American beech in coastal New England:
forest history and dynamics

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Preface

This thesis explores the history and dynamics of coastal beech forests on Naushon Island, Massachusetts. In the first chapter I focus exclusively on forest response to hurricanes, characterizing variation in beech and oak species growth and regeneration responses following several hurricanes that have occurred over the past 150 years. The second chapter explores the long-term history and dynamics of monodominant coastal beech forests in order to clarify the conditions and factors that facilitate single-species dominance. This work is part of a larger effort by ecologists at the Harvard Forest to understand the long-term history of vegetation dynamics in the coastal region.

Moderate intensity disturbances, such as hurricanes, cause varying levels of crown damage, blowdown, and growth change among surviving individuals. However, the range of forest responses to wind storms of moderate intensities has not previously been documented. In Chapter 1, I describe an innovative method developed to characterize forest response to hurricanes. The ‘growth change frequency distribution’ method characterizes response to hurricanes by comparing the range of growth responses observed following known hurricanes to the range of growth responses in non-hurricane years. Using this approach, I found response to hurricanes varied by storm, by species, and by forest structural type. Overall, while most hurricanes had little or no effect on coastal forests, an individual storm caused substantial impacts.

In the second chapter I explore the vegetation history and dynamics of coastal beech forests as a case study in single-species dominance. Monodominant forests occur throughout tropical and temperate regions, but the mechanisms involved in their
development are not well understood. This descriptive study identified several factors that facilitated the development and persistence of monodominant beech forests on Naushon Island. In particular, both disturbance history and species-specific traits enabled beech to dominate forests. In the second chapter, I also characterize beech structural variation with respect to edaphic and environmental conditions, and describe ‘dwarf beech forests’ which have not been documented in the literature.

This thesis represents the first effort to characterize the history and dynamics of coastal beech stands in southern New England. Although uncommon in the modern landscape, this forest type was apparently more widespread prior to the arrival of Europeans. Results of this research suggest that changes in hurricane frequency and intensity or other human or natural disturbances could strongly influence the composition and dynamics of coastal forests.
CHAPTER 1

Variation in forest response to hurricane disturbance in coastal New England

Abstract

Research on disturbance in forest ecosystems has generally focused on either catastrophic disturbances generating stand-replacing successional sequences, or small-scale disturbances (e.g. individual tree-fall gaps) generating tree-by-tree replacement events. The role of moderate disturbances in forest development, in contrast, is poorly understood. While the most severe hurricanes can cause catastrophic disturbance, most hurricanes are moderate disturbances that affect a wide range of forest types from the Caribbean to the northeastern United States. In this study I characterize both individual and population level responses of beech and oak species to hurricanes that varied in intensity in coastal Massachusetts. I explicitly compare the range of growth responses observed following known disturbances to the range of growth responses in non-event years. Beech and oak species exhibited a wide range of responses in growth and regeneration to hurricanes; however, only a single storm caused dramatic increases in growth and new establishment for beech. The results of this study highlight the importance of wind disturbance in the establishment and persistence of beech, and suggest that while some moderate disturbances have little or no effect on species growth and regeneration dynamics, individual storms may have substantial impacts. Variation in forest response to wind storms of varying, but moderate intensities, depended on local site conditions, including environmental, meteorological, topographical, historical and biological factors.
INTRODUCTION

Wind disturbances impact forest composition, structure and function worldwide (Canham and Loucks 1984, Foster 1988a and b, Bellingham et al. 1995, Peterson and Pickett 1995, Robertus et al. 1997, Batista and Platt 2003, Sinton et al. 2000, Kramer et al. 2001, Schulte and Mladenoff 2005), and recent studies indicate ongoing global climate change may result in more intense wind disturbances and substantial changes in storm tracks (Emanuel 2005, Salinger 2005, Webster et al. 2005). The implications of such altered disturbance regimes for forest dynamics are largely unknown, despite the potential for substantial ecological, economic and aesthetic impacts. Unlike more extreme disturbances (e.g. landslides, volcanic eruptions) that initiate primary succession controlled by species dispersal and establishment in a highly altered environment (Veblen and Ashton 1978, Turner et al. 1998), wind disturbances in forests are typically less severe, with forest response determined in part by varying amounts of tree survivorship, seedling establishment and growth change in response to altered resource conditions (Brokaw and Walker 1991, Peterson and Pickett 1995, Batista et al. 1998, Cooper-Ellis et al. 1999).

Wind disturbances, including hurricanes, extra-tropical cyclones, tornados, and other wind storms, result in a wide range of damage to forests, from minor crown damage to extensive blowdown (Runkle 1981, Foster 1988a and b, Brokaw and Walker 1991, Canham et al. 2001). Low intensity wind disturbances create individual tree-fall gaps typically dominated by species present in the understory at the time of gap formation (Runkle 1990). Severe windstorms affect extensive areas (e.g., the 1938 New England hurricane and the 1985 Tionesta, PA tornado) and are thought to “reset” forest
ecosystems compositionally, with subsequent establishment controlled by colonization abilities and propagule availability in an environment characterized by the living and non-living legacies of the pre-disturbance environment (Foster 1988a and b, Peterson and Pickett 1995). Moderate intensity events may cause minor – to – moderate levels of blowdown, crown damage, and growth change among surviving individuals, with community response determined by differences in growth and establishment among species (Canham et al. 2001, Batista and Platt 2003). However, because previous studies have focused on forest response to individual wind storms at the ends of a spectrum in disturbance severity, the range of forest responses to wind storms of moderate intensities over long time periods is poorly understood. Since forest response to wind disturbance is conditioned by stand structure and composition, and environmental, meteorological, topographical, and historical factors (Foster and Boose 1992, Boose et al. 1994, Kramer et al. 2001, Canham et al. 2001), response to even storms of similar intensity may be highly variable.

It is often difficult to determine the timing, intensity and characteristics of wind disturbance events over long time periods. Reconstructions of wind disturbance regimes have typically used surrogate data from analysis of population age structure and annual tree rings to infer disturbance events. Pulses of regeneration and synchronous increases in radial growth among many trees, dubbed “releases,” are used to approximate the timing of stand-level disturbance events; severity is then estimated by the abundance and magnitude of release and establishment (Lorimer 1980, Lorimer and Frelich 1989, Orwig and Abrams 1999). This indirect reconstruction approach assumes that a relationship exists between disturbance intensity, a measure of disturbance strength, and severity, a
measure of response, with more intense events eliciting more abundant release and establishment (Frelich and Lorimer 1991). However, there have been few attempts to rigorously test the relationship between disturbance intensity and subsequent growth change (Nowacki and Abrams 1997, Rentch 2002).

Historical information, when available and accurate, can provide a temporal record of large-scale disturbance events (Foster 1988a and b, McLachlan et al. 2000). Historical reconstructions in the northeastern United States have identified a strong regional gradient in hurricane frequency and intensity from southeastern coastal areas, where intense hurricanes occur frequently, to northwestern inland regions, where hurricanes are relatively uncommon (Boose et al. 1994, 2001). In inland portions of New England, site exposure, tree height, and species composition controlled forest damage caused by the 1938 hurricane (Foster 1988a and b, Foster and Boose 1992, Merrens and Peart 1992). However, the response of coastal forests to more frequent and intense hurricanes is largely unknown, and no study has taken a comprehensive approach to characterizing forest response to multiple hurricane disturbances over a broad time scale.

In this study I examine the response of coastal forests to several hurricanes over the past 150 years, by comparing tree growth following hurricanes to tree growth in years without major hurricanes. Naushon Island, located off the coast of Massachusetts (MA), was chosen for study because hurricanes are the dominant form of natural disturbance; human land use and other natural disturbances have been minimal for the past 150 years; and forests on the island contain only three common tree species, simplifying the task of interpreting species response to disturbance. Additionally, historical sources and a meteorological model allowed me to construct a detailed record of hurricane frequency
and intensity for the study area since European colonization. These conditions present a unique opportunity to explore the relationship between disturbance intensity and population-level responses in terms of tree growth and regeneration. The specific objectives of this study are to 1) characterize the range of species growth responses following a suite of hurricanes of varying but moderate intensities, using a method that compares growth following hurricanes to growth in non-hurricane years, 2) examine patterns of tree establishment with respect to known hurricanes and anthropogenic disturbances, and 3) discuss the role of hurricanes in coastal forest development.

**STUDY AREA**

Study sites are located on Naushon Island (12 km long and 2 km wide), the largest of the Elizabeth Islands. The islands extend southwestward from Woods Hole, MA and are separated from the mainland by Buzzard’s Bay. This chain of islands is part of an end moraine that was formed in the late-Wisconsinan glaciation when the Buzzard’s Bay ice lobe re-advanced during its long-term retreat (Oldale 1992). The landscape is typically morainal with rolling hills (the highest ranging from 30 – 50 m), kettle holes and large surface boulders (Woodworth and Wigglesworth 1934). Soils are composed of medium-to-coarse sands, with finer textured soils found in topographic depressions (Fletcher and Ruffinoli 1986).

Naushon Island has been owned by single families since European colonization, and perhaps as a result, has been characterized by lower population densities and less intensive land use than the surrounding areas (Busby et al. in prep). In particular, anthropogenic disturbance to forests over the past 150 years has been minimal, allowing
for a focused study of forest response to hurricanes. In the early colonial period, the island’s highly valued timber species – cedar, oak, hickory, and sassafras – were selectively cut (Emerson 1935). The last major cutting event on the island occurred from 1824-27 and affected the island’s western forests and portions of the eastern forests (Busby et al. in prep).

In the early colonial period the central portion of the island was cleared for sheep pasturing and has remained open since that time (Schroeder 2002). Sheep were abundant on the island throughout the historical period and grazed largely in pastures. In contrast, native deer have been a significant source of herbivory in continuously forested areas throughout the historical period. The deer population has ranged from 50 – 500 over the past 200 years (2 – 22 deer/km²); however, population estimates at the time of individual hurricanes are not available. In general, population densities greater than 8.5 per km² are thought to negatively affect oak species regeneration (Healy 1997).

There are two large areas on the island that have been continuously forested since European colonization, hereafter referred to as the East and West end forests (Fig. 1). Combined, the East and West end forests cover 1,052 ha of the 2,226 ha island. American beech (Fagus grandifolia) dominates both areas, accounting for 97% of stems in our study plots. Scattered large white oak (Quercus alba) and black oak (Quercus velutina) are also present. Few or no herbaceous plants or shrubs are found in the densely shaded understory. Extensive reconnaissance surveys identified three common and distinct structural stand types that are informally referred to as: tall, intermediate and dwarf (Fig. 2a, b, c). Tall stands occur at the bottom and lower slopes of ice-block
Fig. 1. Map showing the study area along the southern New England coastline. Insets show forested areas on Naushon Island, MA in 1999 (top panel) (MassGIS 2002) and in 1845 (bottom panel) (CGS 1845) with locations of study plots and stone walls.
Fig. 2. Photographs of representative structural forest types on Naushon Island, MA: (a) tall, (b) intermediate, and (c) dwarf.
depressions and other lowlands. Beech trees 40-70 cm in diameter and 20-30 m tall dominate the canopy, and are present in all smaller size classes. Intermediate stands are found in areas with little topographic variation. Many of these stands support dense pole-sized beech trees, while others contain beech trees in all size classes up to 40 cm in diameter and 20 m tall. Dwarf stands are located on ridges or knobs and are dominated by short-stature beech trees 1-5 m tall and less than 25 cm in diameter that apparently develop in response to stressful conditions created by dry, nutrient poor soils, chronic exposure to salt-laden winds, and occasional storms that damage or remove emerging oaks (Busby et al. in prep). A fourth structural type, found along the coastline and characterized by dense, wind-sculpted beech trees 10-30 cm in diameter, was not sampled extensively since it occurred in only a few locations. A notable feature of all stand-types is the limited beech mortality from beech bark disease. Beech bark disease has been present on the island for > 30 years (D. Houston pers. comm.), but has resulted in little mortality, in contrast with high mortality rates throughout the Northeast (Twery and Patterson 1984).

An unusually detailed series of maps depicts land cover change for the island since 1781. Early nautical maps (Des Barres 1781) and a detailed US Coast and Geodetic Survey map (1845, scale: 1:10,000) identified areas that were forested through the 19th C., and a series of aerial photographs were used to track changes in the landscape over the past century. Study sites were subjectively placed in areas that were continuously forested throughout the historical period, which were defined as areas consistently mapped as forested for which I found no contradictory documentary or field data to suggest otherwise (Fig. 1).
METHODS

Field Data

To characterize variation in response to hurricanes, I sampled vegetation in fixed area plots (400 m²) in representative structural forest types in both the East and West end forests (tall N = 6, intermediate N = 12, and dwarf N = 6) (Fig. 1). Whenever possible a tall, intermediate and dwarf stand were selected in close vicinity to document forest response to similar disturbance events across a topographic and forest structural gradient. For each plot, average stand height, slope, aspect, and the presence and orientation of each tip up mound were recorded. Species and dbh were recorded for all trees greater than 10 cm dbh, and an increment core was taken from 15-20 trees greater than 7 cm dbh for age determination and radial growth analysis. Because of the low density of oak species in study plots, and their greater age than the more abundant beech, additional oak trees located outside of plots were cored to facilitate reconstructing long term forest history and dynamics. This included oak trees immediately adjacent to study plots (included in Fig. 3a, b, c), as well as trees not associated with particular study plots (Fig. 3d). In dwarf study plots, a random sample of seedlings (stems < 10 cm basal diameter and not reaching breast height) and saplings (stems < 10 cm dbh) (5-10 per plot) were cut for age determination.

Sound cores were collected from 647 trees: 433 beech, 146 white oak, and 68 black oak (East end N = 347, West end N = 300; tall N = 154, intermediate N = 198, dwarf N = 109 and outside-of-plot oak species N = 132). Additionally, a relatively small number (N = 54) of beech and oak cores were retrieved from stands along the coastline and are included in species analyses, but not in analyses of structural types because of the
limited occurrence of this type. Cores were taken as close to the base of each tree as possible (30 - 40 cm from the base) in order to attain the most accurate establishment date. Cores were dried, mounted, and sanded with increasingly fine sandpaper to reveal the cellular structure. Tree rings were counted and measured to the nearest .01 mm using a Velmex measuring system (East Bloomfield, NY, USA). Cores were used to determine tree ages, excluding rotten cores and cores that substantially missed the pith. All cores were used in the radial growth analysis. A sub-sample of beech ($N = 92$) white oak ($N = 58$) and black oak ($N= 25$) were visually cross-dated, and verified using the program COFECHA (Holmes 1983). Cross-dated cores were used to examine the yearly response to hurricanes.

**Hurricane regime reconstruction**

The first step to characterizing tree response to hurricanes was determining the timing and intensity of hurricane strikes to the study area. Boose et al. (1994, 2001) reconstructed hurricane frequency and intensity in New England from European colonization (1620) to 1997. First, all hurricanes with damaging winds were identified for the region by a comprehensive review of a wide range of sources: personal diaries and town histories for the period 1620-1699, contemporary newspapers from 1700-1997, and meteorological data from 1871-1997. Wind damage reports and meteorological observations for each storm were used to characterize regional patterns of damage. Boose et al. (1994, 2001) then developed a model, HURRECON, parameterized with data from recent hurricanes, which can be used to reconstruct maximum hurricane wind speeds, a measure of hurricane intensity, at specific sites. I used HURRECON to reconstruct hurricane frequency and intensity for Naushon Island for the period 1620 –
1997. However, since the model is designed to characterize hurricane disturbance at landscape to regional scales, I do not attempt to distinguish storm intensities among hurricanes with similar reconstructed values.

HURRECON estimates of hurricane wind speeds are easily translated into a Fujita scale rating of storm severity. The Fujita scale rating system classifies F0 damage as a loss of leaves and branches and the uprooting of shallow rooted trees (sustained wind speeds 18-25 m/s), F1 damage as scattered blowdowns and small gaps (26-35 m/s), F2 damage as extensive blowdowns (36-47 m/s), and F3 damage as almost complete leveling of trees (> 48 m/s) (Boose et al. 1994, 2001). Hurricane intensity is more commonly described in terms of the Saffir-Simpson scale; categories 1 through 5 relate wind speeds and potential damage. A category 1 hurricane is equivalent to the upper range of F1 storms and the lower range of F2 storms. A category 2 hurricane is similar to an F2 storm, and a category 3 hurricane is equivalent to an F3 storm. It is uncommon for category 4 or 5 hurricanes to strike the New England coast since storms lose strength as they travel north over land and cold ocean waters.

Local documentary sources from the study area – personal descriptions, anthologies and annual reports – were used to develop an independent reconstruction of hurricane strikes. I used the documentary reconstruction in combination with the HURRECON reconstruction to identify six hurricanes to examine in detail for which I had an adequate sample of tree ring data. The six hurricanes 1) were characterized by Fujita scale ratings (1.4 – 2.2) greater than the median rating for all hurricanes (1.3); 2) were not preceded or followed (within six years) by another hurricane (Fujita scale rating > 1.4); and 3) impacted the study site according to documentary sources (excluding one
Minor hurricanes were not included because these events were typically not recorded in historical documents, and were not thought to have had an observable effect on population-level growth dynamics. I selected hurricanes not preceded or followed by another hurricane in order to determine growth response to a specific event, recognizing, however, that the effects of a previous hurricane may persist much longer than six years and exert influence on the growth response to a subsequent storm. A longer period of separation between hurricanes was not possible given the high frequency of hurricanes. The selected hurricanes occurred in 1869, 1888, 1924, 1944, 1960, 1991, and had reconstructed Fujita scale ratings of 2.2, 1.4, 1.5, 1.9, 1.8, and 1.9, respectively. An earlier hurricane (1841, 1.8) was also evaluated for white oak, which was the only species that commonly had stems predating this event. These seven hurricanes are representative of the more severe storms that have impacted the study area over the past 150 years.

**Growth change frequency distributions**

To characterize tree response to a range of hurricanes over the past 150 years, I developed a method that explicitly compares the range of growth responses among individuals of a particular species following hurricanes to the range of growth responses in non-event years. I examined forest-wide beech, white and black oak growth responses (all trees of each species living at year y) for this and other analyses. However, the number of trees sampled in each structural type was not sufficient to compare growth responses among structural types for all hurricanes.

Growth in non-event years, those in which a hurricane did not occur, provides an estimate of the range of growth responses that occur in a typical year, and is used as a
benchmark to assess growth response to hurricanes. I distinguish between two types of non-event years: non-hurricane years and quiet years. Non-hurricane years occur throughout the study period, but do not fall on a hurricane year. Quiet years are those which are not preceded or followed (eight years) by a hurricane (> F1), and are distributed in the only two ‘quiet periods’ that occurred in the study period: 1904-1916 and 1969-1983. A greater separation between quiet years and hurricanes was not possible given the high frequency of hurricanes in the study area. I examined a number of quiet \( N = 6 \) and non-hurricane years \( N = 6 \) equal to the number of hurricanes examined. I also examined the effect of a major cutting event on white oak growth. The cutting event took place from 1824-27 \( y = 1826 \) and affected most of the West end forest and portions of the East end forest (Emerson 1935).

Using all cores, I calculated percent growth change (GC) for each hurricane and non-event year \( y \). GC for each core was calculated using prior \( (M_1) \) and subsequent \( (M_2) \) ten-year growth means: \( GC = [(M_2 - M_1) / M_1] \times 100 \). For example, to calculate GC for the year 1944, \( M_1 = 1935-1944 \) and \( M_2 = 1945 - 1954 \) were used (Nowacki and Abrams 1997). I examined growth changes based on ten-year averages to filter out short term tree responses to climate while detecting sustained growth responses caused by disturbance (Lorimer and Frelich 1989, Nowacki and Abrams 1997). However, by using ten-year growth averages, GC in non-event years may overlap the \( M_1 \) or \( M_2 \) of hurricane years. Because GC for beech is correlated with tree size, with smaller trees showing greater GC, I standardized GC by size to compare individuals of varying sizes throughout the 150-year study period. To standardize, I multiplied GC by the diameter at year \( y \), calculated by summing the ring widths from the innermost year to year \( y \). I excluded
cores from this analysis that were rotten or did not reach the pith. Since white and black oak showed a range of GC for all tree sizes, GC was not standardized by tree size.

I generated GC frequency distributions for beech and oak species for the six selected hurricane years and non-event years. Differences among the shapes of GC frequency distributions following the selected hurricane years, and differences between the hurricane years and the non-event years, are interpreted as resulting from the differential impact of hurricanes on growth. Growth change frequency distributions have also been used to assess the likelihood of gaps versus understory origin for seedlings (Lorimer et al. 1988). In non-event years, I expected GC would be tightly distributed, with a relatively small number of individuals exhibiting above or below average growth. In response to stand-level disturbance events, in which a minimum of ~ 25% of trees typically experience growth release (Nowacki and Abrams 1997), I expected distributions would have long right tails and would be characterized by significantly higher third quartile values relative to non-event years. I use the third quartile value as a proxy for the level of GC exhibited by the fastest growing trees. For example, a higher third quartile value in a hurricane year relative to a non-event year would indicate that 25% of trees responded to the hurricane with greater GC than the third quartile value of the non-event year.

I report only the statistics that best characterize differences among hurricanes, and between hurricane and non-event years: 10%, 25%, 75% and 90% quantiles, maximum, mean, median, skewness, and variance. One-way analysis of variance was used to compare these statistics for the three categories (hurricane, non-hurricane and quiet).
also present an illustrative example of GC frequency distributions following a major hurricane, 1944, and a non-event year 1934, for all species.

**Transient patterns of growth following hurricanes**

In order to characterize transient patterns in growth following hurricanes, I examined annual variation in the growth response to hurricanes. First, to determine how mean growth change ($M_2$) varied over the ten-year period following hurricanes, I examined variation in the yearly response around the post-hurricane ten-year mean for the two hurricanes that elicited the greatest growth response (1924 and 1944). For example, in the years immediately following the hurricanes, positive growth relative to the post-hurricane mean would indicate rapid attainment of maximum release, whereas negative growth followed by positive growth would indicate gradual release, or damage followed by recovery. I calculated the year-to-year residuals ($R_y$), the difference between a measured annual ring width ($W_y$) and the ten-year post-hurricane mean ($M_2$), for years one-to-ten for the two hurricanes: $R_y = W_y - M_2$. In order to compare the range of response among trees of differing species, life stages and sizes, I standardized residuals by dividing $R_y$ by $M_2$.

Secondly, I generated mean ring width indexes for beech and oak species to examine variation in annual growth following hurricanes relative to pre-hurricane growth, and more broadly, relative to growth throughout the 150 year study period. Species indexes are composed of standardized mean indices for all cross-dated cores. Standardization involves fitting a curve or straight line to the average tree growth as it changes over time to ‘correct’ for age-related growth trends (Fritts and Swetnam 1989). Each ring width is divided by the value of the curve, and expressed as an index of the
potential average growth for that year. Since I observed no overall age-related growth
trends for beech, which established in the understory and in open conditions and was
characterized by multiple periods of suppression and release, indices were calculated by
dividing annual growth values by the overall mean growth increment (straight line
standardization). In contrast, since oaks showed declining growth with age, indices were
calculated by dividing annual growth values by expected values obtained from fitting a
negative exponential or negative linear curve to measured values. To gauge the impact of
climatic conditions on observed growth patterns I examined the Palmer Drought Severity
Index (PDSI) for the Massachusetts NCDC Climate Division 3. Monthly PDSI values
were averaged to generate a yearly signal for the period 1895 – 2004 (NOAA CLIMVIS).

RESULTS

Forest composition and population age structure

Beech trees dominated all study plots, accounting for 96% of stems in dwarf
plots, 98% in intermediate, and 96% in tall. Oak species accounted for the remaining
stems; other species accounted for < 1% of stems and were excluded from age structure
and growth analyses (*Acer rubrum* and *Ostrya virginiana*). Beech trees ranged in age
from 26 to 204 years, with a median age of 61 years (*N* = 433). Beech establishment is
characterized by two major pulses of establishment – one following the 1824-27 cutting
event that persisted for 50 years (tall and intermediate types) and a second following the
1944 hurricane (all structural types) (Fig. 3a, b, c).
Fig. 3. Establishment patterns for distinct structural forest types (a, b, and c) and scattered oaks (d) (tall \( N = 154 \), intermediate \( N = 198 \), dwarf \( N = 109 \), and scattered oak \( N = 132 \)). White and black oaks sampled immediately adjacent to plots are included in structural forest type figures whereas oaks not associated with plots are depicted in panel d. Tree establishment dates are binned by decades.
The oldest trees found in the study area were white oaks, which ranged in age from 59 to 351 years, with a median age of 181 years \((N = 146)\) (Fig. 3d). The oldest white oak tree sampled in the study area, 351 years, is one of the oldest of this species recorded in New England. Episodic white oak establishment occurred in the late 1700s to early 1800s, and again beginning in the 1820s. The only period of black oak establishment was synchronous with the second period of white oak establishment; black oaks ranged in age from 108 to 196 years, with a median age of 152 years \((N = 68)\) (Fig. 3d).

**Hurricane reconstructions**

The HURRECON model identified 58 storms that have impacted the study area since 1620 (Fig. 4). The higher frequency of hurricanes in the last century is a result of a greater abundance of historical and meteorological data, and is not interpreted as a real change in hurricane frequency (Boose et al. 2001). Fujita scale values ranged from 0.1 to 2.6, with a median value of 1.3. Five storms were assigned Fujita scale values greater than 2: 1635, 1770, 1804, 1815, and 1869. For the period 1620 to 1997, an average of 6.5 years elapsed between hurricanes, 16 years between storms resulting in F0 damage, 13 years between F1 damage, and 75 years between F2 damage. The greater frequency of hurricanes resulting in F1 damage than F0 damage is most likely a consequence of the greater likelihood of a severe storm being recorded by documentary sources, not a positive relationship between storm frequency and intensity. Hurricane frequency and intensity are high in the study area relative to the inland part of New England, where
Fig. 4. Hurricanes affecting the study area since 1620, reconstructed by HURRECON (Boose et al. 1994, 2001). Arrows indicated hurricanes examined using the GC frequency distribution analysis. Intensity of damage is estimated by Fujita scale: F0 damage = wind speeds 18-25 m/s, broken branches and shallow-rooted trees uprooted, F1 damage = 26-35 m/s, single trees or isolated groups blown down, F2 damage = 36-47 m/s, extensive blowdowns, and F3 damage = 48-62 m/s, most trees blown down.
hurricane frequency and intensity decreased from southeast to northwest, and an average of 5 - 85 years elapsed between F0 hurricanes, 10 - 200 years between F1 storms, and 85 - 380 years between F2 storms (Boose et al. 2001).

While the analysis using HURRECON indicates that 58 hurricanes impacted the study area, I found historical descriptions pertaining to Naushon Island for only 16 hurricanes (beginning with the 1815 hurricane), and four of these were not identified by the model (1928, 1954, and two storms in 1955). One of the four storms not reconstructed by HURRECON was described as a minor storm causing no damage (August 13, 1955), whereas the other three caused some damage, including the uprooting of trees. Of the 12 hurricanes for which I have historical documentation that were also reconstructed by HURRECON, Fujita scale values ranged from 0.8 to 2.2, with a median value of 1.8. The range and median value of reconstructed intensities for the storms for which I found historical documentation suggests a bias toward documenting higher severity storms.

Of the 42 hurricanes reconstructed between 1815 and 1997, 10 were defined as F1.5 or greater, and 9 of these 10 storms were described in historical documents from the study area. Historical descriptions suggest high variability in forest damage among the highest intensity storms (Table 1). Descriptions of the 1944 hurricane (F1.9) indicate that damage from that storm was far more severe than damage caused by other storms with similar reconstructed intensities. The 1960 and 1991 storms, for example, were reconstructed as F1.8 and F1.9, but descriptions of these storms and field observations indicate that major damage did not occur.
Table 1. Documentary sources revealing impact of storms selected for GC frequency analysis.

1841  (F-scale 1.8) Oct. 3 1841 “A gale from the north-east commenced in the morning and in the course of the afternoon and night blew most violently and undoubtedly was the heaviest storm which has occurred since the memorable one of 1815….Tuesday afternoon took a ride in the woods; sad havoc the storm has made there. The ground is covered with leaves torn from the trees; large limbs are wrenched and twisted off; many of the time honored and venerable old oaks and beeches lie prostrate with an air of grandeur about them even in their lowly estate. The air is fragrant with the odor of bruised and crushed leaves: the roads and paths are blocked up in many places with trees uprooted and lying across them” (Forbes and Gregg 1979).

1869  (F-scale 2.2) “September…It was the greatest gale since the famous September gale of 1815. The “Apollo” tree in the amphitheatre was rooted up, and many other fine trees” (Hughes 1902).

1888  (F-scale 1.4) No documentation.

1924  (F-scale 1.5) “A hurricane struck the Island in August after three days of heavy rain. It was short-lived but violent, coming from the northwest and laying low a swath of trees from the vicinity of the Green Gate Wall across to the South Shore” (Emerson and Leon 2003). “…we realized that a lot of trees had been blown down, and I went out the next day to clear trees that had fallen on the Main Road” (Forbes 1964). Post-hurricane timber salvage (1926): “Chairman reported that arrangements have been made for the sale of wood now being cleared out and cut up” (Emerson and Leon 2003).

1944 – (F-scale 1.9) Sept. 14. “The hurricane hit Naushon with 134 mph winds. All bath houses were destroyed and wharves and bridges damaged but the greatest destruction was to the trees. In many places the woods were flattened down to the ground in tangled masses” (Forbes 1964). “A survey of the woods after the 1944 hurricane shows that although the damage was very severe in several of the most heavily wooded regions, about two thirds of the island woods containing many very fine trees have not been appreciably injured…The forests were not seriously damaged by the hurricane of 1938, but were hard hit by that of September 1944. The wind came across the island from the southeast and blew down a large proportion of the heaviest stands of timber. The wind was gusty, so that the damage is not entirely uniform, leaving some stands relatively untouched and destroying others almost completely. In general, however, most of the woods containing large trees were more or less affected” (Raup 1945). An estimated 1/5 of trees, or 30,000, blew down in the hurricane (Annual Report 1945). Post-hurricane timber salvage (1946-48): “So far the total amount removed is a little under 1,000 cords of less than 10% of the estimated total” (1946 Annual Report). “To date Smith has sawed up about 330,000 feet of lumber, 90% of which is oak.” (1947 Annual Report) “H.D. Smith sawed over 200,000 board feet, chiefly oak, most of which remains unsold” (1948, Emerson and Leon 2003).

1960 – (F-scale 1.8) “September…the woods, which were just beginning to show signs of recovery from the past hurricanes were again badly battered. Although it seemed that the forest would never recover, nature has reasserted herself, and except for some blow-downs and areas of thickly crowded new growth, the forest has come back and regained much of its former beauty” (Emerson and Leon 2003).

1991 – (F-scale 1.9) “In August, “Bob” hit the Island, going from east to south to west and creating many downed trees and from spray, caused much loss of foliage which sprouted out again later, in some cases flowering” (Emerson and Leon 2003).
Analysis of growth change frequency distributions

Visual comparisons of the GC frequency distributions for all species for a hurricane year (1944) and a non-event year (1934) are instructive for interpreting GC frequency distributions. For beech and white oak, the 1944 distribution has a longer right tail than the 1934 distribution (Fig. 5a, b). Tall and intermediate distributions mirror the overall beech distribution, whereas the 1944 dwarf distribution has a lower median relative to the 1934 distribution (data not shown). Similarly, 1944 black oak growth change is lower than 1934 (Fig. 5c).

Analysis of variance detected no significant differences overall in the beech GC frequency distributions for hurricane, non-hurricane and quiet years (Table 2, Appendix A). However, for beech, two hurricanes (1924 and 1944) had mean, median, maximum, variance, 75% and 90% quantile values that were much larger than during non-event years (1944 also had a higher skewness value) (Fig. 6a, b). The 1960 hurricane had maximum, skewness and variance values greater than non-event years, and the 1869 hurricane had a variance value greater than non-event years (Fig. 6a, b). Overall, four of the six hurricanes (1869, 1924, 1944, and 1960) were characterized by variance values greater than any of the non-event years (Fig. 6a, b).

For white oak, analysis of variance detected a significant difference for the 10% quantile only, with hurricanes characterized by the lowest values (Table 2). Like beech, 1944 was characterized by a high mean, median, maximum, variance, skewness, 75% and 90% quantile values for white oak (Fig. 6a, Appendix A). The 1924 hurricane was characterized by high mean and third quartile values (Fig. 6a). The cutting event (1826) had high mean, median, 75% and 90% quantile values (Fig. 6a).
Fig. 5. Frequency distributions of percent growth change for beech, white oak and black oak for a hurricane (1944) and non-event year (1934). Sample sizes are approximately equal for the two years (1944 N = 159 and 1934 N = 155). Although percent growth change for beech was standardized for the analysis, it is not standardized for this figure to allow a comparison of the range in percent growth change among species.
Table 2. Analysis of variance results comparing GC frequency summary statistics for hurricane, non-hurricane and quiet years.

<table>
<thead>
<tr>
<th></th>
<th>Beech</th>
<th></th>
<th>White oak</th>
<th></th>
<th>Black oak</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p</td>
<td>F</td>
<td>p</td>
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<td>Quantiles:</td>
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<tr>
<td>10%</td>
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<td>0.856</td>
<td>4.64</td>
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<tr>
<td>25%</td>
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<td>0.83</td>
<td>0.778</td>
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<tr>
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<tr>
<td>90%</td>
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<td>Mean</td>
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<td>0.151</td>
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</tr>
<tr>
<td>Median</td>
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<td>0.988</td>
<td>10.88</td>
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<tr>
<td>Maximum</td>
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<td>0.119</td>
<td>3.14</td>
<td>0.094</td>
<td>2.23</td>
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<tr>
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<td>0.077</td>
<td>1.88</td>
<td>0.188</td>
<td>1.92</td>
</tr>
<tr>
<td>Skewness</td>
<td>0.496</td>
<td>0.492</td>
<td>2.8</td>
<td>0.112</td>
<td>2.94</td>
</tr>
</tbody>
</table>

*p < 0.05
Fig. 6. 

a) 75% Quartile

<table>
<thead>
<tr>
<th>Year</th>
<th>GC X dbh</th>
<th>GC</th>
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</thead>
<tbody>
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<td>1924</td>
<td>1944</td>
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<table>
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b) Variance

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<th>GC</th>
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<td>1924</td>
<td>1944</td>
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<table>
<thead>
<tr>
<th>Year</th>
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c) 25% quartile

<table>
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<th>GC</th>
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<tbody>
<tr>
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<td>1944</td>
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<table>
<thead>
<tr>
<th>Year</th>
<th>1824-27 cutting event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1924</td>
<td></td>
</tr>
</tbody>
</table>

1 = quiet year, 2 = non-hurricane, 3 = hurricane, 4 = 1824-27 cutting event

Fig. 6. Third quartile values for beech, white and black oak generated in the GC frequency analysis. First quartile values are also shown for black oak, and variance is shown for beech (variance is the only statistic calculated or reported using decimal percentages). Categories shown on x-axis include: quiet years (1), non-hurricane years (2) and hurricanes (3). A third quartile value for 1826, representing the 1824-27 cutting operation, is shown for white oak (4).
Black oak growth following hurricanes was significantly different from non-event years, with hurricanes characterized by the lowest 10%, 25% and 75% quantiles and median values (Table 2, Appendix A). However, examining individual hurricanes, only 1944 is characterized by median, maximum, variance, skewness, 10%, 25% and 75% quantile values lower than non-event years (Fig. 6a, c).

**Transient patterns of growth following hurricanes**

Analysis of the temporal patterns of growth response following hurricanes in 1924 and 1944 revealed similar patterns for both storms for beech, and among structural types (Fig. 7a, b, c, d). Growth in the 1-2 years immediately following each hurricane was lower than the ten-year post-event mean; growth in years 3-5 was similar to the mean, and growth after year 5 was greater than the mean. This pattern was also observed for oak species following the 1944 hurricane; however, no significant growth pattern was detected for oak species following the 1924 storm (Fig. 7a, b). Although the majority of black oak trees were characterized by negative GC following the 1944 hurricane, the residual pattern mirrors beech and white oak, and indicates that growth showed a positive trend over the ten year period. This pattern is also revealed by the ring width indices; after 1944, indices for all species exhibit a positive trend, however, beech and white oak indices eventually surpass pre-hurricane levels whereas black oak indices remain below pre-hurricane levels (Fig. 8a, b, c).

Beech residuals for 1924 are similar to 1944, but muted; more extreme negative and positive residuals following the 1944 hurricane reveal greater variation in growth
Fig. 7. Mean relative residuals for beech, white and black oak (upper panels), and structurally distinct forest types (beech only) (lower panels) following hurricanes in 1924 and 1944. Bars show the standard error of the mean.
Fig. 8. Standardized mean ring width index for cross-dated beech ($N = 98$), white ($N = 58$) and black oak ($N = 25$). Dashed lines indicate hurricanes examined by the GC frequency distribution method.
over the ten-year period (Fig. 7a, b). Similarly, beech showed greater variation in growth than oak species following the 1944 hurricane (Fig. 7a).

PDSI data indicate that climatic variation must be taken into consideration when interpreting the annual response to the 1924 hurricane (NOAA CLIMVIS) (Appendix B). Specifically, 1925 was characterized by the lowest PDSI value for the entire record (1895-2004), so low growth in 1925 may not indicate response to the 1924 hurricane. Seven of the eight years following the 1944 hurricane were characterized by negative PDSI values (1945 and 1946 were only slightly negative), years nine and ten have slightly positive PDSI values.

**DISCUSSION**

Moderate intensity disturbances, such as hurricanes, are thought to cause intermediate levels of crown damage, blowdown, and growth change among surviving individuals. However, the range of forest responses to wind storms of moderate intensities has not previously been documented. This study characterizes a gradient in forest responses to hurricanes on Naushon Island, MA over the past 150 years. Forest response to hurricanes varied by storm, by species, and by structural type. Beech responses ranged from no change in growth or regeneration, to a greater variation in growth change, to positive growth change of surviving trees but no new establishment, and finally, to dramatic increases in growth and new establishment. White oak growth responses were similar to beech, although, the magnitude of positive white oak growth change following hurricanes was less than beech; black oak exhibited negative growth change following hurricanes. Additionally, I found no evidence to suggest either oak
species regenerated following hurricane disturbance over the 150-year study period (Fig. 3). These results suggest that while some moderately intense hurricanes have little or no effect on coastal forests, individual storms may have substantial impacts.

**Methodological lessons**

The GC frequency distribution method characterizes growth response to hurricanes relative to a broad range of observed tree behavior in event and non-event years. For the dominant tree species, the six moderately intense hurricanes, as a group, were not significantly different from non-event years. Rather, although I expected third quartile values of growth response for the hurricanes to reveal stand-level impacts, third quartile values identified only two storms (1924 and 1944) and the 1824-27 cutting event as distinctive in their effects at the population level (Fig. 6). The absence of demonstrable impacts on tree growth following other hurricanes relative to non-event years strongly suggests that these hurricanes affected only a small percentage of the population. This is supported by stand age structure, with establishment occurring only after the 1944 hurricane, and the historical record, which documents timber salvage following only the 1924 and 1944 hurricanes (Table 1).

In this study, hurricanes that affected a relatively small percentage of trees may have been indistinguishable from non-event years because GC in non-hurricane years (within 3.4 years on average of a hurricane >F1) may have been influenced by a prior or subsequent hurricane strike. In a study site characterized by a high frequency of hurricanes, percent growth change calculated using ten-year averages (thus encompassing a 20-year window) may almost always be influenced by such disturbances. The GC frequency distribution method may be particularly useful for distinguishing disturbances
for sites characterized by a low to moderate disturbance frequency, where GC results may differ more from disturbances to non-event years. However, quiet years, which are within eight years of a hurricane >F1, were also indistinguishable from most hurricane years for beech and white oak, suggesting that prior or subsequent hurricane strikes may not adequately explain the absence of demonstrable hurricane impacts on growth. Rather, most hurricanes apparently had relatively minor stand-level impacts.

An additional factor potentially contributing to the absence of observable growth response to hurricanes is that response to disturbance is not synchronous. A delay in positive growth change following disturbance, resulting from damage to individual trees or to delayed mortality of neighboring trees (Orwig and Abrams 1994, Walker 1995, Cooper-Ellis et al. 1999), may weaken the ten-year growth response signal. Annual residuals relative to the 1944 pre-hurricane growth mean ($M_1$) confirm this hypothesis; on average, beech and white oak growth in the 1-2 years immediately following the hurricane was lower than the pre-event mean ($M_1$) (Appendix C). Most trees exhibited maximum GC from 1946-1950, which may reflect delays in recovery from damage or in mortality of a neighboring tree enabling growth response.

Trees that suffer major hurricane damage are more susceptible to pathogen attack through wounds or blowdown in subsequent years. Cooper-Ellis et al. (1999) found that of the trees damaged (uprooted, snapped, bent or leaning) by an experimental pull-down designed to mimic the effects of the 1938 hurricane, 80% survived and re-leafed in the first growing season. Mortality increased for all species in years 2 and 3, and by year 6 only 18% of damaged trees were alive (Cooper-Ellis et al. 1999). Similarly, mortality caused by hurricane Hugo (1991) was distributed over a 3 year period and mortality
doubled from year 1 to 3 (Walker 1995). These studies, in combination with data from this study, indicate growth release following hurricane disturbance is distributed over multiple years. However, extending the period of observation from ten to fifteen years to capture delayed response would only increase the ‘noise associated with subsequent hurricanes.

When the timing of disturbance events is known, the GC frequency distribution method can be used to characterize species response to disturbances by comparing growth change distributions in event versus non-event years. In contrast, indirect reconstruction approaches use the relative abundance of releases to estimate the timing and severity of disturbances, and to broadly characterize disturbance regimes (Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997). The GC method complements these traditional methods by providing a framework to characterize population response to multiple known disturbances using growth in non-event years as a benchmark to assess disturbance severity.

Without prior knowledge of the timing of disturbance events, comparing GC distributions for all years may help identify individual disturbance events. This approach may even be more appropriate than the release detection method since it is species and site-specific, and because it uses non-event growth instead of arbitrary GC ‘thresholds’ as a means to characterize disturbance severity. Poorly tested GC ‘thresholds’ may not be appropriate for detecting above average growth for particular species, or for trees growing in particular areas within a species’ geographic range (Black and Abrams 2003). For example, in this study, release detection methods would not have been appropriate for black oak, which exhibited negative growth change following hurricanes.
**Dissimilarity in growth responses to hurricanes**

While growth responses to several of the hurricanes investigated was indistinguishable from growth in non-event years for beech and both oak species, two hurricanes had observable impacts on radial growth (1924 and 1944). Several factors may contribute to the dissimilarity in growth responses to hurricanes over the past 150 years. Local site conditions – environmental, meteorological, topographical, historical and biological factors – may have played a major role in determining growth responses to hurricanes (Foster and Boose 1992, Boose et al. 1994, 2001, Sinton et al. 2000, Canham et al. 2001, Kramer et al. 2001). In particular, species composition, stand age and height, meteorological conditions, and the time since the last disturbance event strongly influence the extent to which a particular storm may result in substantial damage (Foster 1988b, Foster and Boose 1992, Merrens and Peart 1992, Bellingham et al. 1995, Batista et al. 1998). For example, the impact of the 1944 hurricane was much greater than the impacts of other hurricanes investigated, despite similar reconstructed intensities. Given that susceptibility to windthrow increases with tree age and size (Foster 1988b, Peterson and Pickett 1991, Foster and Boose 1992, Peterson 2004), the population structure in 1944 (a large portion of trees 80-120 years of age, having established after the 1824-27 cutting event) may have been particularly vulnerable to storm damage in 1944. The opposite effect may have occurred following the 1960 hurricane which occurred soon after substantial removal of vulnerable overstory trees by the 1944 and 1954 hurricanes.

Differences in storm intensity may have also led to the observed variance in species response to hurricanes. In particular, the intensity of the 1944 hurricane may have been under-estimated, or the others over-estimated, by HURRECON.
Documentation of extensive damage on Cape Cod and elsewhere in southeastern MA following the 1944 hurricane provides support for this interpretation (Little 1950, Dunwiddie 1991). A field assessment by H.M. Raup (1945) of forest damage to the study area following the 1944 hurricane found that 1/3 of trees were damaged, including an estimated 1/5 uprooted (1945 Annual Report). Historical documentation of hurricane damage to the study area and surrounding region, and GC frequency distribution results, suggest that the 1944 hurricane was more severe than other hurricanes included in our analyses, despite similar estimates of Fujita ratings. In coastal areas, the effects of the 1944 hurricane were apparently more similar to those documented from central New England from the 1938 hurricane (> 40% of trees uprooted) (Foster 1988b, Cooper Ellis et al. 1999) than to most moderate hurricanes (< 10% mortality) (Brokaw and Walker 1991, Zimmerman et al. 1994, Bellingham et al. 1995, Batista and Platt 2003).

**Hurricane effects on beech population growth and regeneration**

This study found a wide range of beech responses to individual hurricanes, from no observable change in growth or regeneration (1888 and 1991), to a greater variation in growth responses (1869 and 1960), to positive growth change of surviving trees but no new establishment (1924), and finally, to dramatic increases in growth and new establishment (1944). Thus, these results suggest that while some moderately intense hurricanes have little or no effect on beech growth and regeneration dynamics, individual storms may have substantial impacts. In particular, once beech is widely established, individual hurricanes may strongly favor beech establishment and growth. This result confirms that wind disturbance may be of great importance to the establishment and persistence of beech (Russell 1953). Additionally, these findings are consistent with the
broad range of reported beech responses to various types of wind disturbance, including low (Papaik et al. 2005) to high (Abrell and Jackson 1976, Canham et al. 2001) susceptibility to blowdown; positive growth response but no establishment (Merrens and Peart 1992, Peters and Poulson 1994, Batista et al. 1998, Batista and Platt 2003); and substantial increase in establishment (Russel 1953, Williams-Linera et al. 2000).

Abundant beech regeneration occurred following the 1944 hurricane in all structural types (Fig. 3a, b, c). Similarly, a pulse of beech establishment occurred in the 19th C., apparently in response to a major cutting event. Thus, unlike the gap dynamics model of beech regeneration that has been described throughout its geographic range (Ward 1961, Leak 1975, Canham 1990, Tubbs and Houston 1990, Poage and Peart 1993), beech regeneration in the study area has occurred in pulses related to severe disturbance. Since I was unable to determine the exact age of sampled trees, the percentage of tree establishment following this event that resulted from release of advanced regeneration versus seedling establishment is unknown. However, the high frequency of substantial growth increase among understory beech confirms the importance of advanced regeneration in establishing dominance following wind disturbance (Zimmerman et al. 1994, Bellingham et al. 1995, Peterson and Pickett 1995, Cooper-Ellis et al. 1999). In addition, the ability of beech to develop abundant root-suckers in response to crown, stem or root damage, also allows it to successfully regenerate after wind disturbance (Ward 1961, Held 1983, Jones and Raynal 1986, 1988, Putz and Sharitz 1991, Cooper-Ellis et al. 1999). Following a catastrophic tornado in northern Pennsylvania, Peterson and Pickett (1995) reported that 66% of beech stems originated from sprouts and 33% from
seed. I suspect that root suckering was similarly important in beech response to the 1944 hurricane.

Positive growth change following the 1944 hurricane is a second line of evidence suggesting that severe hurricane disturbance may favor beech. The 1944 GC frequency distributions reveal that beech responded to this event with greater increases in growth than associated oak species (Fig. 5). This behavior is similar to beech growth following the severe hurricane that struck New England in 1938 (Merrens and Peart 1992), and to a moderate hurricane, ‘Kate,’ that struck Florida in 1985 (Batista et al. 1998, Batista and Platt 2003). However, unlike results from this study, no long term increase in beech abundance was observed or predicted by Merrens and Peart (1992) or Batista et al. (1998). In Florida, at the southern edge of beech’s geographic range, beech do not resprout (Del Tredici 1995), which may help explain why a positive long term effect of hurricanes on the beech population was not observed (Batista et al. 1998). In central New England, where hurricanes are less severe and occur less frequently than along the coast, a single hurricane may release beech or initiate sprouting, but beech may be quickly overtopped and the positive effects of the disturbance may be short-lived (Peterson and Picket 1995). As a result, in inland northern hardwood forests, beech typically undergoes several periods of release before reaching the canopy (Canham 1990, Poage and Peart 1993).

**Hurricane effects on structurally distinct beech forest types**

Beech populations in structurally distinct forest types responded differently to the 1944 hurricane. Abundant establishment occurred in all structural types, with nearly half of all trees in dwarf study sites establishing in the period 1940 - 1960, compared to
roughly 1/3 in intermediate sites and 1/4 in tall sites. Lower establishment in tall types may reflect higher survival of advanced regeneration. Growth releases were observed only in tall and intermediate sites (data not shown); growth suppression caused by crown damage may have occurred in dwarf types.

Field observations indicate that tip up mounds are absent from dwarf types, whereas tip up mounds from the 1944 hurricane are abundant in tall and intermediate types. This observation confirms a pattern observed following the 1938 hurricane in central New England where the uprooting of trees accounted for approximately 90% of tree damage, with the exception of well-drained, rocky sites, where crown damage was more common than uprooting (Foster 1988b). Heavy rains typically precede hurricanes and frequently saturate soils, leading to increased susceptibility to uprooting. This effect is probably less important for rocky or sandy, well-drained areas, where dwarf types are found.

**Hurricane effects on white and black oak growth and regeneration**

Hurricane disturbance elicited markedly different responses from white and black oak than from beech. The magnitude of positive white oak GC was less than beech (1924 and 1944), which is consistent with observations of a greater potential for release among shade-tolerant trees (Lorimer and Freligh 1989, Nowacki and Abrams 1997, Black and Abrams 2003). Hurricanes had a significant negative impact on black oak growth (and some white oak), with periods of suppression apparently triggered by crown damage. Presumably oaks were in the overstory at the time of most hurricanes and would have been more susceptible to crown damage than understory beech (Foster 1988a). In the mid-19th C., major black oak growth releases did occur when the even-aged cohort was
young; however, once trees were approximately 50 years in age, the percentage of trees showing major release dropped significantly. This is typical for black oak which is not known to experience positive growth in response to thinning once trees are greater than 30 years old (Sander 1990).

No evidence was found to suggest that either oak species have ever regenerated in response to hurricane disturbance (Fig. 3). The most significant pulse in oak regeneration occurred following the 1824-7 cutting event and earlier episodes of white oak establishment probably resulted from cutting related to early farming and shipping activity (Emerson 1935, Busby et al. in prep). These results thus challenge the notion that severe disturbances “reset” the system compositionally (Foster 1988b, Peterson and Pickett 1995, Canham et al. 2001). In this study, response to severe wind disturbance, including abundant beech regeneration and no oak establishment, was fundamentally different from response to a heavy cutting, which removed a much greater percentage of living biomass and allowed the establishment of both oak and beech. However, these interpretations must be tempered by the documented importance of multiple contingencies on forest response to wind disturbance (Peterson and Pickett 1995). For example, deer herbivory, including the preferential browsing of oak seedlings over beech, may have differentially affected oak regeneration following the 1944 hurricane and the 1824-27 cutting event.

Conceptual models

Two conceptual models offer insight into dynamics following disturbance. The first is the gap model, which predicts greater dominance by shade-intolerant pioneer species with disturbances of greater severity (Runkle 1981). In contrast, the ‘severity
model’ predicts dominance based on the regeneration mechanism favored by a particular disturbance severity (Oliver and Larson 1990). Following major wind disturbance, the gap model would predict dominance by the most shade-intolerant species whereas the severity model would predict dominance by surviving advanced regeneration (Peterson and Pickett 1995).

Peterson and Pickett (1995) used both models to explain patterns of regeneration following the 1985 catastrophic (F4) tornado strike to northern Pennsylvania. They concluded that in the wake of severe wind disturbance, species capable of advanced regeneration will dominate only when surviving seedlings and saplings are sufficiently common to prevent the establishment of less shade-tolerant species, and when propagules of shade-intolerant species are sparse or absent (Peterson and Pickett 1995). In their study, advanced regeneration accounted for 82% of beech sprouts and seedlings. However, beech was not sufficiently abundant or distributed to prevent the establishment of shade-intolerant species.

Historical sources indicate beech has been abundant across the study area throughout the study period. This allowed beech advanced regeneration, seedlings and root sprouts to establish dominance following severe hurricane disturbance. In contrast, oak regenerated abundantly after the 1820s cutting event, but did not regenerate in response to any subsequent hurricanes. I offer three explanations for the failure of oak to establish following hurricane disturbance. First, rapid beech establishment from sprouts and/or seedlings may have prohibited oak from establishing from seed, and the advanced age of oaks would have limited their ability to sprout (Roberts 1990, Sander 1990). Second, selective harvesting of oak in the early historical period could account for a
sacricty of oak seed sources following subsequent hurricanes (Busby et al. in prep). And third, high levels of deer herbivory may have negatively impacted the survivorship of oak seedlings (Vera 2000). Response to severe hurricane disturbance on Naushon Island apparently follows the severity model, with beech advanced regeneration and root sprouts favored by severe wind disturbance. In contrast, overstory oaks were damaged by hurricanes, and oaks were unable to establish in the post-hurricane environment.

CONCLUSION

I developed a dendroecological method for interpreting disturbance history that compares growth of surviving trees following known hurricanes to tree growth in years without major hurricanes. The GC frequency distribution method has multiple advantages over indirect reconstruction methods. It is species and site-specific. It uses non-event growth instead of arbitrary GC thresholds as a benchmark to measure disturbance response. Finally, it characterizes the entire range of population-level growth response to disturbance instead of focusing solely on growth release. This method may be particularly useful in areas characterized by a low – moderate disturbance frequency.

Hurricanes that impacted coastal New England over the past 150 years elicited a wide range of responses in growth and regeneration; however, only a single storm (1944) caused dramatic changes in beech growth and establishment and resulted in substantial compositional change (Busby et al. in prep). These results underscore the importance of individual severe disturbance events for forest dynamics, even in an area characterized by a high frequency of hurricanes. Severe disturbance events cause dramatic changes in forest structure and composition, with response determined by storm meteorology in
combination with stand history, composition, structure, local site conditions, and the regeneration mechanism favored by the particular disturbance. Between these events, moderate disturbances occur, but apparently have minimal impacts on growth and regeneration. With anticipated increases in the intensity of hurricanes in the North Atlantic (Emanuel 2005, Webster et al. 2005), major changes in structure, composition and dynamics for a wide range of forest types across the coastal region may occur.
LITERATURE CITED


Annual report from the Trustees to the Shareholders of the Naushon Trust. 1939

Annual report from the Trustees to the Shareholders of the Naushon Trust. 1945.


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Appendix A. First and third quartiles and median values derived from beech, white and black oak growth change frequency distributions.

<table>
<thead>
<tr>
<th></th>
<th>First quartile</th>
<th>Third quartile</th>
<th>Median</th>
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<tbody>
<tr>
<td></td>
<td>Beech</td>
<td>White oak</td>
<td>Black oak*</td>
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<tr>
<td>Quiet</td>
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<td></td>
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<tr>
<td>1914</td>
<td>-243.74</td>
<td>-25.15</td>
<td>-17.45</td>
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<tr>
<td>1970</td>
<td>-333.30</td>
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<tr>
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*p < 0.05
Appendix B. PDSI for Massachusetts NCDC Climate Division 3.
Appendix C. Relative annual release ($\text{RAR}_y$) for cross-dated beech ($N = 92$), white oak ($N = 58$) and black oak ($N = 25$) (upper panels), and structurally distinct forest types (cross-dated beech only: tall $N = 34$, intermediate $N = 31$, dwarf $N = 27$) (lower panels) following hurricanes in 1924 and 1944. Bars show the standard error of the mean. $\text{RAR}_y$ is calculated using the ten-year pre-hurricane growth mean for years one-to-ten following selected hurricanes: $\text{RAR}_y = W_y - M_1$. I standardized the yearly relative annual release by dividing $\text{RAR}_y$ by $M_1$. Unlike Fig. 7, this figure show how the temporal pattern of response varied relative to the growing conditions prior to storms.
CHAPTER 2
Beech dominance in a coastal New England forest

Abstract

Monodominant forests occur in a wide range of tropical and temperate ecosystems, but the mechanism enabling their development are not well understood. This study examines the history and dynamics of beech-dominated forests in coastal New England in order to identify factors which facilitate beech dominance. I also characterize beech structural variation with respect to edaphic and environmental conditions, and describe ‘dwarf beech forests’ which have not been documented in the literature. The development of beech dominance in the study area, Naushon Island, Massachusetts, was influenced by numerous factors – selective oak harvesting in the early historical period, infrequent fire, frequent and occasionally intense hurricanes, intense deer herbivory, minimal anthropogenic disturbance over the past 150 years, and geographic isolation – and facilitated by beech’s ability to persist in the understory and reproduce vegetatively. This study highlights the importance of both disturbance history and species-specific traits in the development of monodominant forests, and suggests these stands can persist for long periods of time in the absence of pest, pathogen, or other disturbances.
INTRODUCTION

Understanding the mechanisms controlling biological diversity is a major focus in ecology. Although considerable attention has been devoted to explaining high levels of species richness in forest ecosystems (Janzen 1970, Condit et al. 1996, Hubbell 2001), relatively little emphasis has been placed on understanding the opposite extreme – monodominant forests (e.g. Veblen and Ashton 1978, Connell and Lowman 1989, Hart et al. 1989, Tori et al. 2001). Individual species that dominate forests often serve as ‘foundation species,’ exerting strong control over community composition and ecosystem function. As a result, the loss of foundation species to species-specific pest, pathogens or other disturbances may result in dramatic shifts in community and ecosystem characteristics (Walker 1992, Peterson et al. 1998, Ellison et al. 2005). However, little is known of the factors facilitating the development and maintenance of monodominance. In particular, few studies have documented the long-term history and dynamics of monodominant forests; such a historical perspective is critical in order to clarify the mechanism and conditions that facilitate single-species dominance, and to assess the likelihood that such forests will persist over time.

South of the boreal forest, few North American tree species are known to form and maintain pure stands over extensive areas. Some species develop monodominant stands as a transient stage in forest succession. These are typically light-demanding, early successional species that establish following disturbance but cannot regenerate beneath their own canopies. For example, quaking aspen (Populus tremuloides) is a shade-intolerant clonal species found in mountainous regions of the western United States that establishes pure stands by root suckers in response to fire or other injury.
(Barnes 1966). In contrast, several late-successional species establish and maintain monodominant stands by reproducing beneath their own canopies. Among these shade tolerant species, Eastern hemlock (*Tsuga canadensis*) may form stands that include >75% density of hemlock stems, although such stands rarely exceed 100 ha in size (D.A. Orwig pers. comm.). American beech (*Fagus grandifolia*), a widely distributed deciduous tree species in eastern North America, occasionally forms and maintains extensive pure stands along the southern New England coast (Good and Good 1970, Greller 1977, Busby et al. in prep). In this region, where the tree species pool is apparently limited by harsh edaphic conditions and frequent fire and hurricane disturbance (Motzkin et al. 2002a, Boose et al. 1994, 2001), beech is the only species with strong vegetative reproduction in combination with shade tolerance.

Beech dominance in the coastal region apparently conforms to a general pattern enabling the development of forest monodominance: vegetative reproduction and pronounced shade-tolerance may facilitate dominance in an environment characterized by frequent or severe disturbance (Barnes 1966, Veblen and Ashton 1978, Hart et al. 1989, Tori et al. 2001). Additionally, the mechanisms facilitating modern beech dominance may have been important over longer time scales, as beech has apparently dominated portions of the coast region at various times beginning ~ 5,000 years BP (Foster et al. in review, Oswald et al. in prep).

In this study, I use detailed historical records and data on stand age structure and growth dynamics to investigate the history and development of extensive beech-dominated forests on Naushon Island, Massachusetts (MA), which contains the largest area (>1,000 ha) dominated by beech (> 90% density of beech stems) in the eastern
United States. Additionally, I describe unusual ‘dwarf beech forests,’ which have not been documented previously, and relate structural variation to edaphic conditions and variation in topography and exposure to wind disturbance. Although several studies have documented the widespread occurrence of monodominant forests in tropical regions (e.g. Connell and Lowman 1989), this study is the first to evaluate the influence of disturbance history and species-traits on the development and persistence of monodominance in temperate forests of the northeastern United States. The specific objectives of this study are to 1) document the history of beech forests in the study area since European colonization, 2) examine the role of disturbances and life history traits in the development and persistence of beech dominance, and 3) determine how site conditions and/or disturbance history influence variation in forest structure and dynamics.

*Study species*

American beech is found throughout eastern North America (Tubbs and Houston 1990), and is considered a late-successional species in northern hardwood forests where it regenerates in gaps and may live for 300 - 400 years (Ward 1961, Leak 1975, Canham 1990, Runkle 1981). In the northeastern United States beech was abundant in pre-Colonial forests (Whitney 1994, Cogbill et al. 2002), but frequent and intense anthropogenic disturbances in the historical period contributed to its region-wide decline (Siccama 1971). Since the 1930s, beech bark disease, a scale-fungus complex, has led to further beech decline and substantial changes in forest structure and dynamics (Twery and Patterson 1984). These historical changes contribute to an ongoing long-term beech decline in the Northeast that began ~ 3,000 years ago (Foster et al. in review, Oswald et al. in prep).
Although the role of beech in northern hardwood forests has received substantial attention from ecologists (e.g. Sicamma 1971, Canham 1990, Poage and Peart 1993, Merrens and Peart 1992), the long term dynamics of coastal beech forests are poorly understood. Whereas paleoecological studies suggest that coastal beech forests were more widespread prior to colonization (Foster et al. 2002, Oswald et al. in prep), witness tree data suggest that beech was absent or of only limited importance at the time of European settlement in the 17th C. (Cogbill et al. 2002). Coastal beech dynamics likely differ from inland beech dynamics because hurricanes, which influence beech dynamics (Busby et al. in prep), are more frequent and severe in coastal forests than inland forests (Boose et al. 1994, 2001). In contrast, fire has the potential to eliminate or limit beech abundance, and has generally been more frequent in the coastal region than most other areas in New England (Parshall et al. 2003).

STUDY AREA

Study sites are located on Naushon Island (12 km long and 2 km wide), the largest of the Elizabeth Islands. The islands extend southwestward from Woods Hole, MA and are separated from the mainland by Buzzard’s Bay. This chain of islands is part of an end moraine that was formed in the late-Wisconsinan glaciation when the Buzzard’s Bay ice lobe re-advanced during its long-term retreat, thrusting and folding glacial deposits into a complex topography characterized by numerous ridges and depressions of varying sizes (Oldale 1992). The modern landscape is typically morainal with rolling hills (the highest ranging from 30 – 50 m asl), kettle holes and large surface boulders (Woodworth
and Wigglesworth 1934). Surface soils are composed of medium-to-coarse sands (Fletcher and Roffinoli 1986).

Two large areas on the island, hereafter referred to as the East and West end forests, have been continuously forested since European colonization (Fig. 1). Combined, the East and West end forests cover 1,052 ha (47%) of the 2,226 ha island. Beech dominates nearly all of these forests, accounting for 97% of stems in our study plots. Scattered large white oak (*Quercus alba*) and black oak (*Quercus velutina*) occur in very low density. Few or no herbaceous plants or shrubs are found in the densely shaded forest understories. Extensive reconnaissance surveys identified three common and distinct structural stand types that were targeted for sampling. I refer to these as: tall, intermediate, and dwarf stands (Fig. 2a, b, c). Tall stands occur at the bottom and lower slopes of ice-block depressions (‘hollows’) and other lowlands. Beech trees 40-70 cm in diameter and 20-30 m tall dominate the canopy, and beech are present in all smaller size classes. Intermediate stands are found in areas with little topographic variation. Many of these stands support dense pole-sized beech trees, while others contain beech trees in all size classes up to ~ 40 cm in diameter and 20 m tall. Dwarf stands are located on knobs or ridges with exposed, sandy or rocky soils and are dominated by short stature beech trees 1-5 m tall and less than 25 cm in diameter. Scattered oak trees in dwarf sites are 30-40 cm in diameter and 5-10 m tall, rising above the beech canopy. A fourth structural type was limited to the coastline and characterized by dense, wind-sculpted beech trees 10-30 cm in diameter and 10 – 20 m in height. This structural type was not sampled extensively since it occurred in only a few locations. A notable feature of all stand-types is the limited beech mortality from beech bark disease. Beech bark disease has been
Fig. 1. Map of the study area along the southern New England coastline. Insets show forested areas on Naushon Island, MA in 1999 (top panel) (MassGIS 2002) and in 1845 (bottom panel) (CGS 1845) with locations of study plots and stone walls.
Fig. 2. Photographs of representative structural forest types on Naushon Island, MA: (a) tall, (b) intermediate, and (c) dwarf.
present on the island for > 30 years (D. Houston pers. comm.), but has resulted in little mortality, in contrast with high mortality rates throughout the Northeast (Twery and Patterson 1984).

**Wind disturbance**

Hurricanes occur frequently in southeastern New England and cause a range of damage to forests, including defoliation, salt spray damage, crown damage, bole snap, and the uprooting of trees (Boose et al. 1994, 2001). From 1620 to 1997, an average of 6.5 years elapsed between hurricane strikes to the study area (Fig. 3) (Busby et al. in prep). A study of hurricane disturbance on Naushon Island found that while most hurricanes over the past 150 years had minimal impacts on beech and oak species growth and regeneration, a severe hurricane in 1944 led to abundant beech growth release and establishment (Busby et al. in prep). Winter storms (“nor-easters,”) also occur frequently, but may cause less severe damage because they occur after leaf-fall when hardwoods may be less susceptible to crown damage and blowdown. In addition to these major storm events, the overall wind regime in coastal New England is characterized by greater daily maximum wind speed than inland areas (Fig. 4). The effects of such chronic wind disturbance are potentially complex; high winds may cause canopy damage, increasing susceptibility to fungal attack and resulting in structural weakening, ultimately rendering trees more susceptible to blowdown. Conversely, chronic wind disturbance may increase the windfirmness of coastal trees (Telewski 1995).
Fig. 3. Hurricanes affecting the study area since 1620, reconstructed by HURRECON (Boose et al. 1994, 2001). Intensity of damage is estimated by Fujita scale: F0 damage = wind speeds 18-25 m/s, broken branches and shallow-rooted trees uprooted, F1 damage = 26-35 m/s, single trees or isolated groups blown down, F2 damage = 36-47 m/s, extensive blowdowns, and F3 damage = 48-62 m/s, most trees blown down.
Fig. 4. Daily maximum wind speeds (two-minute sustained) for the past eight years of meteorological data from Martha’s Vineyard Airport, located approximately ten miles from the study area on adjacent Martha’s Vineyard, MA and Orange Municipal Airport in western Massachusetts (NOAA, National Climate Data Center). Daily maximum winds speeds greater than 17.9 m/s are capable of blowing down trees, and are equivalent to hurricane winds that result in F0 level damage (Boose et al. 1994, 2001).
METHODS

Forest history

An unusually strong record of historical documents and maps exists for the study area (Appendix A and C). I used this record to determine the timing, and in some cases extent, of natural and anthropogenic disturbance events, including agricultural clearing of the surrounding area, forest harvesting, fire, hurricanes, winter gales, insect defoliation events and sheep and deer population estimates. Documentary records were also used to track compositional change in forested areas. Maps were used to characterize forest extent and land use history since European settlement. Early nautical maps (Des Barres 1780) and a detailed US Coast and Geodetic Survey map (1845, scale: 1:10,000) identified areas that were forested through the 19th C., and a series of aerial photographs were used to track changes over the past century. Aerial photo-delineations were georeferenced to US Geological Survey topographic sheets using a zoom-transfer scope, and then digitized (1938, 1951, 1971, and 1999). Study sites were chosen in areas continuously forested throughout the historical period, which I defined as areas consistently mapped as forested for which I found no contradictory documentary or field data to suggest otherwise (Fig. 1).

Modern forest structure and composition

To characterize variation in forest structure and composition, I sampled vegetation in subjectively placed fixed-area plots (400 m²) in representative structural forest types in both the East and West end forests (tall \( N = 6 \), intermediate \( N = 12 \), and dwarf \( N = 6 \)) (Fig. 1). Whenever possible a tall, intermediate and dwarf site were selected in close proximity to document variation in forest structure and dynamics across
a topographic gradient. In each plot, I sampled species composition, tree size and age structure, and recorded average tree height, slope, aspect, and the presence and orientation of tip up mounds.

Within each plot, species and dbh were recorded for all trees > 7 cm dbh, and an increment core sample was taken from 15-20 trees > 7 cm dbh for age determination and radial growth analysis. Because of the low density of oak species in study plots, and their greater age than the more abundant beech, additional oak trees located outside of plots were cored to facilitate reconstructing long term forest history and dynamics. This included oak trees immediately adjacent to study plots (included in Fig. 8a, b, c), as well as trees not associated with particular study plots (Fig. 8d). In dwarf plots, a random sample of seedlings (stems < 10 cm basal diameter and not reaching breast height) and saplings (stems < 10 cm dbh and taller than breast height) (5-10 per plot) were cut for age determination.

I collected sound cores from 647 trees: 433 beech, 146 white oak, and 68 black oak (East end $N = 347$, West end $N = 300$; tall $N = 154$, intermediate $N = 198$, dwarf $N = 109$, and outside-of-plot oak species $N = 132$). Additionally, a small number ($N = 54$) of beech and oak cores were retrieved from stands along the coastline and are included in species analyses, but not in analyses of structural types because of the limited occurrence of this type. Cores were dried, mounted, and sanded with increasingly fine sandpaper to reveal the cellular structure. Tree rings were counted and measured to the nearest 0.01 mm using a Velmex measuring system (East Bloomfield, NY, USA). Cores were used to determine tree ages, excluding rotten cores and cores that substantially missed the pith. All cores were used to examine radial growth dynamics. A sub-sample of beech ($N =$
92), white oak \((N = 58)\), and black oak \((N = 25)\) were visually cross-dated, and checked using the program COFECHA (Holmes 1983). Crossdated cores were used to verify results obtained using the complete sample, and for growth suppression analysis.

**Modern forest dynamics**

To broadly characterize tree response to disturbance in the study area, and to determine whether structural variation is related to disturbance history, I generated stand-level disturbance chronologies for beech and oak species (East and West end data pooled), and by structural type (beech only, East and West end data pooled). By identifying the percentage of trees that experienced growth releases each decade, a disturbance chronology can be used to estimate the average level of decadal release (in the absence of major disturbance), and to approximate the timing of stand-level disturbance events based on pulses in decadal release. The severity of a disturbance event is estimated by the percentage of trees released, with a stand-level disturbance defined as growth release in a minimum of ~ 25% of stems (Lorimer 1980, Nowacki and Abrams 1997).

Criteria used to identify release vary based on tree species and size, and canopy position (Rubino and McCarthy 2004). For example, higher thresholds are typically used for shade-tolerant trees, like beech, that have greater potential for release than less shade-tolerant trees, like oak species. Release events were identified using criteria developed in previous studies of beech and oak growth response to disturbance (Lorimer and Frelich 1989, Nowacki and Abrams 1997, Rentch 2002). First, using all cores, percent growth change (GC) was calculated for all years using prior \((M_1)\) and subsequent \((M_2)\) ten-year growth means: \(GC = \left[\frac{(M_2 - M_1)}{M_1}\right] \times 100\). Running comparisons of sequential ten-
year means were made and release dates were assigned to years in which the maximum GC reached a predetermined threshold (Nowacki and Abrams 1997). I examined growth changes based on ten-year averages to filter out short term tree responses to climate while detecting sustained growth responses caused by disturbance (Lorimer and Frelich 1989, Nowacki and Abrams 1997). Moderate and major releases for beech were defined as a GC of 50-100%, and > 100% (Lorimer and Frelich 1989). Moderate and major releases for oak species were defined as a GC of 25-50%, and > 50% (Nowacki and Abrams 1997).

In addition to causing blowdown, tree death, and release among surviving trees, disturbance events can also cause significant structural damage to surviving trees. Identifying growth suppression caused by structural damage can also be useful in interpreting disturbance history; however, few studies have characterized the range of negative growth response to disturbance (Foster 1988, Orwig et al. 2001, Lafon and Speer 2002, Motzkin et al. 2002b). Growth suppression was identified in a sub-sample of trees using a GC threshold of -50% or less for all species (Foster 1988, Motzkin et al. 2002b). For this analysis I used the sub-samples of crossdated beech (N = 92), white (N = 58) and black oak (N = 25).

Soils

I analyzed mineral soil samples (0-15 cm) taken from study plots to evaluate the relationship between physical and chemical soil properties and forest structure. Since beech is a mesophytic species (Tubbs and Houston 1990, Caspersen and Kobe 2001), I hypothesized that soil texture and landscape position should influence structural variation by affecting moisture availability. Specifically, I expected soil properties and forest
structure to vary along a topographic gradient, with large trees in tall forest structural
types expected to occur on finer textured soils, and stunted trees in dwarf types restricted
to coarse-textured soils. I also analyzed soil nutrients to determine whether nutrient
limitations in dwarf types are likely to contribute to their stunted structure.

Soil samples were oven-dried (105°C for 48 hours) and sieved (2 mm). Samples
were analyzed by Brookside Laboratories (New Knoxville, OH) to determine soil texture,
pH (McLean 1982), total exchange capacity (TEC), percent organic matter (SOM%;
Store 1984), and exchangeable cation and macronutrient concentrations (ppm) (P, Ca,
Mg, K, Na) (Mehlich 1984). Sub-samples were ground (< 250 micro meters) prior to
total carbon and nitrogen analysis, which was determined by the Analytical Chemistry
Laboratory (University of Georgia) by micro-dumas combustion.

RESULTS

Ownership and land use history

Native Americans inhabited coastal New England from the Paleo-Indian period
(9000 – 12,000 BP) onward (Bragdon 1996), although the history of Native use of the
study area is largely unknown. Cultures were semi-sedentary and relied on both marine
and terrestrial resources; maize agriculture was not common until ~ 1300 AD (Bragdon
1996). Although Native Americans are known to have used fire regularly in the region
for a range of purposes, the impact of Native Americans on forest composition and
dynamics in the Northeast remains controversial (Patterson and Sassaman 1988, Clark
Before European settlement in the 17th C., Cape Cod and the adjoining islands apparently supported the highest Native American population densities in New England (Bragdon 1996); therefore, Naushon Island was likely heavily used. Native peoples may have lived on the island full-time, or used it for seasonal hunting and food collection (Banks 1911). The Native American population on Naushon in the mid-17th C. was estimated at 40 families (Fig. 5) (Emerson 1935); the population was probably higher before the 1612-13 epidemic that killed large numbers of coastal Native Americans (Emerson 1935). In 1641 Thomas Mayhew bought the island from the English and the land rights from the resident Native Americans (Emerson 1935). Under European ownership, Native Americans were akin to tenant farmers and cultivated bayberry for wax (Emerson 1935). By 1800 most of the Native Americans had died or left the island (Banks 1911).

Since European settlement, the entire island has been owned by only four families (Mayhew, Winthrop, Bowdoin and Forbes) over a ~350 year period. Starting in 1684, tenant farmers obtained long-term leases of farmland where they raised livestock, primarily sheep and cattle, cultivated vegetables, and processed dairy products (Fig. 5) (Emerson 1935). Tenant farmers were permitted to cut trees for timber and firewood, but were prohibited from cutting cedars or hunting deer (Fig. 5, Appendix A) (Emerson 1935, Forbes and Gregg 1979). Valuable tree species (i.e. sassafras, cedar, and oak) were selectively, and in some cases heavily, cut for shipping timbers and other special uses (Fig. 5, Appendix A) (Emerson 1935). Throughout the colonial period, tenant farming activities were limited to one to four farms (Appendix A) (Yentsch 1974); population
Fig. 5. Timeline of historical information about human activities and livestock and native animal impacts on Naushon Island for the past 400 years. Ownership history is as follows: Thomas Mayhew 1641-1682, Winthrop Family 1682-1730, Bowdoin Family 1730-1843, Forbes Family 1843 – present.
densities on the island were thus substantially lower than in the surrounding areas (Foster et al. 2002).

In addition to early selective logging, cutting also occurred in the late 1700s and early 1800s when Tarpaulin Cove became a popular stop for ships looking to re-supply with fuel wood and food (Appendix A) (Emerson 1935, Forbes and Gregg 1979, Bosworth 1993). Additionally, a major clear-cutting operation employing 10-20 men from 1824-27 affected much of the West end forest; portions of the East end forest may also have been cut (SJC 1823, Emerson 1935). Over the past 150 years, the island has been in single-family ownership and detailed records indicate that there has been minimal cutting in continuously forested areas (Hughes 1902, Forbes and Gregg 1979, Emerson and Leon 2003). However, I found documentary evidence of timber salvage following three wind storms (1898, 1924 and 1944), including the removal of at least 1,000 cords and 530,000 board feet of lumber (the large majority of which was oak) following the 1944 hurricane (Appendix A) (1946 and 47 Annual Reports, Emerson and Leon 2003).

**Animal populations**

Domestic sheep were first introduced to Naushon Island in the late 1600s by tenant farmers (Emerson 1935). The island supported a large sheep population throughout much of the historical period, peaking in the mid 19th C. with > 2,000 sheep (Fig. 6) (Dunwiddie and Adams 1994, Schroeder 2002, Emerson and Leon 2003). “High” and “low” estimates of the sheep population were reported before and after (respectively) British livestock raids during the Revolutionary War (1776-78) completely decimated the island’s livestock; ~ 1,900 sheep and 80 cattle were reportedly stolen
Fig. 6. Historical changes in sheep (introduced to Naushon in 1684) and native deer populations on Naushon Island. Deer populations greater than 8.5 per km² (equivalent to 190 animals on Naushon) are thought to negatively affect regeneration (Healy 1997).
Livestock raids also occurred in the War of 1812 (Emerson 1935). In contrast to much of New England, where dramatic reductions in sheep occurred after the 1840s (Whitney 1994), the number of sheep remained high on Naushon Island through the 19th C. Sheep subsequently decreased through the 20th C.

White-tailed deer (*Odocoileus virginiana*) are native to Naushon Island, and have maintained a population ranging from 50 – 500 over the past 200 years (Fig. 6). In 1868 deer were reportedly scarce, but by the early 1900s deer were abundant and a “serious handicap in raising vegetables and maintaining the pasturage in good condition” (Emerson 1935). In the 1980s, coyotes (*Canis latrans*) swam to the island and quickly reduced the populations of deer and sheep. Within ten years of the coyotes’ arrival the already dwindling sheep population dropped from 200 to 40, and the deer population dropped from 500 to 50 (Emerson and Leon 2003). The deer population has since recovered to ~ 100 animals (G. Leon, unpubl. data).

Sometime between 1780 and 1802 the central portion of the island was cleared for pasture and has remained open since that time. It is unknown how much pasturing occurred in continuously forests areas, however historical maps delineating livestock pasture (Des Barres 1780, Elizabeth Islands 1836, CGS 1845) and descriptions of farm activity indicate that sheep grazing in the historical period was largely restricted to the central portion of the island and open pastures on the far eastern and western portions of the island sheep (Emerson 1935, Raup 1945). Building and maintaining fences to contain livestock was a primary task for farmers. In 1802, James Bowdoin advised the island manager: “examine ye state of ye fences and ye walls and what fences will be necessary to be poled, to keep the sheep at ye West end; begin at each of ye walls that run across ye
Island” (Emerson 1935). Deer browsing, in contrast, undoubtedly occurred in continuously forested areas throughout the historical period.

**Fire history**

I found little documentary evidence of fire on Naushon Island in the historical period. I assume that fires were used in the early historical period to clear forests and establish and maintain pastures, though as is the case in much of New England, I found no specific references to this. Homes and fields were burned by the British during the Revolutionary War (Appendix A) (Emerson 1935). Two fires ignited by parachute flares in the 1940s apparently caused no damage to forested areas (1945 Annual Report). A fire in 1960 burned approximately fifty acres of grassland near the lighthouse pasture at Tarpaulin Cove (Dunwiddie and Adams 1994). Prescribed fires have been used occasionally since the late 1980s to maintain, or ‘reclaim,’ old pastures (Schroeder 2002). Since the historical record for Naushon is unusually detailed, I suspect few substantial fires occurred in the permanently wooded areas of Naushon during the past 200 years.

**Vegetation History**

Historical descriptions of Naushon and nearby islands offer glimpses of pre-settlement vegetation, and document changes in landscape conditions since colonization (Appendix A). In 1602 English explorer Bartholomew Gosnold landed on Cuttyhunk Island, ~ 6 miles southwest of Naushon Island and also part of the Buzzard’s Bay moraine, and claimed it for England. John Brereton, a member of Gosnold’s voyage described forests on Cuttyhunk: “…full of high timbered oaks, their leaves thrice as broad as ours, cedars, straight and tall; beech, elm, holly, walnut trees [hickory] in abundance” (Appendix A) (Brereton 1602, in Quinn and Quinn 1983). Given the close
proximity and similar geologic history of these islands, the vegetation on Naushon Island may have been comparable at this time, with oak, beech and hickory dominating upland forests, and cedar (Chamaecyparis) restricted to wetlands (Foster et al. 2002).

I found very few descriptions of forests on Naushon Island from the 17th and 18th C. In 1682, Wait Winthrop, having recently purchased the island, described it as: “mostly good land…tho something unsubdued…a very rugged place” (Emerson 1935). Historical descriptions indicate that beech and oak were the dominant tree species on Naushon from at least the early 19th C. (Appendix A). For example, in 1815 it was estimated that 3/5 of the island’s trees were beech, while the remaining trees were white and black oak, hickory, and pine (MHS 1815). In 1856, Henry David Thoreau visited Naushon Island and wrote: “I was surprised to find such a noble primitive wood, chiefly beech, such as the English poets celebrate, and oak (black oak, I think), large and spreading like pasture oaks with us, though in a wood” (Torrey and Allen 1962). Documentary records from the early 1900s indicate that beech dominance persisted into the 20th C. In 1901, Arthur Hollick described beech as the majority tree, and he identified stands where nine-tenths of the trees were beech (Hollick 1901). In 1930, J.M. Fogg reported that: “In some regions, like the area near French Watering Place, these woods present an almost pure stand of beech, in others there is considerable admixture of oak, hickory, hop hornbeam, maple and black gum” (Fogg 1930).

Modern forest conditions

Beech trees dominated all study plots, accounting for 96% of basal area in tall structural types, 94% in intermediate types, and 73% in dwarf types. Oak species accounted for 3% of basal area in tall types, 5% in intermediate types, and 27% in dwarf
types; other species (*Acer rubrum* and *Ostrya virginiana*) accounted for < 1% of basal area. Beech basal area differed among structural types (*F* = 48.603, *p* < 0.001), with the greatest basal area in sites dominated by the tall structural type and the least in sites dominated by the dwarf type (Fig. 7). Beech density also differed among structural types (*F* = 10.150, *p* = .004), with higher tree density in dwarf and intermediate types compared to tall types (Fig. 7). Structural types did not differ in aspect, oak density, or beech seedling and sapling density (data not shown).

The age structures of distinct structural types show strong similarities and are characterized by two major pulses of establishment – one following the 1824-7 cutting event that persisted for 50 years and a second following the 1944 hurricane (Fig. 8a, b, c, d). Beech trees (> 7 cm dbh) ranged in age from 26 to 204 years, with a median age of 61 years (*N* = 433). The oldest trees found in the study area were white oak, which ranged in age from 59 to 351 years, with a median age of 181 years (*N* = 146) (Fig. 8d). The oldest white oak tree sampled in the study area (351 years) is one of the oldest of this species recorded in New England. Episodic white oak establishment occurred in the late 1700s to early 1800s, with a larger pulse of establishment beginning in the 1820s. The only period of black oak establishment was synchronous with the second period of white oak establishment; black oaks ranged in age from 108 to 196 years, with a median age of 152 years (*N* = 68) (Fig. 8).

**Forest dynamics**

Throughout the study period 3-10% of beech trees experienced moderate release each decade (averaging 6%) (Fig. 9a). Excluding decades where releases occurred in >20% of stems (1870, 1920, and 1940), the average level of decadal major release is 6%,
Fig. 7. Basal area (m²/ha) and density (stems/ha) of beech (trees >7cm dbh) in tall, intermediate and dwarf study plots. In one dwarf study plot all trees were below breast height so basal area and density are reported as zero.
Fig. 8. Establishment patterns for distinct structural forest types (a, b, and c) and scattered oaks sampled (d). White and black oaks sampled immediately adjacent to plots are included in structural forest type figures whereas oaks not associated with plots are depicted in panel d. Tree establishment dates are binned by decades.
Fig. 9. Disturbance chronologies for beech, white and black oak. Bars above the x-axis indicate the percentage of released stems (moderate and major), whereas bars below the x-axis represent the percentage of suppressed stems. The sample size of trees used in the release analysis is shown above the panels; the size of the sub-sample used for the suppression analysis is shown below. I report the percentage of stems showing release or suppression only for $N > 10$. 
resulting in an average total release (moderate and major) of 12% of stems per decade. An average of 10% of beech trees show suppression every decade.

Greater than 25% of beech trees were released in the 1920s (28%) and 1940s (37%) (Fig. 9a). Most release events in these decades were ‘major’ (>100% GC); moderate releases do not distinguish these decades from others. Comparing structurally distinct types, abundant beech were released in the 1940s in tall and intermediate types (55% and 53% of trees, respectively), but not in dwarf types (Fig. 10a, b, c). Peaks in major release also occurred in the 1920s (41%) and 1870s (31%) in tall types, in the 1840s (30%) in intermediate types, and in the 1870s (43%) in dwarf types.

Decades with greater than 25% moderate and major releases in the white oak chronology were: 1820 (38% of trees), 1840 (35%), 1860 (27%), 1880 (27%), 1920 (32%), 1940 (50%) (Fig. 9b). Excluding these decades, the average level of white oak release per decade is 13% (6% of trees with moderate release, 7% with major release). Abundant white oak suppression occurred in two decades (1810, 1830) which were also characterized by low levels of release (Fig. 9b).

The average level of decadal moderate and major black oak release (excluding decades where releases occurred in >20% of trees: 1840, 1950, 1960 and 1970) is 13%, with major release events occurring when the even-aged cohort was young (1840-70), and varying levels of moderate release occurring thereafter (Fig. 9c). Two decades were characterized by >25% black oak release: 1840s (33%) and 1960s (40%) (Fig. 9c). Black oak suppression occurred in the 1940s (9%) (Fig. 9c).
Fig. 10. Disturbance chronologies for distinct beech structural types. Bars above the x-axis indicate the percentage of released stems (moderate and major), whereas bars below the x-axis represent the percentage of suppressed stems. The sample size of trees used in the release analysis is shown above the panels; the size of the sub-sample used for the suppression analysis is shown below. I report the percentage of stems showing release or suppression only for $N > 10$.  

Decade

Fig. 10.
**Soil properties**

Surface soils in the study area are typically loamy sands and follow a topographic gradient, with a deepening and darkening of the A horizon and a shallowing of the E horizon from knobs to hollow bottoms, presumably as a result of the downslope movement and accumulation of fine textured soil particles and organic matter. Soil texture differed among structural types (sand $F = 4.934$ and $p = 0.037$, and clay $F = 33.469$ and $p < 0.001$) (Table 1), with dwarf types characterized by the highest sand (67 - 92%) and lowest clay content (0 - 4%) and tall types characterized by the lowest sand and highest clay context (Table 1). Significant differences were also detected for organic matter ($F = 6.248$, $p = 0.020$) and phosphorous (ppm) ($F = 7.049$, $p = 0.014$), with dwarf types characterized by the lowest levels and tall types by the highest levels (Table 1). Dwarf types were also characterized by the highest C:N ratio ($F = 7.716$, $p = 0.003$). No significant differences were found for pH, total exchange capacity, sulfur, K, Ca, Mg, and Na.

**DISCUSSION**

The extent of beech dominance and the variation in beech forest structure on Naushon Island are unique in the northeastern United States. Beech accounts for an average of 92% of basal area within study plots that are representative of forest composition across the East and West end forests. Beech abundance is thus considerably higher than typically occurs in beech’s geographic range, where it averages 2.3% and ranges from 1 – 51% (Cogbill in prep.). Additionally, Naushon Island is apparently one of the only sites in the Northeast characterized by a rise in beech abundance in the
Table 1. Naushon Island mineral soil properties grouped by structural type. Values are means and ANOVA F and p values. Similar exchangeable cation concentrations among sites are consistent with uniform parent material. N = number of study plots sampled.

<table>
<thead>
<tr>
<th></th>
<th>Tall</th>
<th>Intermediate</th>
<th>Dwarf</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
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<tr>
<td>N</td>
<td>N = 6</td>
<td>N = 12</td>
<td>N = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand (%)</td>
<td>67.32</td>
<td>73.13</td>
<td>84.62</td>
<td>4.93</td>
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<td>Silt (%)</td>
<td>23.53</td>
<td>22.13</td>
<td>13.69</td>
<td>1.99</td>
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<tr>
<td>Clay (%)</td>
<td>9.15</td>
<td>4.74</td>
<td>1.69</td>
<td>33.47</td>
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<tr>
<td>Phosphorous (ppm)</td>
<td>28.29</td>
<td>25.08</td>
<td>17</td>
<td>7.05</td>
<td>0.014*</td>
</tr>
<tr>
<td>Calcium (ppm)</td>
<td>132.71</td>
<td>150.58</td>
<td>123.6</td>
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<td>0.91</td>
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<tr>
<td>Magnesium (ppm)</td>
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<td>35.75</td>
<td>26.8</td>
<td>2.24</td>
<td>0.149</td>
</tr>
<tr>
<td>Potassium (ppm)</td>
<td>26.57</td>
<td>25.33</td>
<td>16.4</td>
<td>3.215</td>
<td>0.087</td>
</tr>
<tr>
<td>Sodium (ppm)</td>
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<td>28.92</td>
<td>26.4</td>
<td>1.15</td>
<td>0.295</td>
</tr>
<tr>
<td>Sulfur (ppm)</td>
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<td>30.08</td>
<td>24.4</td>
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<tr>
<td>Organic matter (%)</td>
<td>4.12</td>
<td>3.94</td>
<td>1.84</td>
<td>6.25</td>
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<tr>
<td>pH</td>
<td>4.49</td>
<td>4.2</td>
<td>4.22</td>
<td>2.86</td>
<td>0.105</td>
</tr>
<tr>
<td>Total exchange capacity</td>
<td>3.51</td>
<td>4.1</td>
<td>3.23</td>
<td>0.047</td>
<td>0.831</td>
</tr>
<tr>
<td>Nitrogen (%)</td>
<td>0.12</td>
<td>0.13</td>
<td>0.06</td>
<td>3.02</td>
<td>0.069</td>
</tr>
<tr>
<td>Carbon (%)</td>
<td>2.6</td>
<td>2.77</td>
<td>1.69</td>
<td>1.56</td>
<td>0.231</td>
</tr>
<tr>
<td>C:N ratio</td>
<td>22.04</td>
<td>21.54</td>
<td>27.75</td>
<td>7.72</td>
<td>0.003*</td>
</tr>
</tbody>
</table>
historical period (Cogbill in prep.). Although the increase in beech dominance on Naushon Island in the historical period suggests the importance of anthropogenic activity, beech abundance was apparently equally high in some coastal moraine areas at various times before European colonization (Foster et al. 2002, Oswald et al. in prep). In particular, pollen records from the study area indicate several periods prior to European arrival when levels of beech abundance were comparable to modern levels (D.R. Foster unpubl. data), suggesting that beech dominance of the study area is not exclusively an artifact of historical human activity. Although the factors influencing beech dominance in the pre-European period are unknown, low charcoal levels in sediments suggest that fires were infrequent in areas with high beech abundance (Oswald et al. in prep). In addition, a period of beech dominance from 1350-1550 AD developed soon after a severe pre-colonial hurricane that affected southern New England (Donnelley et al. 2001a, b), suggesting that hurricanes may have influenced vegetation dynamics before European colonization (Busby et al. in prep).

**Stand development**

The development and persistence of modern beech stands on Naushon Island has been influenced by the island’s unique ownership history. Single-family ownership and low population density since European colonization have protected the island from fragmentation, intensive land use, and development that has occurred elsewhere along the southern New England coastline throughout the historical period (Barbour et al. 1998, Breunig 2003). While it is tempting to speculate that Naushon contains remnants of the pre-European forest (e.g. Kobbé 1898, Appendix A), historical records and age structure
analyses indicate that forest composition has changed dramatically in the historical period, in response to both natural and human disturbances.

Early historical descriptions and paleoecological data suggest beech and oak were both widespread on Naushon at the time of European settlement; however, selective logging of oak may have reduced its abundance since then. Both in New England and Europe the selective removal of oak, a highly valued timber, has caused significant declines in its abundance (Björkman and Bradshaw 1996, Vera 2000, Cogbill et al. 2002, Abrams 2003). For example, the disappearance of oak in an old growth beech forest in Sweden was linked to intense oak cutting followed by a sharp reduction in fires (Niklasson et al. 2002). Beech, a minor component in the forest during the period of high fire frequency, increased substantially in response to low fire frequency (Niklasson et al. 2002).

Unlike the selective removal of oak, clearcutting may favor oak over associated species; following heavy cutting oak typically re-sprouts from the root collar or establishes from seed, with sprouts and seedlings thriving in open conditions (Roberts 1990, Sander 1990, Abrams 2003). A clear-cut that affected the West end forest and portions of the East end forest (1824-27) initiated abundant white and black oak (and beech) establishment and the second biggest pulse in white oak release in the study period (38% in the 1820s). Earlier white oak establishment may have been initiated by cutting associated with farming activity. However, a lack of substantial cutting in the past 150 years has contributed to poor conditions for oak species establishment in the continuously wooded stands.
In New England, fire-adapted ecosystems often contain oak species capable of surviving fires and establishing from seed or sprouts under open conditions (Abrams 2003). In contrast, beech is easily damaged by fire (Tubbs and Houston 1990). Fire suppression in the Northeast, in combination with selective cutting, may have contributed to a region-wide decline in oak regeneration (Abrams 2003). However, on Naushon Island, documentary and sedimentary charcoal records indicate fire was infrequent both before and after European colonization (D.R. Foster unpubl. data), suggesting that oak may have persisted in the area in the absence of frequent fire. The lack of fire in the historical period has presumably contributed to oak declines by maintaining conditions unfavorable to oak establishment. Additionally, the eradication of squirrels, which are known to be important dispersal agents for oak, sometime in 20th C. (Emerson and Leon 2003), may have also contributed to oak regeneration failures. However, oak regeneration does occur in the openlands, around the perimeter of the island, and occasionally in abandoned pastures.

Unlike fire, hurricanes occur frequently on Naushon Island (Fig. 3), and may be responsible for frequent gap formation. Average decadal release is higher in the study area than levels reported for inland forests (Lorimer 1980, Lorimer and Frelich 1989), suggesting that gaps are created more frequently in the coastal region. Additionally, gaps may be larger in the study area than inland areas, where beech requires two or more gap episodes to reach the forest canopy (Runkle and Yetter 1987, Canham 1990, Poage and Peart 1993). In this study, beech experienced an average of 1.5 release events (ranging from one to four) before reaching the canopy (data not shown), with many trees requiring only one episode (typically 1944). These differences may reflect gap size, with
hurricanes creating large gaps that persist in time long enough for beech to reach the canopy. These results are consistent with previous studies documenting a regional gradient in hurricane frequency and intensity from southeastern coastal areas, where hurricanes occur frequently, to northwestern inland regions, where intense hurricanes are relatively uncommon (Boose et al. 1994, 2001).

Winter gales, ice storms, or insect defoliation events (affecting oak species) may also be responsible for gap formation. I found documentation of only one winter storm that caused substantial blowdown and subsequent salvage logging (1898, Appendix A), but no record of ice storm damage. I found no record of substantial oak defoliation by gypsy (*Lymantria dispar*) or browntail (*Euproctis chrysorrhoea*) moths; however, minimal defoliation occurred occasionally in the early 20\(^{th}\) C. (Emerson and Leon 2003).

The disturbance chronologies suggest that the most significant disturbance affecting the study area in the past 200 years occurred in the 1940s, which I interpret as the 1944 hurricane based on abundant historical information documenting severe damage (~1/5 of trees island-wide were uprooted) and subsequent salvage operations (Appendix A) (1945 Annual Report). Although the proportions beech and oak uprooted by the hurricane are unknown, age structure data and oak suppression following the hurricane suggest that most oak were in the overstory at the time of the hurricane and were highly susceptible to damage and blowdown, whereas beech was presumably both in the overstory and understory (Busby et al. in prep). Following the 1944 hurricane, a high percentage of surviving beech experienced substantial growth releases and beech established abundantly in all structural types. Thus while most studies have emphasized the importance of single-tree gap dynamics in beech recruitment, in areas like coastal
New England, severe wind disturbance is important to the long term establishment and persistence of beech (Busby et al. in prep). Beech’s extreme shade tolerance enables it to establish and persist beneath overstory canopies, and its ability to re-sprout from roots enables it to respond rapidly to hurricane damage (Jones and Raynal 1986, 1988).

Sprouting is generally thought to be an important factor in short term recovery (Cooper-Ellis et al. 1999) and long term compositional change following wind disturbance (Putz and Sharitz 1991). However, some of the root sprouting following the 1944 hurricane may also have been associated with soil disturbance caused by the timber salvage operation.

Unlike beech, I observed no oak stems in the continuous woodlands that dated to the 1944 hurricane. Thus, the 1944 hurricane apparently resulted in a dramatic increase in the proportion of beech relative to oaks. Both species were blown down but only beech regenerated. In the absence of fire, clear cutting, or other major disturbances that allow oak to regenerate, I expect the relative importance of beech to increase further in the coming decades as mature oaks begin to die off.

High levels of herbivory may have differential impact on tree species establishment (Vera 2000). Both European beech (*Fagus sylvatica*) and American beech increase in abundance in response to intensive browsing and grazing since they are less palatable than nearly all other woody species (Björkman and Bradshaw 1996, Vera 2000 Tripler et al. 2005). In particular, oak species are considered more palatable to deer than beech and may decline in response to high browsing pressure (Tubbs and Houston 1990, Vera 2000, Tripler et al. 2005).
Deer browsing has probably been the most significant source of herbivory in continuously forested areas on Naushon Island since sheep were generally restricted to the openlands. Competition with sheep (especially at times when sheep densities were high) on open areas of the island may have forced deer to browse primarily in forests. In 1945, H.M. Raup suggested that deer browsing in forested areas restricted oak and hickory regeneration, while beech sprout reproduction was apparently abundant (Raup 1945). Currently, with oak regeneration lacking, deer browse abundantly on beech. Elsewhere in the Northeast, deer population densities greater than 8.5 animals per km² can reduce red oak (*Quercus rubra*) sapling abundance and overall sapling species richness (Healy 1997); densities on Naushon Island in the historical period have ranged from 2-22 deer/km² (8.5 deer/km² is equivalent to 190 animals on Naushon) (Fig. 6).

I suspect that deer herbivory favored beech versus oak through much of the historical period. However, if herbivory alone was prohibiting oak species establishment, oak regeneration would have been expected following a drastic reduction in the sheep and deer populations in the 1980s; this did not occur. Rather, oak regeneration requires not only release from herbivore pressure but also fire, extensive cutting, or other disturbance that creates open conditions sufficient for establishment. White oak establishment in the late 1770s may have resulted from a combination of such factors, including: 1) British livestock raids that decimated the sheep population (the deer population was also apparently low), 2) forest harvesting for firewood and barrack construction for 70-80 Revolutionary war soldiers (Appendix A), and 3) wartime fire activity that may have spread into wooded areas. Additionally, oaks may have
established in gaps created by an intense hurricane in 1770 (third greatest in intensity of all hurricanes reconstructed by HURRECON, Fig. 3).

In addition to natural and human disturbances, geographic isolation may have influenced the rise in beech dominance on Naushon Island, which has been separated from the mainland from 8,800 – 6,800 cal yr BP onward (Oldale and O’Hara 1980, Gutierrez et al. 2003). Species with the potential to attain dominance may do so more easily on islands, where competitors are limited by invasion barriers and post-isolation extinction events (MacArthur and Wilson 1963, Kadmon and Pulliam 1993). Selective cutting in the historical period may have reduced or eliminated the abundance of species (i.e. oak, hickory, pitch pine) that have been unable to recover or re-establish in an isolated environment dominated by beech. Although isolation may have influenced the development of modern forest composition on Naushon Island, similar beech-dominated forests in nearby Woods Hole, MA suggest that at least small stands (~ 5 ha) of this forest type can develop without isolation. Thus while no single driver appears response for beech dominance, I conclude that numerous factors have influenced the rise in beech dominance on Naushon over the past 400 years – selective oak harvesting in the early colonial period, frequent and intense hurricanes, infrequent fire, intense herbivory, minimal anthropogenic disturbance over the past 150 years, and isolation.

**Soil variation parallels structural variation across a gradient in topography**

Beech forests on Naushon Island are characterized by distinct structural types. In particular, dwarf types are characterized by stunted beech vegetation that is apparently unique, with no similar stands documented in the literature. Dwarf types are characterized by low growth rates and basal area, high stem density (Fig. 7), and
contorted growth forms, with several factors apparently contributing to the vegetation structure. Analysis of physical and chemical soil properties confirmed the hypothesis that dwarf types are characterized by extremely sandy, nutrient-poor soils, whereas tall types that support large trees contain finer-textured soils with greater nutrient availability (Table 1). Intermediate types are characterized by transitional soil conditions. Coarse soil textures and low organic matter concentrations may limit soil water holding capacity on dwarf types, potentially contributing to the stunted growth forms of the beech. Interestingly, oaks, which are less water-demanding than beech (Tubbs and Houston 1990), grow larger and taller than associated beech trees in dwarf types and contribute a significant portion of the total basal area. Additionally, leaf litter is consistently blown off dwarf types resulting in areas of exposed mineral soils and extensive bryophyte cover. Chronic removal of litter inputs to the sites presumably results in long-term nutrient depletion (Nadelhoffer et al. 2004), and may contribute to the stunted growth forms and slow growth rates. In one dwarf site, annual beech growth averaged 0.79 mm (mean of ~1,700 years of ring width data from 13 trees), with some individuals growing < 0.1 mm per year for greater than 25 years.

An island-wide survey of dwarf types located > 40 sites, primarily on northwest to southwest aspects (data not shown), the direction of predominant winter and summer winds, respectively. Chronic wind perturbation to dwarf types may contribute to the unusual structure of these stands in a variety of ways. Wind exposure may cause desiccation and reduced photosynthetic activity in trees (Telewski 1995), potentially contributing to lower diameter growth rates of trees in windward versus leeward sites (Taylor 1923). Similarly, chronic wind perturbation has been shown to restrict height
growth (Telewski and Jaffe 1986, Holbrook and Putz 1989), and I have observed beech dieback of stems emerging above the “dwarf” canopy. In coastal areas, wind-deposited salt spray is an additional stress, leaching into soils and causing reduced water absorption and transpiration (Oosting and Billings 1942, Griffiths et al. 2006), and altered growth forms (Good and Good 1970). Although I found no significant difference in sodium concentration among structural types, infrequent salt deposition from storm events could still be important.

I did not find any evidence to suggest that variation in disturbance history contributes to the structural gradient. Nonetheless, beech and oak growing in structurally distinct forest types responded differently to two of the most severe disturbances in the study period, the 1824-27 cutting event and the 1944 hurricane. Following the cutting event, a pulse in beech and oak regeneration occurred in tall and intermediate types but not dwarf types, suggesting that dwarf types may have supported low stature vegetation that was not cut. The 1944 hurricane had a profound impact on beech growth and regeneration in all structural types. Abundant establishment occurred following the 1944 hurricane, with nearly half of all trees in dwarf study sites establishing in the period 1940-1960, compared to roughly 1/3 in intermediate sites and 1/4 in tall sites. Lower establishment in tall types may reflect greater survival of beech. However, tip up mounds from the 1944 hurricane are common in both tall and intermediate types, suggesting that trees in tall types were not “protected” from hurricane winds by topographic position. In fact, the crowns of trees in tall types would presumably be exposed given their average height of 20-30 m. Short trees in dwarf types may be less susceptible to uprooting, although crown damage was apparently high enough to initiate substantial establishment
of new stems, presumably from root sprouts. Island-wide, damage was not uniform; some intermediate stands were nearly completely blown down with few surviving stems, while others experienced no release or establishment following the storm (Raup 1945, Appendix B).

Although I have not determined the specific mechanisms that cause the unusual dwarf growth forms of beech in dwarf types, I suspect that they develop in response to stressful conditions created by dry, nutrient poor soils, chronic exposure to salt-laden winds, and occasional storms that damage or remove emerging oaks. Likewise, I have no direct evidence of the long term history of stunted beech in dwarf types, however, soils data, tree ring data, and historical references (Kobbé 1898, Appendix A) suggest that they have persisted for >100 years. At times of greater island-wide oak abundance, I suspect all structural types were more heavily dominated by oak. Dwarf types, therefore, may not always be dominated by the characteristic short stature beech. Alternatively, harsh edaphic and environmental conditions may favor beech dominance even at times of greater overall oak abundance (Russel 1953). In this case, dwarf sites may be similar to the beech gaps of the Great Smoky Mountains where dense monodimnant stands of small, gnarled beech trees occur on windy south slopes adjacent to sheltered mixed spruce-fir forests (Russel 1953, Good and Good 1970).
CONCLUSION

Beech has been abundant on Naushon Island for thousands of years, forming either pure stands, or mixed stands with oak, hickory, and pine. In the pre-European period, I suspect low fire frequency and occasionally severe hurricanes enabled coastal beech dominance while limiting oak regeneration. Although I am unable to disentangle the potentially confounding mechanisms for modern beech dominance, results of this study have demonstrated the likely importance of both natural and human disturbances and species life history characteristics in the development of this compositionally and structurally unusual beech forest.

Beech and oak were both widespread at the time of European settlement, and both species persisted throughout the early historical period when forests were occasionally cut. However, forest harvesting in the past 150 years has been limited and of low intensity, resulting in little or no oak establishment in the continuous woodlands. A severe hurricane in 1944 resulted in substantial growth releases among widely established understory beech and abundant beech establishment, but no oak establishment (Busby et al. in prep). Native deer herbivory throughout the historical period presumably exerted negative pressure on oak establishment, as deer prefer oak to beech. This combination of natural and human disturbances has led to the development and persistence of beech dominance on Naushon Island. Thus, as with other monodominance studies (Hart et al. 1989, Torti et al. 2001), species life history characteristics (especially shade tolerance and the ability to re-sprout) and disturbance history have contributed to the development of extensive monodominant stands in a region where such stands are otherwise rare. With
anticipated increases in the intensity of hurricanes in the North Atlantic (Emanuel 2005, Webster et al. 2005), beech dominance of the study area will likely persist.
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Appendix A. Historical descriptions of Naushon and nearby Elizabeth Islands.

1602 “On the outside of this Island [Cuttyhunk] are many plane places of grass, abundance of strawberries and other berries...This Island is full of high timbered oaks, their leaves thrice as broad as ours, cedars, straight and tall; beech, elm, holly, walnut trees in abundance” (Brereton, Quinn and Quinn 1983). “[Cuttyhunk]...is overgrown with wood and rubbish, viz. oaks, ashes, beech, walnut, witch-hazel, sassafras and cedars...” (Archer, Quinn and Quinn 1983). Cedar and sassafras were harvested from the Elizabeth Islands by Bartholomew Gosnold’s crew (Emerson 1935).

1682 “mostly good land...tho something unsubdued...a very rugged place” (Winthrop, in Emerson 1935).

1684 First tenant farmer on Naushon Island (Emerson 1935).

1696 From the Captain’s Log, H.M.S. Falkland: “In this place [Naushon Island] is but one small house in which live one family the Island affords wood and sum deare for other convenient very barren land but being obledged for severall reasons and necessaries we are happy in our safe arrival” (Emerson 1935).

1699 Lease, Winthrop to tenant farmer: “And shall not cut or fell any the red cedar trees nor make any strip or waste of the white cedar trees upon the said land except such of the white cedars as shall be needful for the building and fences upon the said farme and the repairs thereof” (Emerson 1935).

1700 Letter from Matthew Mayhew to Wait Winthrop: “Sr. you may please call to mind you promised to let me have cedars [1,000] for inclosing my field, out of the swamps at Nashawna” (Emerson 1935).

1718 Letter from Thomas Lechemere regarding illegal sale of cedar by Naushon tenant farmer: “…more accounts are told me concerning his carrying cedars to Nantucket whereupon I wrote him and told him it would not be allowed and directed him to desist there from” (Emerson 1935).

1765 “Bill for the Preservation of Moose and Deer on Tarpaulin Cove Island and Nennemessett Island” passed in the Massachusetts Legislature (Emerson 1935).

1776 “The said Commissary, be and hereby is directed with the assistance, or the soldiers on said station, to build as many log houses with timber on said Island as will be sufficient for the reception of 70 or 80 men [rebels]” (Emerson 1935). British soldiers set fire to “everything that would burn, so that neither house, barn, hay nor Indian corn that could be met with escaped the Flames, nor did the live stock share a better fate for what could not be carried off was shot” (Emerson 1935).

1801 Diary of Josiah Quincy: “The soils of this Island are weak and sandy. All of the cluster appeared destitute of wood, although I was assured there was enough in the interior. On Nashant deer run wild and are protected to the proprietor by an act of Legislature” (Emerson 1935).

1807 James Bowdoin to Albert Gallatin: “…the Island of Naushon is appropriated to grazing and to the rearing of horses, cattles and sheep principally the latter; as the Island is long and narrow and has many landing places, it is much exposed to be robbed of its stock; owing to the circumference I have obliged to erect houses and to attach families to them unprofitably for the sake of protecting stock. The same circumstance required me to build a house and connect there with 200 acres of land for a Tavern for the accommodation of the sea men belonging to vessels which anchors on Tarpaulin Cove
Harbor...[who]...frequently kill the stock and steal both timber and fire wood from ye island” (Emerson 1935).

1813 From the Captain’s Log, H.M.S. Albion: “Still in Tarpaulin Cove. Daylight sent the boat for wood and water” (Emerson 1935).

1814 From the Captain’s Log, H.M.S. Nimrod: “Anchored in Tarpaulin Cove...sent boats for water...carpenters on shore cutting wood” (Emerson 1935).

1815 “There are on it [Naushon] four farms, four dwelling houses, at which are milked 40-50 cows. The soil in the eastern part is a sandy loam and good; in the western part it is light, and not so good. The principal part of the mowing land is at the east end...Nashaun is well wooded: the other Elizabeth Islands, except Nanamesset, have no wood. About 3/5 of trees are beech: the remainder of the wood is white and black oak, hickory, and a little pine. About ½ of the island is in wood and swamps; and in the swamps grow white cedar. Some fire wood is sold, and transported from the island. Very little ship timber remains, not more than 300 tons; but it is of a superior quality” (Thomas Winthrop, MHS 1815).

1817 “While all the Elizabeth islands west of it have been stripped of their woods, the trees here, consisting of beech, pine, oak, and hickory, have been carefully preserved, and afford shelter to a hundred deer, one of which bounded across our path at a little distance before us” (American Review 1817).

1823 “…[West end forest] generally to be in a state of decay and great deterioration...the wood on the aforesaid large tract which is oak and particularly the larger and older oak are in a state of actual decay and that they are growing worse daily...Quantity of beech is great, but great deal of wood is in a state of decay and deterioration. No walnut wood, except some dead or dying trees...the woodland at this end [East End] is more valuable and the growths more thrifty – there is a large proportion of oak on the same and that it is young and sound generally and that the beech wood is also thrifty and healthy and valuable...The oak timber on this said east end is also generally better than on the west end of this Island” (SJC 1823).

1824 “I have taken a partial view of the timber on Naushon Island. I find there is a tract of the best timber land I have seen in this part of the country, say, timber suitable for ships, from 300 to 400 tons...the timber is white oak and yellow bark oak” (Emerson 1935). “And as there are many places where the trees are all old and going to decay and no young wood to sprout and therefore no matter what season cut, it might be well to continue the ten best men through the season chopping – the foregoing calculation upon the supposition that about 3,000 cords are to be cut the next spring” (Salem Towne, Emerson 1935). “When the wood choppers had come and gone, leaving behind them a great denuded area, the island returned to its peaceful routine. Many vessels still stopped at the Cove and vegetables, meat and cheese were still in demand, but the farms were on the wane. Those at the French Watering Place and the Tall Farm were abandoned” (Emerson 1935).

1825 “The Island is extremely well wooded, a great number of men being now employed cutting timber from it, about thirty horses are annually raised for market from
the farm, and a vast number of sheep find rich pasture in its forest and upon its waste land” (Emerson 1935).

1838 “Account of Wood on Hand, 121 cords at the Cove, 20 ½ at North Wharf, 2 ½ at Lower Landing, and 5 in Cottage Woods” (Emerson 1935).

1856 “…I was surprised to find such a noble primitive wood, chiefly beech, such as the English poets celebrate, and oak (black oak, I think), large and spreading like pasture oaks with us, though in a wood. The ground under the beeches was covered with withered leaves and peculiarly free from vegetation. On the edge of the swamp I saw great tupelos running up particularly tall, without lower branches, two or three feet in diameter, with a rough, light colored bark….No sight could be more primeval…” (Thoreau, Torrey and Allen 1962).


1870 “…nearly the whole of the rugged isle is covered with thick woods, in which paths and carriage tracks have been cut…rich oak and beech woods” (Bryce 1870).

1898 “We were at the bottom of a hollow, where the trees grew straight and tall; but as I looked about me, following the sides of the hollow up, I observed that the trees immediately about me grew no taller than the top of the hollow. They were tall because their growth started from the very bottom; and by just so much as the other trees were rooted higher along the sides of the hollow, but just so much they were shorted than those rooted in the depths. All growth was checked at the top of the hollow. Those trees which grew near the top, where the wind could dive in upon them, were like the cedars you see in the sand hollow along a beach. Their branches had been blown on so from one direction that they all grew leeward” (Kobbé 1898).

1898 Winter gale: “probably wrecked 1,000 trees on Naushon…you would be surprised to see the tremendous number of trees that are down everywhere through the woods…that whole hillside sloping north looks like a battleground; it is so thick with the fallen bodies of trees” (Forbes and Gregg 1979).

1902 “Probably 50 chords (of firewood) this winter will round up all traces of the gale of 1898, and the dead and dying trees that have fallen since, as well” (Emerson and Leon 2003).

1901 “The forest growth was a revelation, as most of it had all the appearance of never having been disturbed by civilization. The trees are in every stage of growth, from seedling and small saplings to those which are in their prime or past it, while lying on the ground, where they have fallen naturally, are the decaying trunks of former generations…In certain sections there are acres of forest where this tree [beech] monopolized fully nine-tenths of the growth, and a complete tree census of the island would undoubtedly show it to be in a considerable majority…Another peculiar effect is also produced by these conditions in the relative heights of trees. The trunks of those which grow in the bottom of any depression are tall, while those on the sides are successively shorter and shorter, according as their location approaches the summits” (Holliick 1901).

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1 The accuracy of this description of sheep grazing in forests is questionable. The quote is taken from an article written in the Barnstable Gazette, which falsely described 200 British soldiers stationed on Naushon Island in the Revolutionary War (Emerson 1935).
1911  “The Forbes family, as the last ‘Masters of Naushon,’ has emulated successfully its predecessors in the high ideals of the establishment created by the Winthrops and Bowdoins, and it bids fair to pass on under their tenure with this unique reputation untainted by commercial exploitation” (Banks 1911).
1918  “…Naushon alone attests to the noble forests of the past” (Pratt, Dunwiddie and Adams 1994).
1916  “Trees, in stretches of miles; beeches, oaks, most numerous; -- many of them hung with moss, looking like bearded Druids; some coiled in the clasp of huge, dark-stemmed grape-vines” (Holmes 1916).
1930  “The most conspicuous vegetational feature of the islands, aside from the open grassy downs, is the dense growth of rather low beech woods which clothes the greater part of Naushon and smaller areas on some of the other islands…In some regions, like the area near French Watering Place, these woods present an almost pure stand of beech, in others there is considerable admixture of oak, hickory, hop hornbeam, maple and black gum. Almost the only portions of Naushon which are not wooded are those right along the shore or some of the higher exposed ridges in the central part of the island” (Fogg 1930).
1944  Sept. 14. “The hurricane hit Naushon with 134 mph winds. All bath houses were destroyed and wharves and bridges damaged but the greatest destruction was to the trees. In many places the woods were flattened down to the ground in tangled masses” (Forbes 1964). “A survey of the woods after the 1944 hurricane shows that although the damage was very severe in several of the most heavily wooded regions, about two thirds of the island woods containing many very fine trees have not been appreciably injured…The forests were not seriously damaged by the hurricane of 1938, but were hard hit by that of September 1944. The wind came across the island from the southeast and blew down a large proportion of the heaviest stands of timber. The wind was gusty, so that the damage is not entirely uniform, leaving some stands relatively untouched and destroying others almost completely. In general, however, most of the woods containing large trees were more or less affected” (Raup 1945). An estimated 1/5 of trees, or 30,000, blew down in the hurricane (Annual Report 1945).
1945  “Forests composed primarily of white and black oaks, beech and hickory cover a large portion of the island of Naushon. Other species that appear commonly or occasionally are hop hornbeam, red maple, red oak, pitch pine, coastal white cedar, flowering dogwood, holly tupelo, red cedar, etc” (Raup 1945).
1946  Description of timber salvage: “So far the total amount removed is a little under 1,000 cords or less than 10% of the estimated total” (1946 Annual Report).
1947  Description of timber salvage: “To date Smith has sawed up about 330,000 feet of lumber, 90% of which is oak” (1947 Annual Report).
1948  Description of timber salvage: H.D. Smith sawed over 200,000 board feet, chiefly oak, most of which remains unsold (Emerson and Leon 2003).
2005  Beech dominates areas continuously forested throughout the historical period (Busby et al. in prep). In dwarf study plots, 96% of stems are beech and 4% are oak species. In intermediate sites, 98% are beech and 1% oak species, and in tall plots 93% are beech and 6% oak species. Other species found in study plots, but not used for age or growth analysis, included red maple (Acer rubrum) and hop hornbeam (Ostrya...
*virginiana*. No oak regeneration was observed in continuously wooded area, although oak have established in open areas.
Appendix B. Individual plot tree establishment (x-axis, wide bars) and beech growth release (y-axis, lines). Location of study plots are on ‘Naushon Island study sites’ map at the end of this appendix.
Intermediate, East end

Deer Parlor

Year

1750 1800 1850 1900 1950 2000

0 25 50 75 100

beech

J200a

Year

1750 1800 1850 1900 1950 2000

0 20 40 60 80 100

beech

I9g

Year

1750 1800 1850 1900 1950 2000

0 10 20 30 40 50

beech

J200b

Year

1750 1800 1850 1900 1950 2000

0 20 40 60 80 100

beech

L5g

Year

1750 1800 1850 1900 1950 2000

0 10 20 30 40 50

beech

Fern

Year

1750 1800 1850 1900 1950 2000

0 10 20 30 40 50

beech

black oak

white oak
Intermediate, West end

**V2000**

- Number of stems established
- Year
- Black line: beech

**S22g**

- Percentage of beech GC >100%
- Year
- Black line: beech

**P5generic**

- Year
- Black line: beech

**T1000g**

- Year
- Black line: beech
- Dark line: black oak

**Q19g**

- Year
- Black line: beech
- White line: white oak

**Q5generic**

- Year
- Black line: beech
Naushon Island study sites

Legend
- stone wall
- dwarf, N = 6
- intermediate, N = 12
- tall, N = 6
- 1999 Forest
- Major lakes and wetlands
Appendix C. Historical and contemporary maps of Naushon Island (Harvard Forest Archives).

Naushon Island 1780 (Des Barres)

Legend
- Structures
- Other
- Endosed field
- Wetland
Naushon Island 1938 (J. Stone unpub. data)
Naushon Island 1971 (MacConnell 1973)

Legend
- Stone wall
- Major lakes and wetlands
- Hardwood/softwood mix (1-20 ft)
- Hardwood/softwood mix (21-40 ft)
- Hardwood/softwood mix (41-60 ft)
- Hardwoods (1-20 ft)
- Hardwoods (21-40 ft)
- Hardwoods (41-60 ft)
- Hardwoods (61-80 ft)
- Open
- Residential
- Softwoods
- Swamp
Naushon Island 1999 (MassGIS 2002)

Legend
- stone wall
- developed
- forest
- open
- water
- wetland

0 1,500 3,000 Meters

N
Naushon Island Soils (Fletcher and Roffinoli 1986)