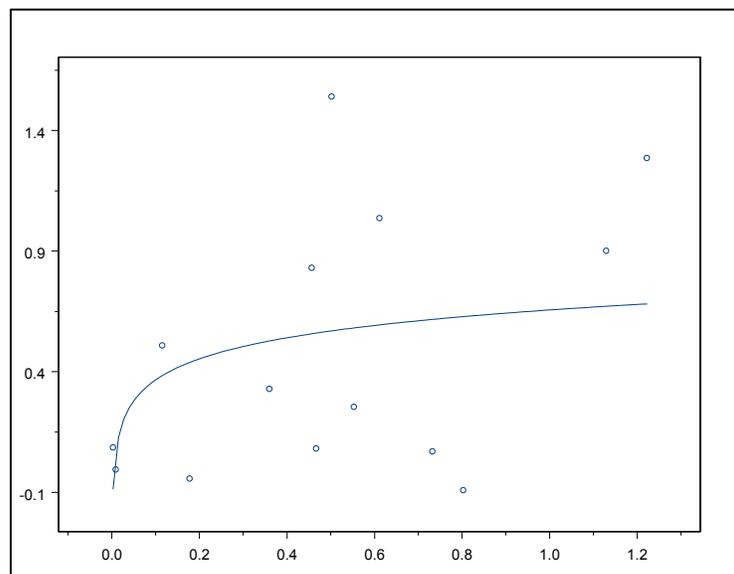


Figure 5.4. The relationship between canopy damage intensity and change in species diversity on (a) a 1.3 ha loblolly pine stand and (b) a 1.96 ha mixed-aged oak stand in the Duke Forest. X-axis is the damage index (by definition, from 0-3, 0 means no damage stems and 3 is maximum, means that all the stems are severely damage). Y-axis is the difference of tree diversity (as $\exp H'$) between 2001 (5 years after Hurricane Fran) and 1992 (4 years before Hurricane Fran). The two mapped plots were divided into numerous ca 1000 m² subplots. This result supports “Intermediate Disturbance Hypothesis” proposed by Connell (1978).

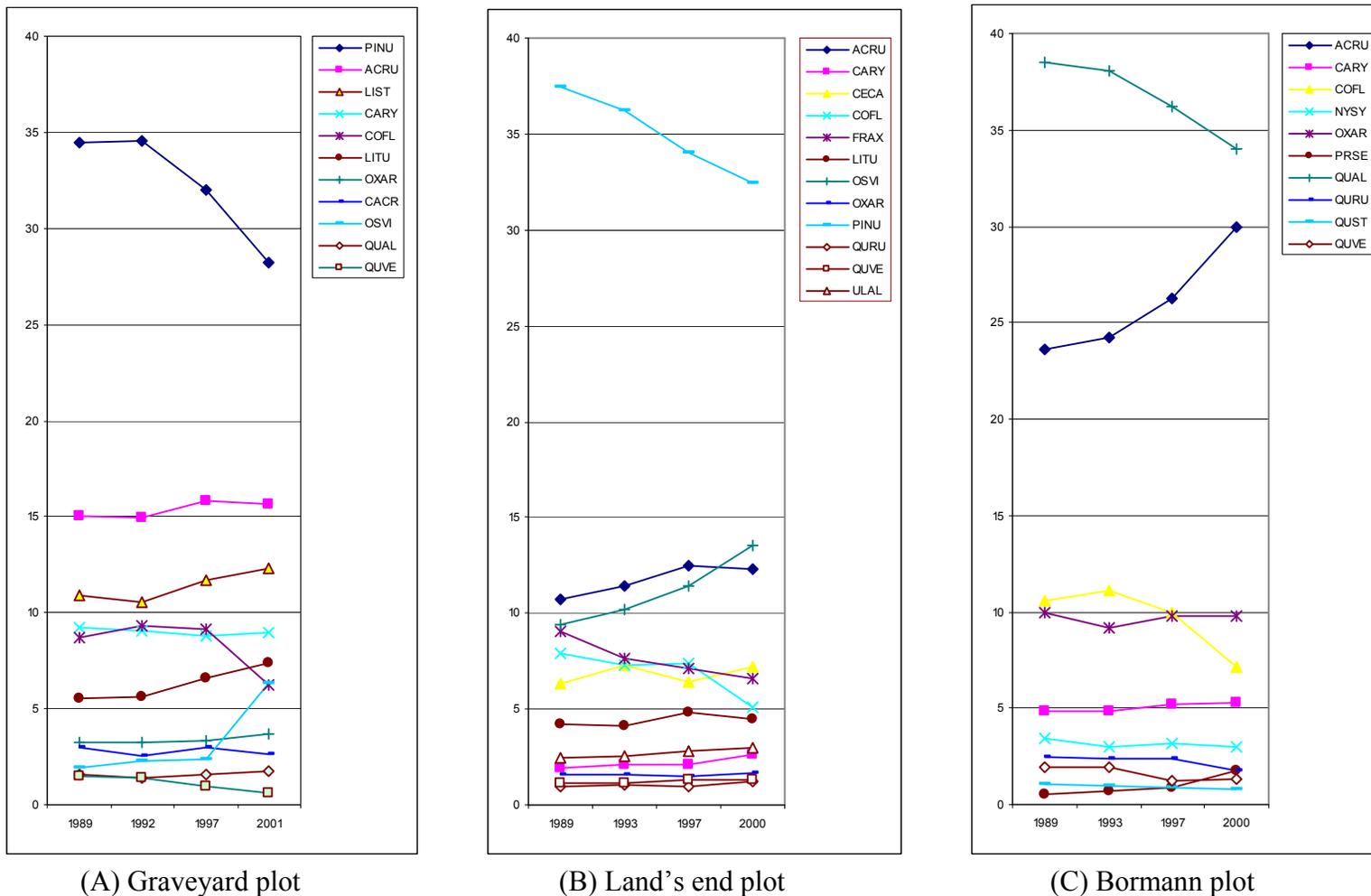


Figure 5.5. Change in IV (importance value) of major tree species in three mapped plots in three periods (pre-hurricane, hurricane period and post hurricane) over 10 yr. Data are shown for all species that IV ≥ 1 over the three periods. The total value of IV is 100. The survey years for each plot pre-hurricane vary from 1989 – 1993, and post hurricane vary from 2000 – 2001. (a) Graveyard plot and (b) Bormann plot. Increases in some species such as *Acer rubrum* reflect their disproportionate abundance in the understory of forests that experienced significant mortality of the larger trees.

Note: Species Abbreviation in **Figure 5.5**:

ACRU	- <i>Acer rubrum</i>	CARY	- <i>Carya spp</i>
COFL	- <i>Cornus florida</i>	FRAX	- <i>Fraxinus spp.</i>
JUVI	- <i>Juniperus virginiana</i>	LIST	- <i>Liquidambar styraciflua</i>
LITU	- <i>Liriodendron tulipifera</i>	NYSY	- <i>Nyssa sylvatica</i>
OSV I	- <i>Ostrya virginiana</i>	OXAR	- <i>Oxydendrum arboreum</i>
PINU	- <i>Pinus spp.</i>	QUAL	- <i>Quercus alba</i>
QURU	- <i>Quercus rubra</i>	QUVE	- <i>Quercus velutina</i>
QUST	- <i>Quercus stellata</i>	QUFA	- <i>Quercus falcata</i>

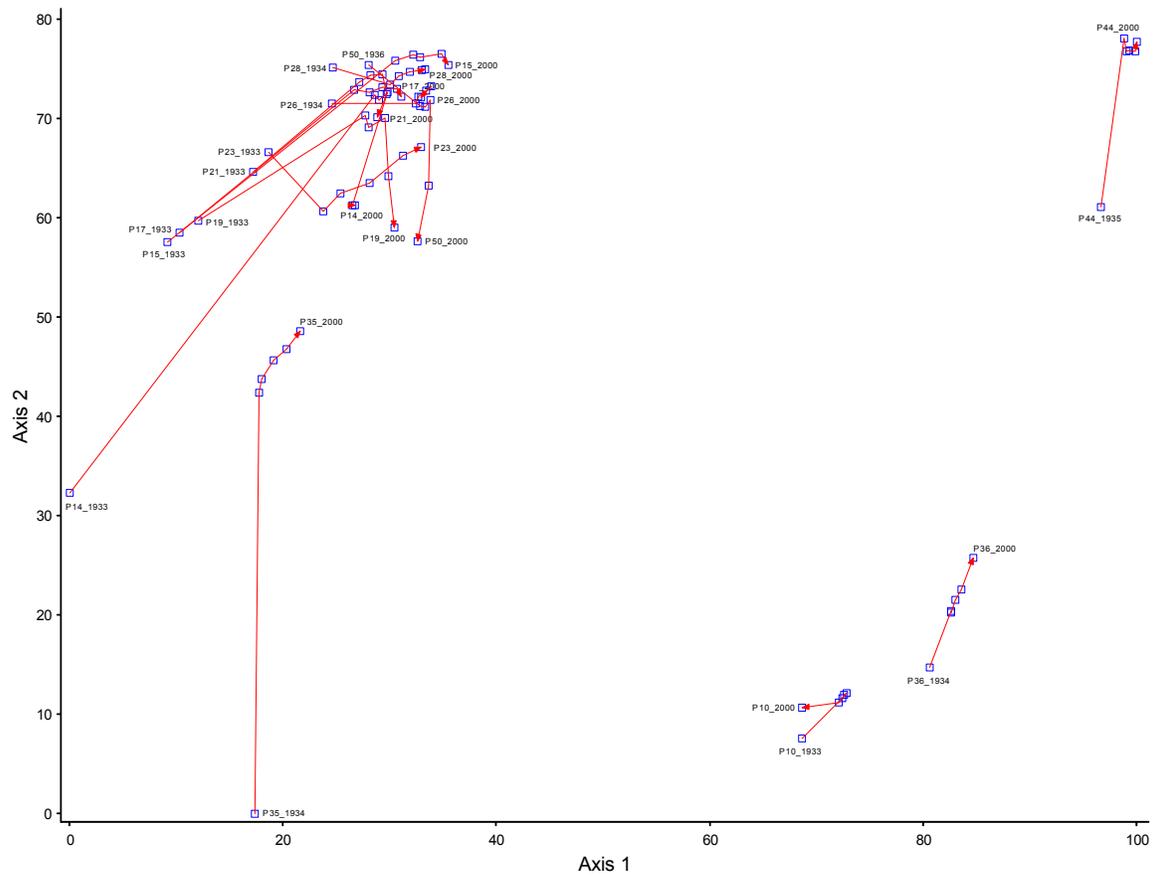


Figure 5.6. Nonmetric Multidimensional Scaling (NMS) ordination of 13 control permanent sampling plots in the Duke Forest Vectors indicate sequences of observations of a single plot over the interval 1933 to 2000

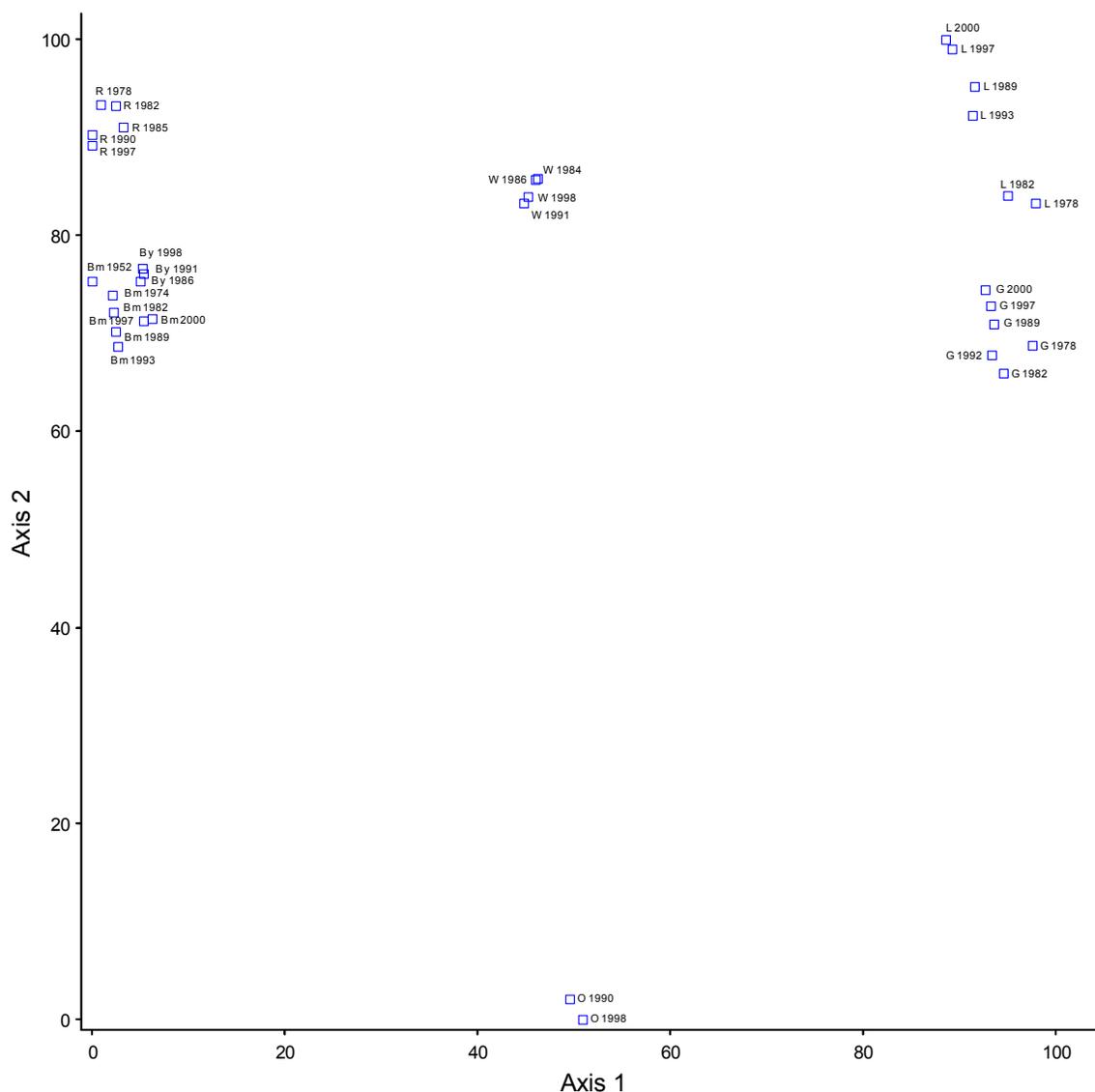


Figure 5.7. Nonmetric Multidimensional Scaling (NMS) ordination of seven mapped plots measured in mostly from 1978 through 2000. Squares are plot locations in two-dimensional NMS ordination space over time. Observations are label with specific plot and year (G = Graveyard, L = Land's end, R = Rocky, W = Wooden Bridge, Bm = Bormann, By = Bryan Center, and O = Oosting plot). Hardwood plots on the left and bottom, whereas successional pine plots are in the upper right.

CHAPTER 6

GENERAL CONCLUSIONS

This study focused on the impacts of hurricanes on Piedmont forests and the subsequent recovery patterns. It provides insights into the role of hurricanes in the structure and composition of temperate forests. The availability for the Duke Forest of long-term monitoring data for trees, seedling and saplings spanning the years before and following the 1996 Hurricane Fran provided a unique opportunity to separate hurricane-induced changes from the background successional dynamics. Overall, this study has shown that large, infrequent hurricanes play an important role in shaping forest structure and composition in the Piedmont region. However, the effects on tree composition and diversity vary greatly and depend on damage severity, pre-hurricane stand characteristics, and the temporal and spatial scales at which the changes are observed.

Hurricane Fran's strong wind and high precipitation resulted in a highly heterogeneous pattern of forest disturbance across the landscape of the Duke Forest and adjacent areas. Stand-level damage severity varied substantially across the dispersed array of established permanent plots. The variance in stand-level tree mortality and basal area loss was high. This complexity of hurricane damage was a result of interactions among meteorological, topographical and biological factors. Wind speeds undoubtedly were the primary determinant of damage severity. Rainfall was also a critical factor influencing damage severity and tree damage type. Uprooting was the dominant damage

type for canopy trees during Hurricane Fran due to soil saturation by the heavy rain immediately prior to and associated with the storm. Much of the damage was concentrated at the topographic extremes, particularly along stream bottom areas where the wettest soils were located.

This study demonstrates the importance of scale in observations of tree damage patterns and the value of the long-term, pre-disturbance data for understanding wind damage impacts. At the landscape scale, the predictability of tree damage and mortality risk was found to be correlated with site exposure, topographic position, and tree size. At the stand scale, the predictability of tree damage was low due to highly variable wind gusts and complex interactions among individual trees. Nonetheless, tree death, stem damage and the pre-hurricane tree size were positively correlated.

Hurricane Fran significantly increased within-stand spatial heterogeneity as a result of the patchy nature of tree damage and death. Spatial point pattern analysis revealed a generally clumped distribution of hurricane-induced tree mortality and increased aggregation of surviving trees at the stand scale. In addition, the hurricane resulted in a substantially increased tree-gap size and a dramatic rise in understory light. Stand height, stem density, and basal area significantly decreased as a consequence of the hurricane. On average, tree mortality of large-size trees approximately doubled during the five-year period that spanned the hurricane event compared to the pre-hurricane level, although this increased mortality was not uniformly distributed across species. In addition, increased mortality of hardwood trees was not confined to the year of the hurricane, but continued for several years following the hurricane. These significant structural and dynamic

changes in the forest appear likely to have a substantial and continuing influence on stand development and future composition.

The hurricane significantly diversified the live-tree size distribution in damaged forest stands. Overall, the predominant tree species of the upper canopy layer in both pine and hardwood forests decreased substantially due to the higher mortality of large-size trees. In the damaged pine stands, the mean size of the dominant loblolly pines (*Pinus taeda*) increased whereas the density of pines decreased in all size classes. Hurricane Fran also greatly affected pine stands by decreasing the relative abundance of small size-class oaks (*Quercus spp.*) and hickories (*Carya spp.*). Several light-demanding and more shade intolerant hardwood species, such as tuliptree (*Liriodendron tulipifera*) and sweetgum (*Liquidambar styraciflua*) increased dramatically in density in the small size class (1-3 cm) during the 5 years following the hurricane, whereas dogwood (*Cornus florida*), the most damaged tree in the pine stands, decreased in stem density in all tree sizes.

In a pattern consistent with that of loblolly pine in the mapped pine stand, the mean size of trees, and particularly that of the predominant white oak (*Quercus alba*), increased after Hurricane Fran in the damaged hardwood stands, whereas the density of trees decreased in all size classes. Particularly conspicuous was the increase in stem density of red maple (*Acer rubrum*) in smaller size classes 5 years after the hurricane. As in pine stands, dogwood decreased in stem density in all size classes in the 5-year following the hurricane.

Tree species susceptibility to windthrow can partially explain within-stand variation in damage. Tree susceptibility is determined by tree canopy characteristics, leaf features,

and the characters of root systems. Among large trees of the Duke Forest, Hurricane Fran caused a higher incidence of damage in hardwoods than pines. This is because hardwoods usually have broad, spreading canopies and flat leaves that can catch the force of the wind much more readily than the smaller canopies and the needle leaves of pine trees. Moreover, hardwoods often have shallow root systems that increase their susceptibility to uprooting during hurricanes.

The most rapid changes following Hurricane Fran were seen in the understory seedling layer. Seedling density and species richness experienced an immediate drop. This was followed by a rapid rebound in seedling density and more gradual recovery and enhancement in richness and diversity. Seedling recruitment did not increase continuously over time and overall seedling density was relatively low compared to pre-hurricane level. This study supports the hypothesis that canopy disturbances can promote local tree species diversity. However, these disturbance-induced changes must be viewed in the context of variation in pre-disturbance tree species composition resulting from differences in habitat and stand history.

Changes in sapling population density and diversity were varied. Mostly, sapling diversity increased slightly in the five years following the hurricane, although not where canopy damage was extreme. Sapling recruitment increased due to the release of understory seedlings. This observation is consistent not only with the hypothesized relaxation of competition, but also the hypothesis that windthrows contribute greatly to tree diversity in the Piedmont forests.

Piedmont forests exhibit remarkable resilience to hurricane damage because of widespread advanced regenerations. Canopy gaps created by the hurricane resulted in

release of established shade-intolerant or mid-tolerant seedlings and saplings, and thereby reversed the negative correlation previously observed between relative growth in successive years. Most seedlings and saplings approximately doubled their relative growth rates after the hurricane, although not uniformly across tree species. Resprouting of damaged individuals and vegetative production of additional shoots were also common.

In contrast to the profound structural changes experienced, hurricane-induced changes in tree species composition and diversity were modest. Tree diversity increased slightly or was maintained in most of the damaged forest stands as a result of colonization by new, light-demanding species. The disturbed forests experienced an increase in certain exotic trees such as princess tree (*Paulownia tomentosa*) and tree-of-heaven (*Ailanthus altissima*). In addition, analysis of the effects of the 1954 Hurricane Hazel has shown that hurricane effects on tree species composition and diversity can be long lasting. In a heavily damaged oak stand (i.e., basal area loss > 30%), tree diversity was substantially increased even 50 years after the storm.

Finally, historical hurricanes appear to have reduced the predictability of stand composition and to have accelerated the existing trend of late successional oaks and hickories being replaced by more light-demanding red maple. Large hurricane disturbances appear to be responsible for increased variance in regeneration, which contributes to a diverse but temporally relatively stable canopy layer. The occurrence of Hurricane Fran has served to further document and clarify the variable and non-equilibrium nature of late-successional, mixed-aged hardwood forests of the southeastern Piedmont.

LITERATURE CITED

- Bormann, F. H. and G. E. Likens. 1979. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag New York Inc. New York, USA.
- Carpino, E. 1998. Ecological determinants of hurricane damage in a southeastern piedmont forest. Master thesis. Duke University, Durham, North Carolina, USA.
- Christensen, N. L. and R. K. Peet. 1981. Secondary forest succession on the North Carolina piedmont. Pages 230-245 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest Succession: concepts and application*. Springer-Verlag, New York, USA.
- DeCoster, J. K. 1996. Impacts of tornados and hurricanes on the community structure and dynamics of North and South Carolina forests. Ph.D. Dissertation. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.
- Emanuel, K. A. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* **486**:686-688.
- Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, southwestern New Hampshire, USA. *Journal of Ecology* **76**:105-134.
- Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology* **76**:135-151.
- Foster, D. R. and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology* **80**:79-98.
- Glitzenstein, J. S., P. A. Harcombe, and D. R. Streng. 1986. Disturbance, succession, and maintenance of species-diversity in an east Texas forest. *Ecological Monographs* **56**:243-258.
- Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nunez, and W. M. Gray. 2001. The recent increase in Atlantic hurricane activity: causes and implications. *Science* **293**:474-479.
- Harcombe, P. A., C. J. Bill, M. Fulton, J. S. Glitzenstein, P. L. Marks, and I. S. Elsik. 2002. Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. *Journal of Ecology* **90**:947-957.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina piedmont. *Castanea* **67**:84-95.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of piedmont, North Carolina. *American Midland Naturalist* **28**:1-126.

- Peet, R. K. 1992. Community structure and ecosystem properties. Pages 102-151 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman and Hall, London, UK.
- Peet, R. K. and N. L. Christensen. 1980. Succession - a population process. *Vegetatio* **43**:131-140.
- Peet, R. K. and N. L. Christensen. 1987. Competition and tree death. *Bioscience* **37**:586-595.
- Peet, R. K. and N. L. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina piedmont. Pages 233-245 in H. J. During, M. J. A. Werger, and J. Willems, editors. Diversity and pattern in plant communities. SPB Publishers. The Hague. The Netherlands.
- Philippi, T. E., R. K. Peet, and N. L. Christensen. 1993. Tree seedling demography in old-field *Pinus taeda* and mature mixed hardwoods stands in a piedmont forest. *Bulletin of the Ecological Society of America* **74 (Suppl.)**:393.
- Pickett, S. T. A. and P. S. White. 1985. Editors. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida, USA.
- Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* **82**:424-435.
- Reice, S. R. 2001. The silver lining: the benefits of natural disasters. Princeton University Press, Princeton, New Jersey, USA.
- Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* **1**:511-523.
- Walker, L. R. 1999. Editor. Ecosystems of Disturbed Ground. Ecosystems of the World. Volume 16. Elsevier Science, Amsterdam, The Netherlands.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229-299.
- White, P. S. and A. Jentsch. 2004. Disturbance, succession, and community assembly in terrestrial plant communities. Pages 342-366 in V. M. Temperton, R. J. Hobbs, T. Nuttle and S. Halle 2004. Assembly Rules and Restoration Ecology - Bridging the gap between theory and practice. Island Press, Washington D.C. USA.
- White, R. D. 1999. The impacts of hurricane Fran on a North Carolina piedmont woodland. Master thesis. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.

Appendix I:

Tree, shrub and liana species in the Duke Forest with common names and codes (Nomenclature follows the USDA PLANTS v 4.0)

Code	Scientific Name	Common name	Growth Form*
ACBA	<i>Acer barbatum</i>	Southern Sugar Maple	1
ACNE	<i>Acer negundo</i> var. <i>negundo</i>	Boxelder	1
ACRU	<i>Acer rubrum</i>	Red Maple	1
AESY	<i>Aesculus sylvatica</i>	Painted Buckeye	2
AIAL	<i>Ailanthus altissima</i>	Tree of Heaven	1
ALJU	<i>Albizia julibrissin</i>	Silktree	1
ALSE	<i>Alnus serrulata</i>	Hazel Alder	2
AMAR	<i>Amelanchier arborea</i>	Common Serviceberry	1
ASPA	<i>Asimina parviflora</i>	Smallflower Pawpaw	2
ASTR	<i>Asimina triloba</i>	Pawpaw	2
BENI	<i>Betula nigra</i>	River Birch	1
CAAL	<i>Carya alba</i>	Mockernut Hickory	1
CAFL	<i>Calycanthus floridus</i>	Eastern Sweetshrub	2
CARA	<i>Campsis radicans</i>	Trumpet Creeper	3
CACR	<i>Carpinus caroliniana</i>	American Hornbeam	1
CACA	<i>Carya caroliniae-septentrionalis</i>	Southern Shagbark Hickory	1
CACO	<i>Carya cordiformis</i>	Bitternut Hickory	1
CAGL	<i>Carya glabra</i>	Pignut Hickory	1
CAOL	<i>Carya ovalis</i>	Red Hickory	1
CAOV	<i>Carya ovata</i>	Shagbark Hickory	1
CAPA	<i>Carya pallida</i>	Sand Hickory	1
CARY	<i>Carya</i> sp.	Hickory	1
CADE	<i>Castanea dentata</i>	American Chestnut	1
CAPU	<i>Castanea pumila</i>	Chinkapin	2
CELA	<i>Celtis laevigata</i>	Sugarberry	1
CEOC	<i>Celtis occidentalis</i>	Common Hackberry	1
CECA	<i>Cercis canadensis</i>	Eastern Redbud	1
CHVI	<i>Chionanthus virginicus</i>	White Fringetree	2
COAL	<i>Cornus alternifolia</i>	Alternatleaf Dogwood	2
COFL	<i>Cornus florida</i>	Flowering Dogwood	1
COST	<i>Cornus foemina</i>	Stiff Dogwood	2

Appendix I:

Tree, shrub and liana species in Duke Forest with common names and codes (Continued)

Code	Scientific Name	Common name	Growth Form*
COAM	<i>Corylus americana</i>	American Hazelnut	2
CRCR	<i>Crataegus crus-galli</i>	Cockspur Hawthorn	1
CRFB	<i>Crataegus flabellate</i>	Fanleaf Hawthorn	1
CRFL	<i>Crataegus flava</i>	Yellowleaf Hawthorn	1
CRMA	<i>Crataegus marshallii</i>	Parsley Hawthorn	1
CRPH	<i>Crataegus phaenopyrum</i>	Washington Hawthorn	1
CRPU	<i>Crataegus punctata</i>	Dotted Hawthorn	1
CRAT	<i>Crataegus sp.</i>	Hawthorn	1
CRUN	<i>Crataegus uniflora</i>	Dwarf Hawthorn	1
DIVI	<i>Diospyros virginiana</i>	Common Persimmon	1
ELPU	<i>Elaeagnus pungens</i>	Thorny Olive	2
EUAM	<i>Euonymus americanus</i>	Bursting-heart	2
FAGR	<i>Fagus grandifolia</i>	American Beech	1
FRAX	<i>Fraxinus spp.</i>	Ash	1
GABA	<i>Gaylussacia baccata</i>	Black Huckleberry	2
GLTR	<i>Gleditsia triacanthos</i>	Honeylocust	1
HAVI	<i>Hamamelis virginiana</i>	American Witchhazel	2
HYAR	<i>Hydrangea arborescens</i>	Wild Hydrangea	2
ILAM	<i>Ilex ambigua</i>	Carolina Holly	2
ILDE	<i>Ilex decida</i>	Possumhaw	2
ILOP	<i>Ilex opaca</i>	American Holly	1
JUNI	<i>Juglans nigra</i>	Black Walnut	1
JUVI	<i>Juniperus virginiana</i>	Eastern Redcedar	1
KALA	<i>Kalmia latifolia</i>	Mountain Laurel	2
LIJA	<i>Ligustrum japonicum</i>	Japanese Privet	2
LISI	<i>Ligustrum sinense</i>	Chinese Privet	2
LIBE	<i>Lindera benzoin</i>	Northern Spicebush	2
LIST	<i>Liquidambar styraciflua</i>	Sweetgum	1
LITU	<i>Liriodendron tulipifera</i>	Tuliptree	1
LOJA	<i>Lonicera japonica</i>	Japanese Honeysuckle	3
MAGR	<i>Magnolia grandiflora</i>	Southern Magnolia	1

Appendix I:

Tree, shrub and liana species in Duke Forest with common names and codes (Continued)

Code	Scientific Name	Common name	Growth Form*
MATR	<i>Magnolia tripetala</i>	Umbrella-Tree	1
MASP	<i>Malus spp.</i>	Crabapple	2
MORU	<i>Morus rubra</i>	Red Mulberry	1
MYCA	<i>Morella caroliniensis</i>	Southern bayberry	2
NYSY	<i>Nyssa sylvatica</i>	Blackgum	1
OSVI	<i>Ostrya virginiana</i>	Hophornbeam	1
OXAR	<i>Oxydendrum arboreum</i>	Sourwood	1
PAQU	<i>Parthenocissus quinquefolia</i>	Virginia Creeper	2
PATO	<i>Paulownia tomentosa</i>	Paulownia	1
PIEC	<i>Pinus echinata</i>	Shortleaf Pine	1
PINU	<i>Pinus sp.</i>	Pine	1
PITA	<i>Pinus taeda</i>	Loblolly Pine	1
PIVI	<i>Pinus virginiana</i>	Virginia Pine	1
PLOC	<i>Platanus occidentalis</i>	American Sycamore	1
PRAM	<i>Prunus americana</i>	American Plum	1
PRAN	<i>Prunus angustifolia</i>	Chickasaw Plum	1
PRSE	<i>Prunus serotina</i>	Black Cherry	1
QUAL	<i>Quercus alba</i>	White Oak	1
QUCO	<i>Quercus coccinea</i>	Scarlet Oak	1
QUFA	<i>Quercus falcata</i>	Southern Red Oak	1
QULY	<i>Quercus lyrata</i>	Overcup Oak	1
QUMA	<i>Quercus marilandica</i>	Blackjack Oak	1
QUMI	<i>Quercus michauxii</i>	Swamp Chestnut Oak	1
QUNI	<i>Quercus nigra</i>	Water Oak	1
QUPH	<i>Quercus phellos</i>	Willow Oak	1
QUPR	<i>Quercus prinus</i>	Chestnut Oak	1
QURU	<i>Quercus rubra</i>	Northern Red Oak	1
QUSH	<i>Quercus shumardii</i>	Shumard's Oak	1
QUER	<i>Quercus sp.</i>	Oak	1
QURG	<i>Quercus sp.</i>	Red Oak Subgenus	1
QUWG	<i>Quercus sp.</i>	White Oak Subgenus	1

Appendix I:

**Tree, shrub and liana species in Duke Forest with common names and codes
(Continued)**

Code	Scientific Name	Common name	Growth Form*
QUST	<i>Quercus stellata</i>	Post Oak	1
QUVE	<i>Quercus velutina</i>	Black Oak	1
RHCA	<i>Rhododendron catawbiense</i>	Catawba Rosebay	2
RHNU	<i>Rhododendron periclymenoides</i>	Pink azalea	2
RHAR	<i>Rhus aromatica</i>	Fragrant Sumac	2
RHCO	<i>Rhus copallinum</i>	Winged Sumac	2
ROCA	<i>Rosa carolina</i>	Carolina Rose	2
ROPA	<i>Rosa palustris</i>	Swamp Rose	2
RUOC	<i>Rubus occidentalis</i>	Black Raspberry	2
SAAL	<i>Sassafras albidum</i>	Sassafras	1
SMRO	<i>Smilax rotundifolia</i>	Roundleaf Greenbrier	3
STTR	<i>Staphylea trifolia</i>	American Bladdernut	2
STGR	<i>Styrax grandifolius</i>	Bigleaf Snowbell	2
TORA	<i>Toxicodendron radicans</i>	Eastern Poison Ivy	3
ULAL	<i>Ulmus alata</i>	Winged Elm	1
ULAM	<i>Ulmus americana</i>	American Elm	1
ULRU	<i>Ulmus rubra</i>	Slippery Elm	1
ULMU	<i>Ulmus sp.</i>	Elm	1
VAAR	<i>Vaccinium arboreum</i>	Farkleberry	2
VAAT	<i>Vaccinium fuscatum</i>	Black Highbush Blueberry	2
VACO	<i>Vaccinium corymbosum</i>	Highbush Blueberry	2
VAST	<i>Vaccinium stamineum</i>	Deerberry	2
VAVA	<i>Vaccinium pallidum</i>	Blue Ridge Blueberry	2
VIAC	<i>Viburnum acerifolium</i>	Mapleleaf Viburnum	2
VIDE	<i>Viburnum dentatum</i>	Southern Arrowwood	2
VIPR	<i>Viburnum prunifolium</i>	Blackhaw	2
VIRA	<i>Viburnum rafinesquianum</i>	Downy Arrowwood	2
VIRU	<i>Viburnum rufidulum</i>	Rusty Blackhaw	2
VIAE	<i>Vitis aestivalis</i>	Summer Grape	3
VIRO	<i>Vitis rotundifolia</i>	Muscadine	3

* Note: Growth form: 1- tree; 2 – shrub; 3 - liana.

Appendix II:

Shade tolerant class of the major tree species in the Duke Forest, North Carolina, USA

1. Very tolerant (able to survive in very deep shade):

<i>Acer barbatum</i>	Southern Sugar Maple
<i>Carpinus caroliniana</i>	American Hornbeam
<i>Fagus grandifolia</i>	American Beech
<i>Ilex opaca</i>	American Holly
<i>Ostrya virginiana</i>	Eastern Hophornbeam

2. Tolerant (able to survive in deep shade):

<i>Acer rubrum</i>	Red Maple
<i>Carya cordiformis</i>	Bitternut Hickory
<i>Celtis occidentalis</i>	Common Hackberry
<i>Cercis canadensis</i>	Eastern Redbud
<i>Cornus florida</i>	Flowering Dogwood
<i>Fraxinus americana</i>	White Ash
<i>Fraxinus pennsylvanica</i>	Green Ash
<i>Magnolia grandiflora</i>	Southern Magnolia
<i>Morus rubra</i>	Red Mulberry
<i>Oxydendrum arboretum</i>	Sourwood
<i>Ulmus rubra</i>	Slippery Elm

3. Intermediate (able to survive in modest shade):

<i>Acer negundo</i>	Boxelder
<i>Carya alba</i>	Mockernut Hickory
<i>Carya glabra</i>	Pignut Hickory
<i>Carya ovata</i>	Shagbark Hickory
<i>Celtis laevigata</i>	Sugarberry
<i>Diospyros virginiana</i>	Common Persimmon
<i>Juglans nigra</i>	Black Walnut
<i>Juniperus virginiana</i>	Eastern Redcedar
<i>Nyssa sylvatica</i>	Black Tupelo
<i>Prunus serotina</i>	Black Cherry
<i>Quercus alba</i>	White Oak
<i>Quercus michauxii</i>	Swamp Chestnut Oak
<i>Quercus prinus</i>	Chestnut Oak
<i>Quercus velutina</i>	Black Oak
<i>Quercus nigra</i>	Water Oak
<i>Quercus pagoda</i>	Cherrybark Oak
<i>Quercus phellos</i>	Willow Oak
<i>Quercus rubra</i>	Northern Red Oak
<i>Ulmus alata</i>	Winged Elm
<i>Ulmus americana</i>	American Elm

Appendix II:

Shade tolerant class of the major tree species in the Duke Forest, North Carolina, USA (Continued)

4. Intolerant (generally unable to survive very long in deep shade):

<i>Betula nigra</i>	River Birch
<i>Liquidambar styraciflua</i>	Sweetgum
<i>Liriodendron tulipifera</i>	Yellow Poplar
<i>Pinus echinata</i>	Slash Pine
<i>Platanus occidentalis</i>	American Sycamore
<i>Quercus coccinea</i>	Scarlet Oak
<i>Quercus falcata</i>	Southern Red Oak
<i>Quercus marilandica</i>	Blackjack Oak
<i>Quercus stellata</i>	Post Oak

5. Very intolerant (unable to survive very long in very deep shade):

<i>Robinia pseudo-acacia</i>	Black Locust
<i>Paulownia tomentosa</i>	Princess tree
<i>Pinus taeda</i>	Loblolly Pine
<i>Pinus virginiana</i>	Virginia Pine

Note: This shade tolerance classification was compiled mainly based on Burns, Russell M., and Barbara H. Honkala, Tech. Coords. 1990. *Silvics of North America*: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. Vol.2, 877 p.. Adjustment of the shade tolerance class has been made for some tree species based on our observations in Piedmont forests.

Appendix III:

Resistance of tree species to hurricane damage for the major trees in North Carolina Piedmont region, USA*

Uprooting	Breakage	Flood tolerant	Deterioration by insect and disease
<i>Celtis occidentalis</i>	<i>Celtis occidentalis</i>	<i>Acer rubrum</i>	<i>Juniperus virginiana</i>
<i>Juniperus virginiana</i>	<i>Juniperus virginiana</i>	<i>Fraxinus sp.</i>	<i>Liquidambar styraciflua</i>
<i>Carpinus caroliniana</i>	<i>Liquidambar styraciflua</i>	<i>Liquidambar styraciflua</i>	<i>Quercus nigra</i>
<i>Ostrya virginiana</i>	<i>Nyssa sylvatica</i>	<i>Platanus occidentalis</i>	<i>Platanus occidentalis</i>
<i>Nyssa sylvatica</i>	<i>Ostrya virginiana</i>	<i>Juglans nigra</i>	<i>Ostrya virginiana</i>
<i>Liquidambar styraciflua</i>	<i>Cornus florida</i>	<i>Betula nigra</i>	<i>Carpinus caroliniana</i>
<i>Platanus occidentalis</i>	<i>Magnolia grandiflora</i>	<i>Morus rubra</i>	<i>Quercus rubra</i>
<i>Ulmus alata</i>	<i>Carpinus caroliniana</i>	<i>Ulmus americana</i>	<i>Quercus alba</i>
<i>Ulmus rubra</i>	<i>Quercus rubra</i>	<i>Diospyros virginiana</i>	<i>Quercus coccinea</i>
<i>Quercus rubra</i>	<i>Quercus nigra</i>	<i>Carpinus caroliniana</i>	<i>Quercus falcata</i>
<i>Quercus alba</i>	<i>Quercus alba</i>	<i>Ostrya virginiana</i>	<i>Quercus phellos</i>
<i>Quercus coccinea</i>	<i>Quercus coccinea</i>	<i>Juniperus virginiana</i>	<i>Quercus prinus</i>
<i>Quercus falcata</i>	<i>Quercus falcata</i>	<i>Nyssa sylvatica</i>	<i>Quercus stellata</i>
<i>Quercus phellos</i>	<i>Quercus phellos</i>	<i>Quercus nigra</i>	<i>Quercus velutina</i>
<i>Quercus prinus</i>	<i>Quercus prinus</i>	<i>Quercus alba</i>	<i>Cercis canadensis</i>
<i>Quercus stellata</i>	<i>Quercus stellata</i>	<i>Quercus coccinea</i>	<i>Fagus grandifolia</i>
<i>Quercus velutina</i>	<i>Quercus velutina</i>	<i>Quercus falcata</i>	<i>Liriodendron tulipifera</i>
<i>Cercis canadensis</i>	<i>Cercis canadensis</i>	<i>Quercus phellos</i>	<i>Magnolia grandiflora</i>
<i>Fagus grandifolia</i>	<i>Fagus grandifolia</i>	<i>Quercus prinus</i>	<i>Nyssa sylvatica</i>
<i>Liriodendron tulipifera</i>	<i>Liriodendron tulipifera</i>	<i>Quercus stellata</i>	<i>Carya cordiformis</i>
<i>Magnolia grandiflora</i>	<i>Platanus occidentalis</i>	<i>Quercus velutina</i>	<i>Carya glabra</i>
<i>Pinus taeda</i>	<i>Pinus echinata</i>	<i>Cercis Canadensis</i>	<i>Carya ovata</i>
<i>Pinus echinata</i>	<i>Pinus virginiana</i>	<i>Celtis occidentalis</i>	<i>Carya alba</i>
<i>Quercus nigra</i>	<i>Pinus taeda</i>	<i>Fagus grandifolia</i>	<i>Acer rubrum</i>
<i>Acer rubrum</i>	<i>Prunus serotina</i>	<i>Liriodendron tulipifera</i>	<i>Acer barbatum</i>
<i>Acer barbatum</i>	<i>Carya cordiformis</i>	<i>Quercus michauxii</i>	<i>Cornus florida</i>
<i>Cornus florida</i>	<i>Carya glabra</i>	<i>Magnolia grandiflora</i>	<i>Ulmus alata</i>
<i>Prunus serotina</i>	<i>Carya ovata</i>	<i>Carya cordiformis</i>	<i>Ulmus rubra</i>
<i>Carya cordiformis</i>	<i>Carya alba</i>	<i>Carya glabra</i>	<i>Pinus taeda</i>
<i>Carya glabra</i>	<i>Acer barbatum</i>	<i>Carya ovata</i>	<i>Prunus serotina</i>
<i>Carya ovata</i>	<i>Acer rubrum</i>	<i>Carya alba</i>	<i>Celtis occidentalis</i>
<i>Carya alba</i>	<i>Juglans nigra</i>	<i>Ulmus alata</i>	
<i>Juglans nigra</i>	<i>Ulmus alata</i>	<i>Ulmus rubra</i>	
<i>Oxydendrum arboreum</i>	<i>Ulmus rubra</i>	<i>Prunus serotina</i>	

* Note: In descending order of resistance mainly based on 1) Patrick J. Barry, Coleman A. Doggett, Robert C. Anderson and Kenneth M. Swain. 2001. How to Evaluate and Manage Storm-Damaged Forest Areas. Forest Landowner: 22-26; 2) my own field observations on the uprooting and breakage damage in the Duke Forest; and 3) consultations with the experienced foresters Drs. Henry McNab and Coleman Doggett.

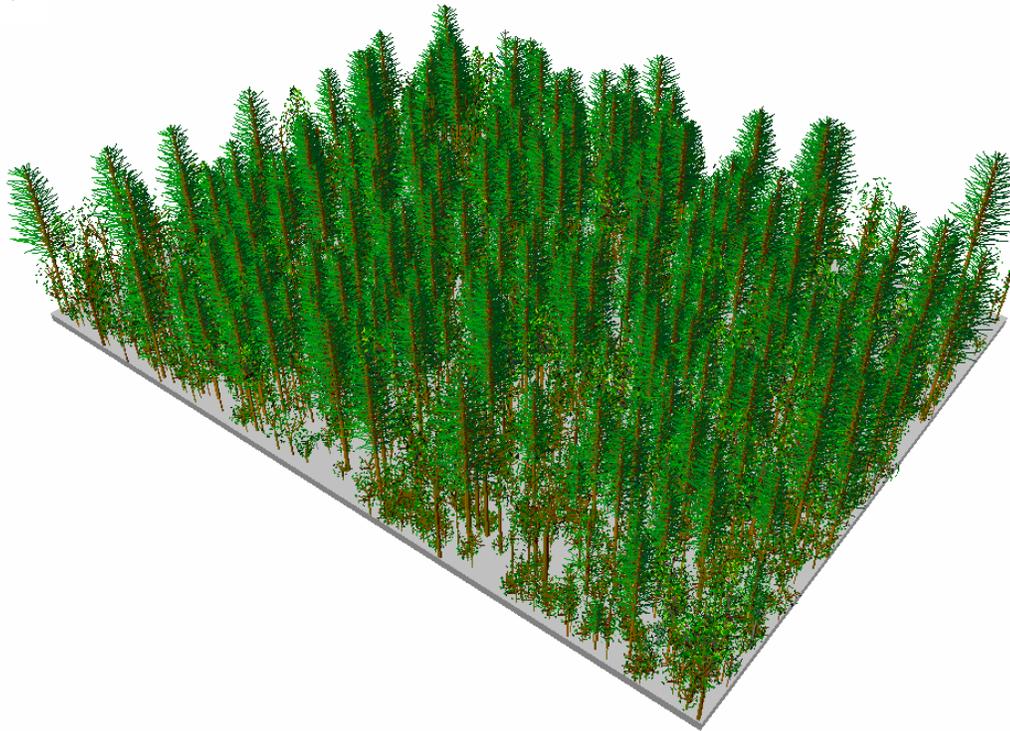
Appendix IV:

Visualization of forest stand dynamics before and after 1996 Hurricane Fran in the Duke Forest, North Carolina, USA

Figure 1. Visualization of forest stand dynamics before and after 1996 Hurricane Fran in the Graveyard plot of Duke Forest, North Carolina, USA. The 3-Dimesion graphic images were generated using the Stand Visualization System (SVS) developed by the Pacific Northwest Research Station of the USDA Forest Service with data from field survey records of the forest stand from 1989 to 2000. These images provide a representation of dynamics of stand conditions in the Graveyard plot over a 13-year period including 1989, 1993, 1997, and 2001.

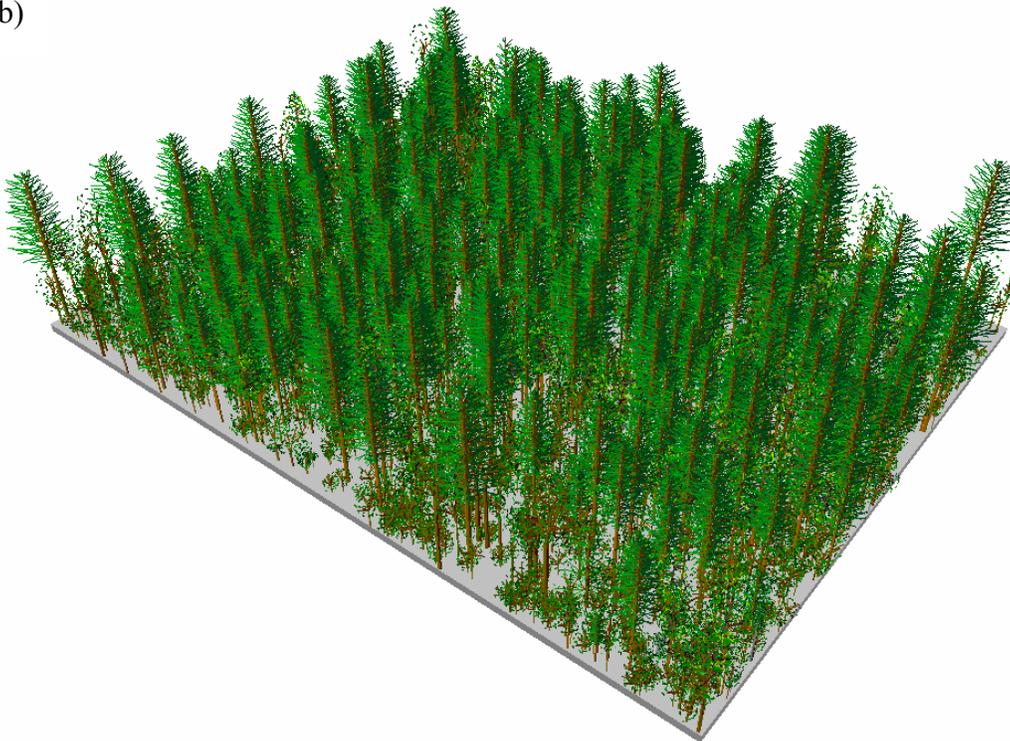
Graveyard_Plot_1989

a)



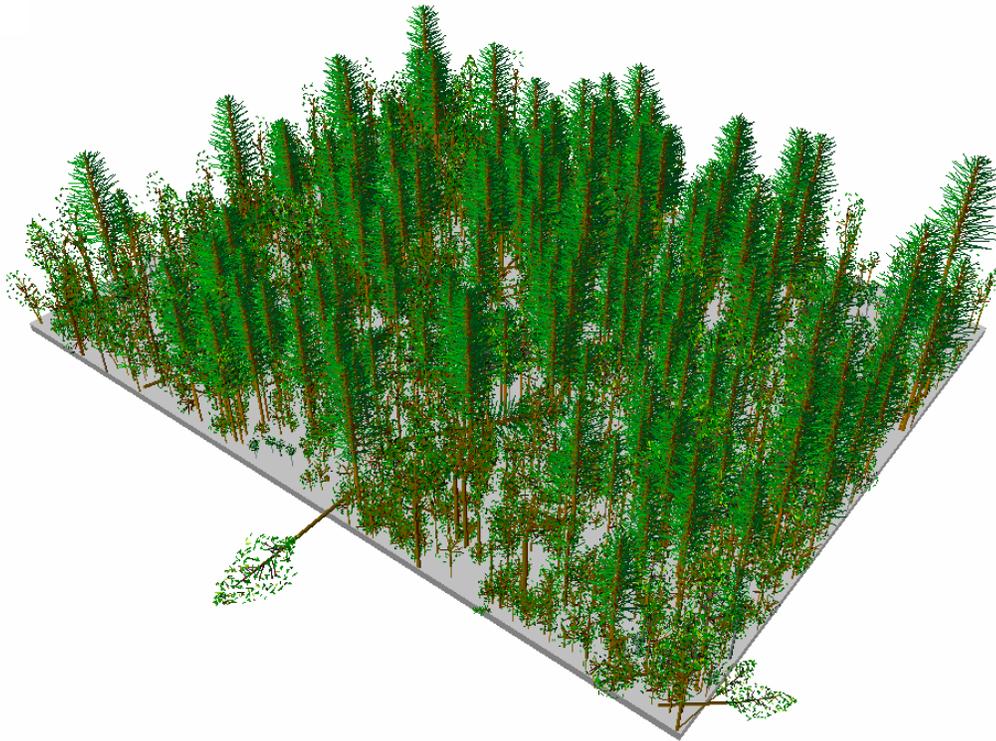
Graveyard_Plot_1992

b)



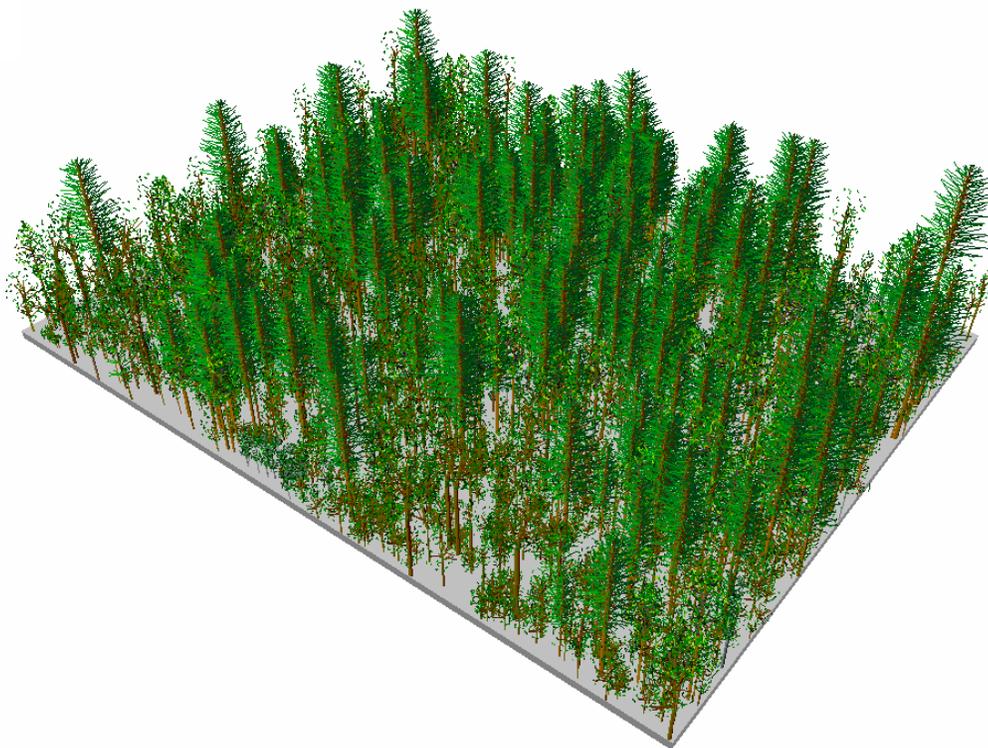
Graveyard_Plot_1997

c)



Graveyard_Plot_2001

d)



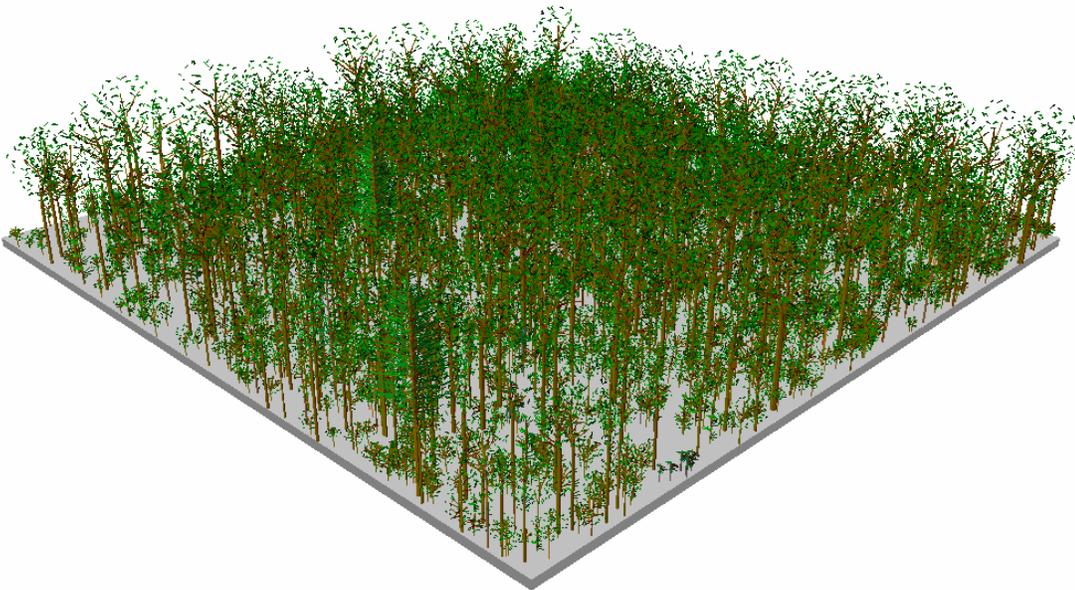
Appendix IV:

Visualization of forest stand dynamics before and after 1996 Hurricane Fran in the Duke Forest, North Carolina, USA (Continued)

Figure 2. Visualization of the forest stand dynamics before and after 1996 Hurricane Fran in the Bormann plot of Duke Forest, North Carolina, USA. The 3-Dimesion graphic images were generated using the Stand Visualization System (SVS) developed by the Pacific Northwest Research Station of the USDA Forest Service with data from field survey records of the forest stand from 1983 to 2000. These images provide a representation of dynamics of stand conditions in the Bormann plot over a 12-year period including 1989, 1993, 1997, and 2000.

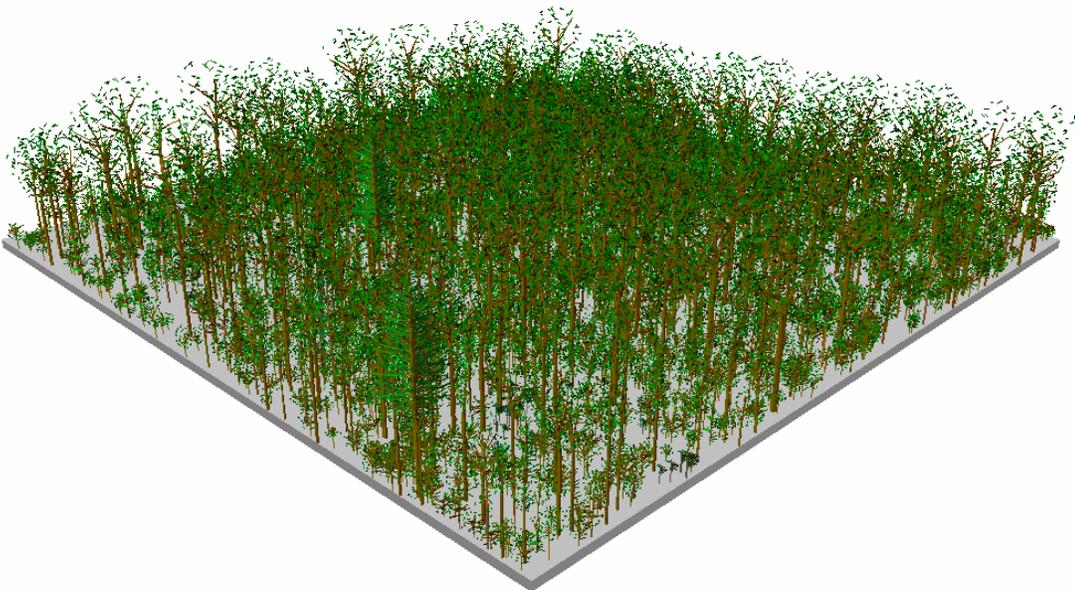
Bormann_Plot_1989

a)



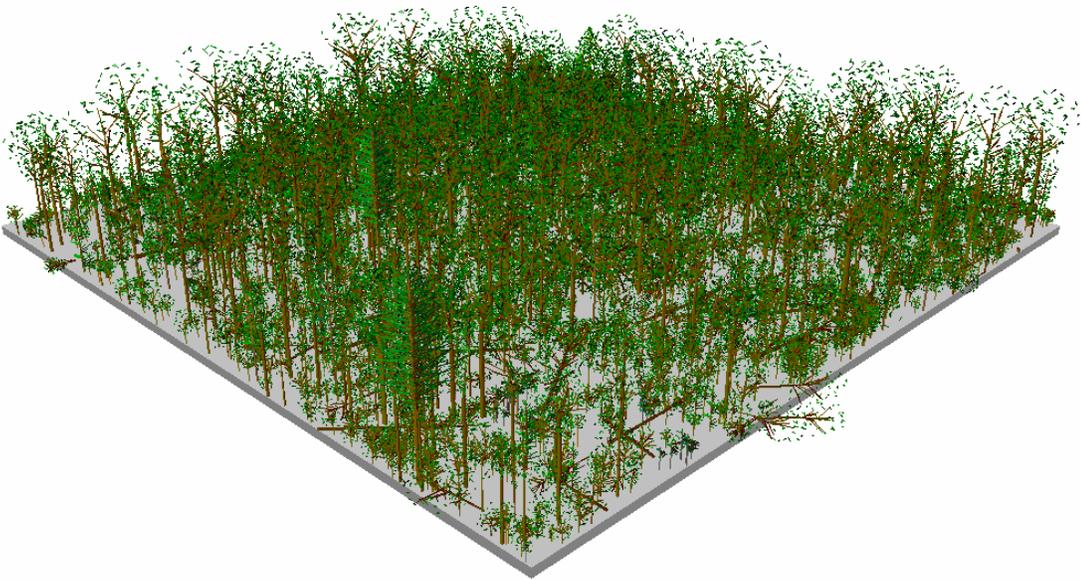
Bormann_Plot_1993

b)



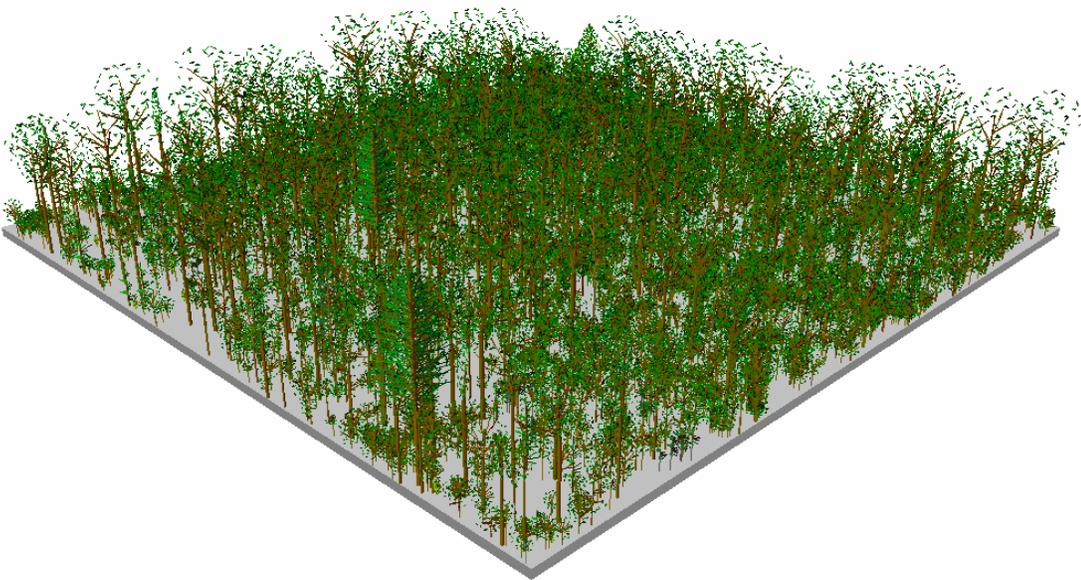
Bormann_Plot_1997

c)



Bormann_Plot_2000

d)



Appendix V:

Photographs illustrating forest damage in Duke Forest by the 1996 Hurricane Fran and understory regenerations after this major windstorm. Photographs are by the author except where otherwise noted.

An introductory description for the following selected photographs:

The 1996 Hurricane Fran was a large, infrequent disturbance in Piedmont forests ([Photo 1](#)). Fran caused substantial tree damage across the Duke Forest. Uprooting was the major form of damage for the medium and large trees during Hurricane Fran due to the heavy rainfall ([Photo 2](#), [Photo 3](#), and [Photo 4](#)). The strong winds also caused substantial stem breakage for some large canopy trees. Forest canopy losses were common ([Photo 5](#), [Photo 6](#), and [Photo 7](#)).

Hurricane Fran created various sizes of forest canopy gaps that greatly increased understory light ([Photo 8](#), [Photo 9](#)). With increased light, major microsite factors play an important role by influencing understory composition, species diversity, growth, and dynamics.

In addition to increasing light, windstorms generate a highly diverse substrate with treefall mounds and pits, stumps, leaf litter, and rotting logs ([Photo 10](#)), allowing greater and more diverse tree species establishment ([Photo 11](#)).

Hurricane Fran significantly increased within-stand spatial heterogeneity as a result of the patchy nature of tree damage and death. However, some portions of the forest escaped significant windstorm damage ([Photo 12](#), [Photo 13](#), and [Photo 14](#)).

The rapid recovery of wind-damaged forests largely resulted from the increased recruitment of the light demanding tree seedling and advanced growth of the surviving trees and the established understory saplings in the new environment of increased light, soil moisture, and nutrients ([Photo 15](#), and [Photo 16](#)).

Tree blowdowns often generated a pit and mound topography, characterized by contrasting moisture conditions, but in both cases by decreased competition and increased seedling establishment ([Photo 17](#), [Photo 18](#), [Photo 19](#), and [Photo 20](#)).

Regrowth plays an important role in tree recovery from catastrophic wind disturbances in temperate hardwood deciduous forests ([Photo 21](#)). After damaged by intensive winds, a high portion of hardwood trees can regrow from sprouting of their damaged stems ([Photo 22](#) and [Photo 23](#)).

In addition, Hurricane Fran created forest gaps that facilitated establishment of invasive tree species and allowed increased growth of previously established invasive individuals ([Photo 24](#)).

Various management practices have been applied for restoring the forest (e.g., restoring loblolly pine forests) in the Duke Forest after the 1996 Hurricane Fran ([Photo 25](#)).

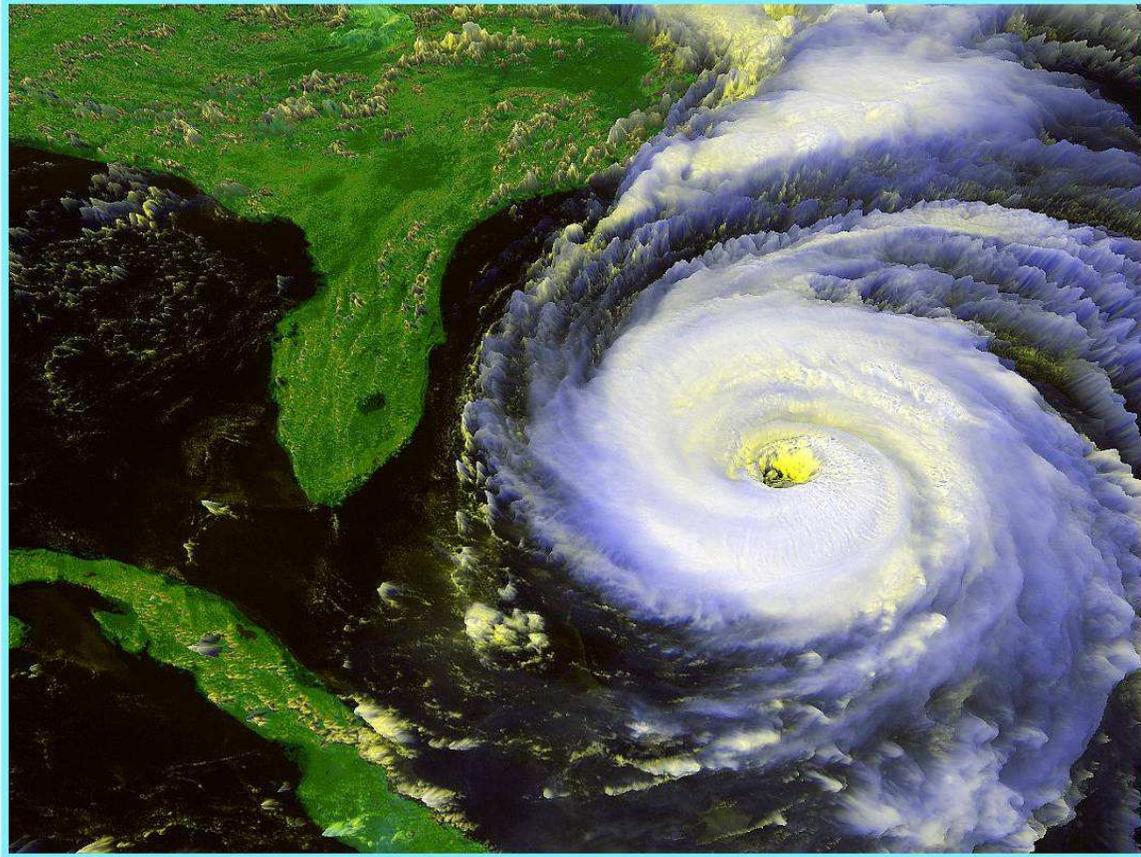


Photo 1. Satellite image of Hurricane Fran on September 4, 1996. Fran was a category 3 hurricane when it made landfall near Cape Fear on the southeast coast of North Carolina on September 5, 1996. After making landfall, Fran moved from southeast to the northwest across North Carolina's Coastal Plain and Piedmont, its eye passing about 24 km east of the Duke Forest. Although wind intensity had begun to decrease, Fran caused substantial forest damage in central North Carolina Piedmont forests. (Image from the Laboratory for Atmospheres, NASA Goddard Space Flight Center; <http://rsd.gsfc.nasa.gov/images/Fran.html>).



Photo 2. Uprooting was the major form of damage for the medium and large trees during Hurricane Fran. This 2001 photograph shows two large uprooted oak trees (*Quercus sp.*) in the Bormann plot in Duke Forest. The explanation for uprooting being the major damage type was that heavy rainfall occurred before and during the storm, saturating the soil. Hurricane Fran brought about 224 mm of rainfall to Duke Forest and adjacent areas during the two-day hurricane period. Perhaps equally important was a heavy rainfall (ca. 76 mm) two days before Hurricane Fran, causing the surface soil to be saturated prior to the arrival of the major windstorm.



Photo 3. Uprooting of medium and large trees during Hurricane Fran caused significant soil disturbance and greatly increased microsite variation in the damaged forest areas, providing a diverse set of habitats for colonization by pioneer herbs, shrub, and trees. This photograph, taken in 2001, shows a large pit and mound formed by a large the uprooting of a large white oak tree during the 1996 Hurricane Fran. Note the size of this pit and mound by comparing it with the 1-m ruler on the pit. Also note the large hickory seedling (*Carya sp.*) and small oak seedling (*Quercus sp.*) on the edge of the pit on the right side of this photograph.



Photo 4. Uprooting was also the major damage type for large pine trees in the even-aged loblolly pine (*Pinus taeda*) stands of the Duke Forest during the 1996 Hurricane Fran. This photograph, taken in 2001, shows a large pit and mound that was formed by a loblolly pine tree uprooted by Fran near the Graveyard plot of the Duke Forest. Increased woody debris and leaf litter caused by wind damage increased seed germination and seedling establishment after the windstorm disturbance.



Photo 5. Although uprooting was the dominant damage type in Duke Forest during Hurricane Fran, the strong winds also caused substantial forest damage and tree mortality via stem breakage. This 2001 photograph shows the aftermath of stem breakage of a large oak tree in the Graveyard plot of Duke Forest by Hurricane Fran. The fallen tree branches and tree canopy caused significant damage to understory saplings, seedlings, and small trees.



Photo 6. Forest canopy losses due to tree stem breakage were common in the damaged mixed-aged deciduous hardwood forest stands of Duke Forest during the 1996 Hurricane Fran. This 2002 photograph shows one standing tree within the Bormann plot that lost its whole canopy due to high winds during Fran. Canopy disturbance caused by Hurricane Fran increased light penetration to the forest understory and ground layer, which facilitated release of established understory seedlings, saplings and small trees.



Photo 7. The strong winds of Hurricane Fran resulted in significant snapping of less resistant tree stems, thereby diversifying the forest community structure and increasing the understory light availability in damaged forests. This 2002 photograph shows the snapped stem of a middle-size loblolly pine tree in PSP 19 damaged by Hurricane Fran. Understory hardwood tree species such as red maple increased growth due to increased light availability.



Photo 8. Canopy damage by Hurricane Fran substantially increased understory light availability in damaged portions of the Duke Forest. This 2001 photograph taken 5 years after the hurricane shows the consequences of stem breakage and increased understory light in the Bormann plot.



Photo 9. 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 10. With increased light, other microsite factors play an important role by influencing understory composition, species diversity, growth, and dynamics. In addition to increasing light, windstorms generate a highly diverse substrate with treefall mounds and pits, stumps, leaf litter, and rotting logs. These newly formed microsites differ from intact forests in their greater light, soil moisture and nutrient availability, thereby allowing greater and more diverse tree species establishment. This 2004 photograph taken 8 years after Hurricane Fran shows tree stem breakage and log decomposition in the Wooden Bridge plot.



Photo 11. In the Duke Forest, recruitment from seeds and growth of established seedlings and saplings was promoted by the large increase of light in the forest gaps following Hurricane Fran. This 2001 photograph shows relatively high understory light in the vicinity of a large pit and mound in the Graveyard plot of the Duke Forest.



Photo 12. Hurricane Fran significantly increased within-stand spatial heterogeneity as a result of the patchy nature of tree damage and death. However, some portions of the forest escaped significant windstorm damage. This 2001 photograph shows a relatively undamaged area of the Graveyard Plot loblolly pine stand of Duke Forest. The Graveyard plot was an even-aged (ca. 80year-old), post-agriculture loblolly stand in transition to hardwood dominance. At the time of Hurricane Fran the canopy of this stand was dominated by loblolly pine, along with scattered red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), tuliptree (*Liriodendron tulipifera*) and hickories (*Carya spp.*). The understory, contained few pine saplings, but instead was dominated by generalist hardwoods such as dogwood (*Cornus florida*), and red maple, as well as other hardwoods characteristic of the site, such as sourwood (*Oxydendrum arboreum*) and American hornbeam (*Carpinus carolina*).



Photo 13. While some areas of the affected forest experienced heavy damage, other areas experienced much less forest damage and tree mortality. In general, most of less-damaged areas or undamaged forest stands were located at less exposed middle slopes. This 2001 photograph shows a relatively little damaged loblolly pine stand in the Korstian Division of Duke Forest.



Photo 14. Hurricane-induced forest damage was patchy. This 2001 photograph shows a less damaged oak-dominated hardwood stand (PSP 10) five years after Hurricane Fran.



Photo 15. 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 seeding regeneration in the Graveyard plot of the Duke Forest four years after Hurricane Fran.



Photo 16. The rapid recovery of wind-damaged forests largely resulted from the increased recruitment of the light demanding tree seedling and advanced growth of the surviving trees and the established understory saplings in the new environment of increased light, soil moisture, and nutrients. This 2001 photograph from the Bormann plot of Duke Forest shows several loblolly pine and tuliptree saplings established immediately after the Hurricane Fran.



Photo 17. Piedmont pine forests are mostly secondary forests in the transition phase of old-field succession to late successional hardwood forests. These pine stands were dominated by loblolly pine in the canopy, along with red maple, sweetgum, tuliptree and hickories. The understory, contained few pine saplings, but instead was dominated by hardwoods such as dogwood and red maple, as well as other hardwoods characteristic of the site, such as sourwood or American hornbeam. This 2002 photograph shows rapid growth of a loblolly pine sapling on a tipup mound in the Graveyard plot of the Duke Forest after the major hurricane disturbance.



Photo 18. Pits and Mounds created by fallen large trees are potential areas for new seedling establishment and growth. This 2001 photograph shows a pit and mound caused by the uprooting of a large oak tree in the Bormann plot of the Duke Forest during the 1996 Hurricane Fran. For scale note the 1 m ruler next to the mound. Note the recently established loblolly pine seedling on the top of the mound.



Photo 19. Tree diversity was enhanced in most of the damaged forest stands as a result of colonization by new, more light-demanding species. This 2001 photograph shows tuliptree, sweetgum and loblolly pine seedlings in a pit caused by a treefall in the Bormann plot of the Duke Forest after Fran.



Photo 20. This pit caused by the uprooting of a tree in the 1996 Bormann Plot during Hurricane Fran provided a suitable area for colonization of light-demanding tree species. Note in this 2001 photograph the rapid growth of several tuliptree seedlings.

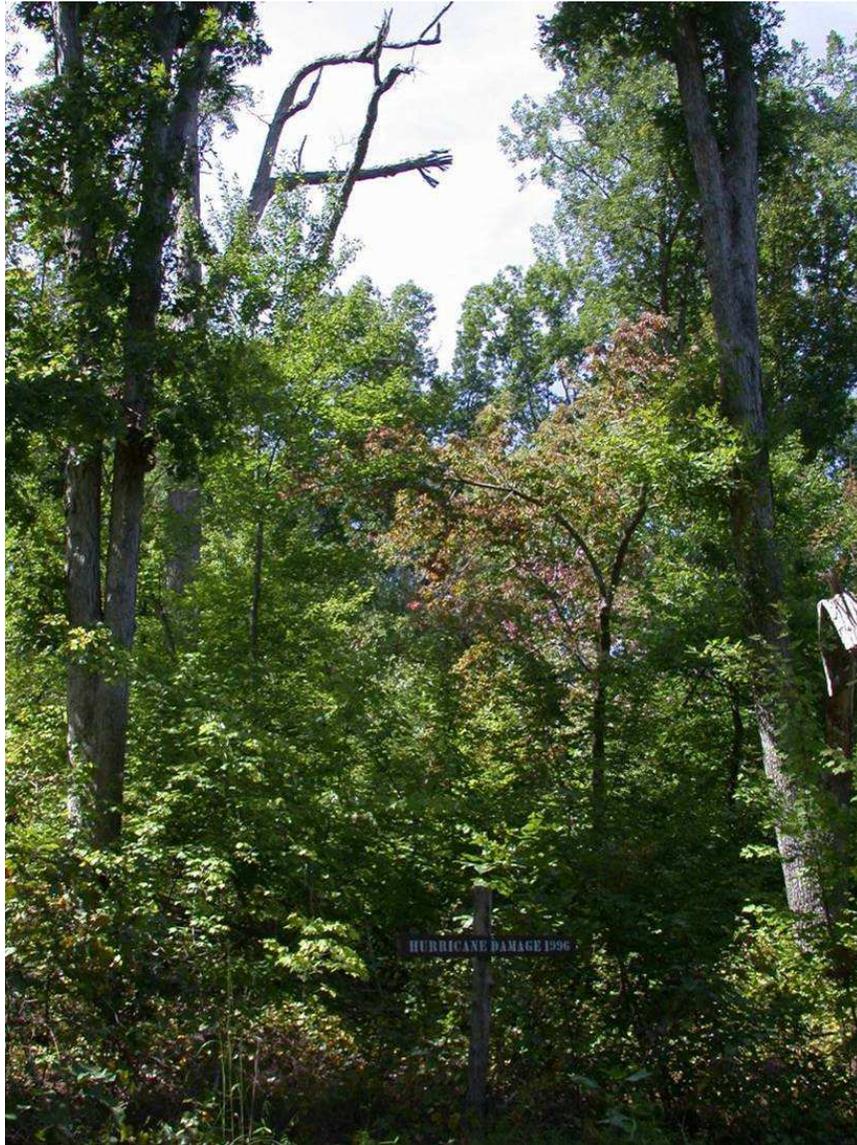


Photo 21. The understory of damaged forests plays a major part in forest response to windstorms in temperate forests. This photograph of the Bormann Plot of the Duke Forest shows the rapid recovery of wind-damaged forests largely resulting from stem sprouting and enhanced growth of the surviving saplings and trees in the new environment of increased light, soil moisture, and nutrient resources.

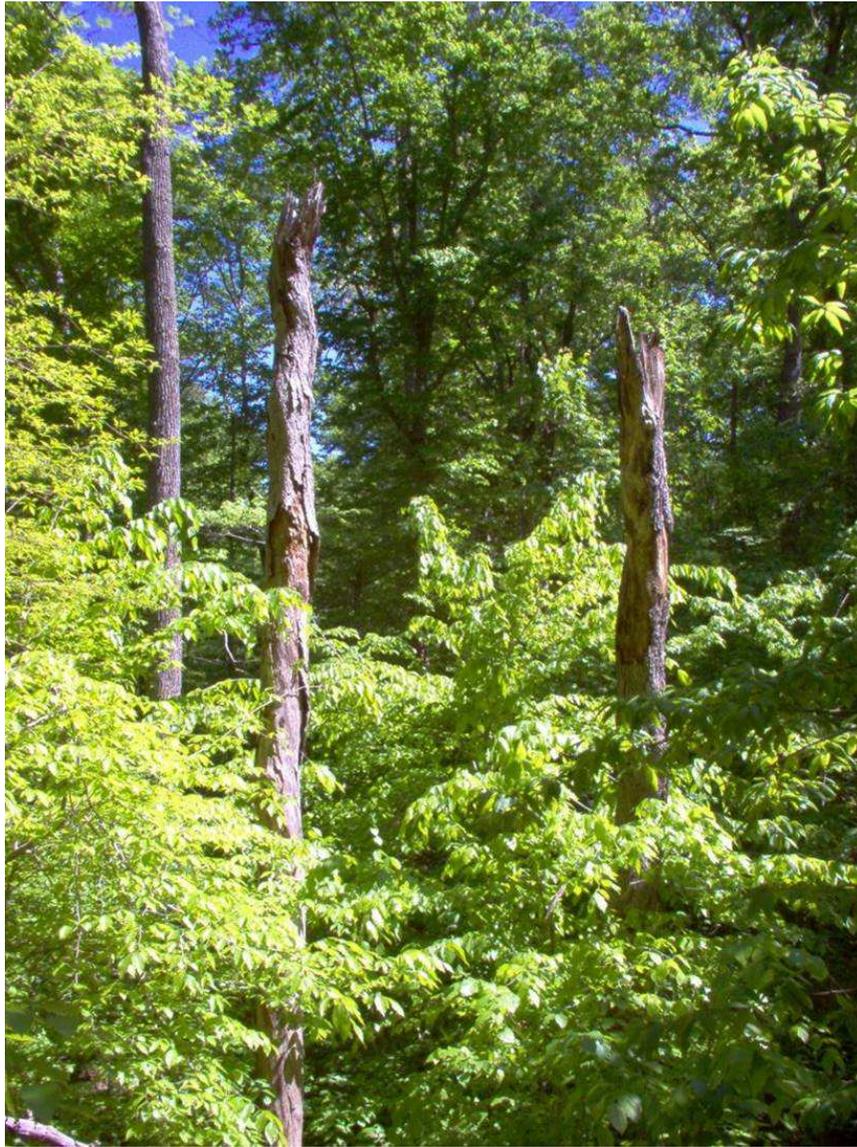


Photo 22. Piedmont forests are remarkable resilience to hurricane damage because of widespread advanced regeneration. This 2004 photograph, taken eight years after Hurricane Fran illustrates the rapid regrowth (i.e., advanced regeneration) of established understory hardwood trees in a forest gap in the Wooden Bridge plot of the Duke Forest.



Photo 23. Regrowth plays an important role in tree recovery from catastrophic wind disturbances in temperate hardwood deciduous forests. After damaged by intensive winds, a high portion of hardwood trees can regrow from sprouting of their damaged stems. This 2004 photograph shows resprouting of an uprooted tuliptree in the Wooden Bridge plot eight years after the 1996 Hurricane Fran.



Photo 24. Hurricane Fran created forest gaps that facilitated establishment of invasive tree species and allowed increased growth of previously established individuals. The exotic princess tree (*Paulownia tomentosa*) and tree-of-heaven (*Ailanthus altissima*) both increased significantly as a result of the Hurricane Fran. This photograph shows invasion of a princess tree into a pit in the Bormann plot of the Duke Forest after Fran. However, overall, invasive species have not yet widely spread in our permanent plots across the Duke Forest.



Photo 25. The Duke Forest managers applied a wide array of management practices for restoring loblolly pine forests after the 1996 Hurricane Fran. This sign shows the 100-year land use history and various management practices have been conducted after the 1996 Hurricane Fran for this damaged area, including salvaging, chopping, site preparation burning, and planting of loblolly pines. This unique sign was located between the Graveyard plot and the Wooden Bridge over the New Hope Creek in Duke Forest.