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# Multiple and interacting disturbances lead to *Fagus grandifolia* dominance in coastal New England

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Busby, P. E., G. Motzkin, and D. R. Foster (Harvard Forest, Harvard University, Petersham, MA 01366). Multiple and interacting disturbances lead to *Fagus grandifolia* dominance in coastal New England. J. Torrey Bot. Soc. 135: 000–000. 2008.—Recent studies have emphasized the importance of multiple and interacting disturbances in controlling plant community dynamics. However, detailed information on disturbance history and changes in species abundance are unavailable for many forest ecosystems. As a result, it is often difficult to evaluate the influence of disturbance interactions on changes in species composition over time. This study examines the history and dynamics of *Fagus grandifolia*-dominated forests in coastal New England to evaluate the role of multiple disturbances in the development of *Fagus* dominance. Detailed historical and dendroecological data were used to reconstruct disturbance history and compositional trends for the past > 300 years. At the time of European settlement, the study area supported mixed forests of *Quercus*, *Fagus*, *Carya*, and *Pinus*. Intensive harvesting in the early 19th century resulted in abundant *Quercus alba*, *Q. velutina*, and *Fagus* regeneration. Thereafter, harvesting and fire were limited, but repeated low-moderate intensity hurricanes allowed *Fagus* but not *Quercus* species to establish and persist in the forest understory. A severe hurricane in 1944, accompanied by intense herbivory from a high deer population, accelerated the development of *Fagus* dominance by releasing *Fagus* saplings, initiating *Fagus* establishment, and preventing *Quercus* establishment. The extreme shade tolerance of *Fagus*, in combination with its flexible regeneration strategy (i.e., the ability to regenerate from seed or from root sprouts), and low palatability to deer, contributed to the increase in abundance of *Fagus* in response to this complex disturbance history. Thus, long-term changes in forest composition and reduced species richness resulted from species-specific responses to multiple, interacting disturbances.

Key words: beech, disturbance interactions, *Fagus grandifolia*, herbivory, hurricane, monodominance, oak, *Quercus*.

Forest composition and dynamics are heavily influenced by disturbance history. While most studies emphasize the importance of individual disturbance events, or disturbance regimes of a particular type (e.g., fire, wind, or cutting), in driving forest dynamics, in fact, most temperate forest ecosystems are characterized by complex histories of natural and anthropogenic disturbance (Whitney 1994, Foster and Aber 2004). Recent studies demonstrate that multiple disturbances often interact to shape landscape-level patterns of forest vegetation (e.g., Veblen et al. 1994, Bigler et al. 2005). For example, intense herbivory may prevent the regeneration of species otherwise expected to establish following severe wind disturbance (Peterson and Pickett 1995), and prior disturbance may strongly influence the probability and severity of subsequent disturbance (Veblen et al. 1994, Bigler et al. 2005). Thus, disturbance interactions influence patterns of species composition in ways that are not easily predicted based on the independent effects of each disturbance.

In this study, we examine the role of natural and anthropogenic disturbances over the past > 300 years in the development of extensive forests dominated by *Fagus grandifolia* Ehrh. on Naushon Island, Massachusetts (MA). *Fagus* is common in northern hardwood forests across the northeastern U.S., but is uncommon in coastal New England where it occasionally forms unusual 'monodominant' stands, with *Fagus* representing > 90% of stem density (Good and Good 1970, Busby 2006). The study area contains the largest (approx-

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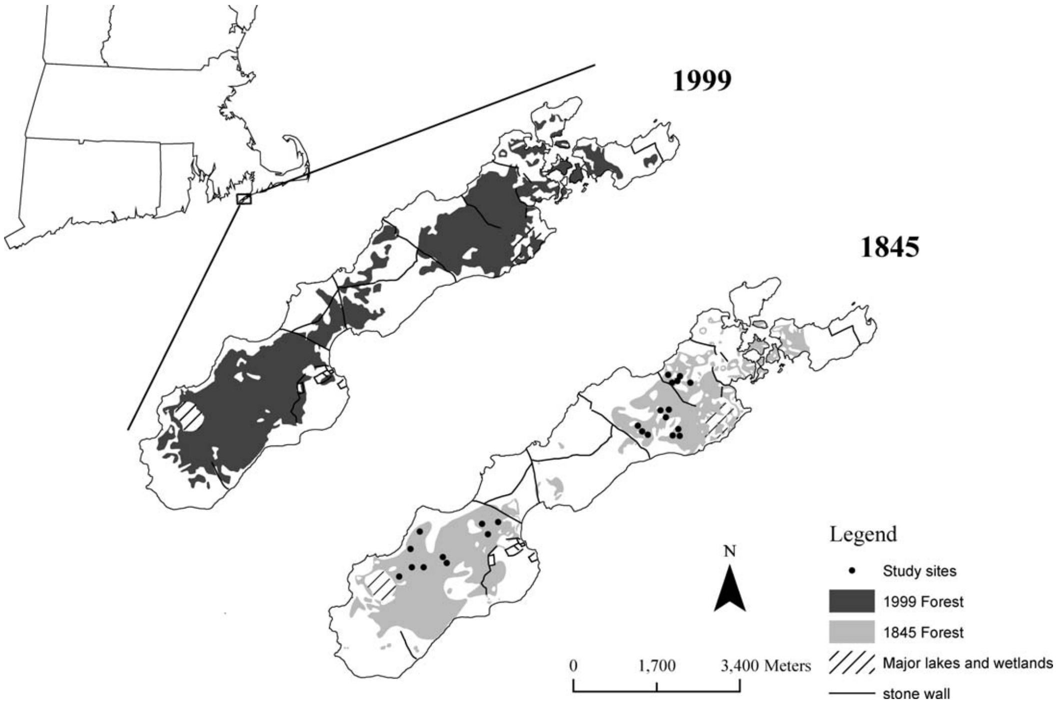


FIG. 1. Map of the study area along the southern New England coast. Forested areas on Naushon Island, MA in 1999 (top panel) (MassGIS 2002) and in 1845 (bottom panel) (USCGS 1845) are shown with locations of study plots and stone walls.

imately 1,000 ha) known monodominant *Fagus* forest in the eastern U.S. Although considerable attention has been devoted to understanding the influence of disturbance on high species richness in forests (e.g. Janzen 1970, Connell 1978), the role of disturbance in the development of species-poor forests is not well-understood (but see Hart et al. 1989). In particular, few studies have documented the long-term history and dynamics of monodominant forests, despite the widespread occurrence of such forests in tropical, temperate, and boreal regions (Connell and Lowman 1989).

We use detailed historical records of disturbance and vegetation change, data on stand age structure and growth dynamics, and information on life history traits of the study species to investigate the influence of a complex disturbance history on long-term forest development. The specific objectives of this study are to: 1) document the history and development of *Fagus* forests in the study area since European colonization, and 2) examine the role of multiple disturbances and life history traits in the development of single-species dominance.

**Materials and Methods.** STUDY SITE. Study sites are located on Naushon Island, MA (12 × 2 km), the largest of the Elizabeth Islands (Fig. 1). The island is morainal, with medium-to-coarse sandy soils (Fletcher and Roffinoli 1986). Two large areas on the island, hereafter referred to as the East and West End forests, cover 1,052 ha (47%) of the 2,226 ha island. *Fagus* dominates nearly all of these forests, with scattered large *Quercus alba* L. and *Quercus velutina* Lam. occurring at very low densities. Beech bark disease has been present on the island for > 30 years (D. Houston pers. comm.), but has resulted in little decline or mortality, in contrast with high mortality rates throughout the northeastern U.S. (Twery and Patterson 1984, Morin et al. 2006).

Naushon Island has an unusual history of ownership and land use that has ensured the preservation of this landscape, and may have facilitated the development of extensive forests characterized by single-species dominance. Before European settlement, the nearby and substantially larger islands of Martha's Vineyard and Nantucket supported the highest Native American population densities in New

England (Bragdon 1996), suggesting that Native peoples may have lived on Naushon and used it extensively for hunting and gathering. The Native population in the mid-17th century was 40 families, but may have been larger before the 1612–1613 epidemic that killed large numbers of coastal Native Americans (Emerson 1935, Banks 1911). Since European settlement (1641 AD), the entire island has remained in single-family ownership, with only four different families through time. The current ownership was established in 1843. Population densities on the island were thus substantially lower than in surrounding areas through the historical period (Yentsch 1974, Foster et al. 2002).

Study Species. *Fagus grandifolia* is found throughout eastern North America, and is considered a late-successional species in northern hardwood forests where it regenerates in gaps created by small-scale wind disturbance (Runkle 1981, Canham 1990). *Fagus* reproduction occurs both by seed and vegetatively by root sprouts that develop in response to above or below-ground injury (Jones and Raynal 1988). In the Northeast, *Fagus* was abundant in pre-Colonial forests (Cogbill et al. 2002), especially in northern New England and at higher elevations, but frequent and intense anthropogenic disturbances in the historical period have contributed to its region-wide decline (Siccama 1971). Since the 1930s, beech bark disease, a scale-fungus complex, has led to further *Fagus* decline and substantial changes in forest structure and dynamics in most inland locations (Twery and Patterson 1984, Morin et al. 2006). These historical changes contributed to a long-term *Fagus* decline in the Northeast that began 1,000–2,000 years ago due to broad-scale climate change (Russell et al. 1993, Fuller et al. 1998).

Although the role of *Fagus* in northern hardwood forests has received substantial attention (e.g., Siccama 1971, Canham 1990, Merren and Peart 1992, Poage and Peart 1993), the long term dynamics of coastal *Fagus* forests are poorly understood. Coastal *Fagus* dynamics likely differ from inland dynamics because hurricanes, which may facilitate *Fagus* forest development, are more frequent and intense in the coastal region (Boose et al. 1994, 2001). In addition, fire, which has the potential to limit or restrict *Fagus*, has been more frequent in the coastal region historically than in most other areas in New England (Parshall et al. 2003).

Forest History. A detailed historical record for the study area was used to determine the timing, and in some cases extent, of natural and anthropogenic disturbance events, and to track compositional changes in forested areas (Appendix). Early nautical maps (Des Barres 1780), municipal land cover maps (Crapo 1837), and a detailed US Coast and Geodetic Survey map (USCGS 1845, scale: 1:10,000) identified areas that were forested through the mid-19th century. Documentary sources, aerial photographs, and land-cover maps were used to track changes over the past century (MacConnell 1951, 1973, MassGIS 2002). Study sites were established in areas continuously forested throughout the historical period, defined as areas consistently mapped as forested for which we found no documentary or field data to suggest otherwise (Fig. 1).

Wind Disturbance. We used the HURRECON model (Boose et al. 1994, 2001) to reconstruct hurricane frequency and intensity for Naushon Island for 1620–1997. Boose et al. (1994, 2001) identified all hurricanes with damaging winds for the Northeast based on 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. The HURRECON model predicts the frequency and intensity of hurricanes at a specific site based on wind damage reports and meteorological observations for each storm. In addition, we used local documentary sources from Naushon Island (e.g., personal descriptions, anthologies, and annual reports) to develop an independent reconstruction of hurricane strikes.

Modern Forest Structure and Dynamics. To characterize forest development, we sampled vegetation in 24 fixed-area plots (400 $m^2$) in continuously wooded areas. Within each plot, species and dbh were recorded for all trees $>$ 10 cm dbh, and increment cores were taken from 15–20 trees $>$ 7 cm dbh for age determination and radial growth analysis. Because of the low density of *Quercus* spp. in study plots, and their greater age than the more abundant *Fagus*, additional *Quercus* trees outside of study plots were cored to facilitate reconstructing long term forest dynamics.

We collected sound cores from 647 trees: 433 *Fagus*, 146 *Quercus alba*, and 68 *Q. velutina*. Tree rings were counted and measured to the nearest 0.01 mm using a Velmex measuring system (East Bloomfield, NY). Cores were used to determine tree ages, excluding those that were rotten or substantially missed the pith. All cores were used to examine growth releases. Because our analyses did not require precise chronologies, we did not cross-date the complete sample. However, a sub-sample of cores (*Fagus* N = 92, *Q. alba* N = 58, and *Q. velutina* N = 25), cross-dated using the program COFECHA (Holmes 1983), was used to validate results obtained using the complete sample. This comparison indicated that partially or completely missing rings were extremely uncommon, and thus were not significant for our analyses (Busby 2006). Cross-dated cores were used for the growth suppression analysis.

To characterize patterns of tree response to disturbance across the study area, we generated island-wide (East and West End data pooled) disturbance chronologies for *Fagus*, *Quercus alba*, and *Q. velutina*. By identifying the percentage of trees that experienced growth releases each decade, a disturbance chronology is used to estimate the average level of decadal small-scale 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).

We identified growth releases using criteria developed in previous studies of *Fagus* and *Quercus* growth response to disturbance (Lorimer and Frelich 1989, Nowacki and Abrams 1997). Moderate and major releases for *Fagus* were defined as growth changes of 50–100% and > 100% (Lorimer and Frelich 1989). Moderate and major releases for *Quercus* species were defined as growth changes of 25–50% and > 50% (Nowacki and Abrams 1997). Using all cores, percent growth change (GC) was calculated for all years using prior ($M_p$) and subsequent ($M_s$) ten-year growth means: $GC = [(M_s - M_p) / M_p] \times 100$. Running comparisons of sequential ten-year means were made and release dates were assigned to years in which the maximum GC reached the pre-determined threshold (Nowacki and Abrams 1997). We 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). Disturbance events resulting in growth suppression (GC = 50% or less) from structural damage to surviving trees were identified using crossdated subsamples (Foster 1988).

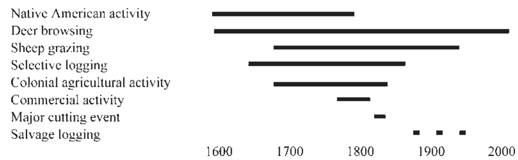


FIG. 2. Timeline of human activities and livestock and deer impacts on Naushon Island for the past 400 years.

**Results.** FOREST HARVESTING. In the early colonial period, valuable tree species (i.e., *Quercus* spp., *Sassafras albidum* Nutt., and *Chamaecyparis thyoides* L.) were selectively, and in some cases heavily, cut from the study area for shipping timbers and other special uses (Fig. 2, Appendix, Emerson 1935). Additionally, a major logging operation from 1824–1827, employing 10–20 men, clear-cut much of the West End and portions of the East End forest (Fig. 2). Detailed records indicate that there has been minimal cutting in continuously forested areas over the past > 150 years under the current ownership (Appendix).

DOMESTIC AND NATIVE HERBIVORES. Naushon Island supported a large domestic sheep population through much of the historical period, peaking in the mid 19$^{th}$ century with > 2,000 sheep (Figs. 2, 3; Emerson and Leon 2003). The number of sheep remained high through the 19$^{th}$ century, and then declined in the 20$^{th}$ century. 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. 3). Whereas sheep grazing was largely restricted to open pastures in the central and far eastern and western portions of the island (Emerson 1935, Raup 1945), deer browsing undoubtedly occurred in continuously forested areas throughout the historical period. In the

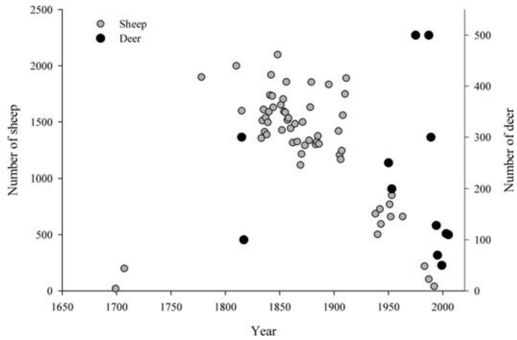


Fig. 3. Historical changes in sheep (introduced to Naushon in 1684) and native deer populations on Naushon Island (Emerson and Leon 2003). Deer populations > 10 per km$^2$ (equivalent to 224 animals on Naushon) are thought to negatively affect tree regeneration (Healy 1997).

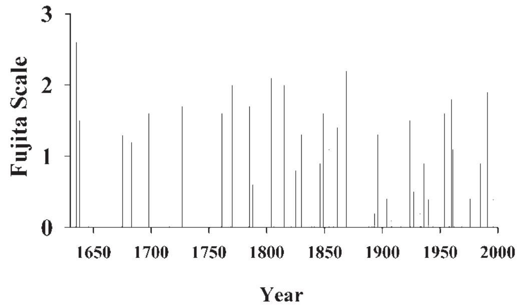


Fig. 4. HURRECON reconstruction of hurricanes affecting the study area (1620–1997). An average of 6.5 years elapsed between hurricanes. F0 = wind speeds 18–25 m s$^{-1}$, minor damage to buildings and broken branches and shallow-rooted trees uprooted; F1 = 26–35 m s$^{-1}$, buildings unroofed or damaged and single trees or isolated groups blown down; F2 = 36–47 m s$^{-1}$, buildings blown down or destroyed and extensive tree blowdowns; F3 damage = 48–62 m s$^{-1}$, buildings blown down or destroyed and most trees blown down (see Boose et al. 1994, 2001 for details of HURRECON).

1980s, coyotes (*Canis latrans*) established on the island and quickly reduced the populations of both deer and sheep. The deer population has since recovered to > 100 animals, but the sheep population remains low (G. Leon, unpubl. data).

Wind Disturbance and Fire History. The HURRECON model identified 58 storms that impacted the study area since 1620 (frequency = 0.15/year, Fig. 4). We found historical descriptions of storms affecting Naushon Island for only 16 hurricanes. Historical descriptions were restricted to the most intense storms and indicate high variability in forest damage among storms (Appendix, Busby 2006).

We found little documentary evidence of fire on Naushon Island for the historical period. Large forest fires would almost certainly have been recorded in the detailed historical records available for the island. The absence of such records suggests that few fires occurred in permanently wooded areas during the past 200 years.

Vegetation History. Historical descriptions of Naushon and nearby islands provide information on pre-settlement vegetation, and help to document changes in landscape conditions since colonization. In 1602, forests on Cuttyhunk Island, approximately 10 km southwest of Naushon and also part of the Buzzard's Bay moraine, were described as: "…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). Given the close proximity and similar geological history of these islands, the vegetation on Naushon Island may have been comparable at the time, with *Quercus* spp., *Fagus*, and *Carya* spp. dominating upland forests, and *Chamaecyparis thyoides* restricted to wetlands (Foster et al. 2002).

Although we found few descriptions of forests on Naushon Island from the 17th and 18th Centuries, paleoecological reconstructions indicate that *Quercus* spp. and *Fagus* were common, with lesser amounts of *Carya*, *Pinus*, *Acer*, and *Nyssa* (Foster et al. 2006, W. W. Oswald and D. R. Foster unpub. data). Historical descriptions indicate that *Fagus* and *Quercus* spp. were the dominant tree species on Naushon from at least the early 19th century. (Appendix). In 1815 it was estimated that three fifths of the island's trees were *Fagus*, while the remaining trees were *Quercus* spp., *Carya* spp. and *Pinus* spp. (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)…" (Torrey and Allen 1962). *Fagus* and *Quercus* spp. persisted into the 20th century. In 1930, J. M. Fogg reported that: "In some regions…these woods present an almost pure stand of beech, in others there is considerable admixture of oak, hickory, hop

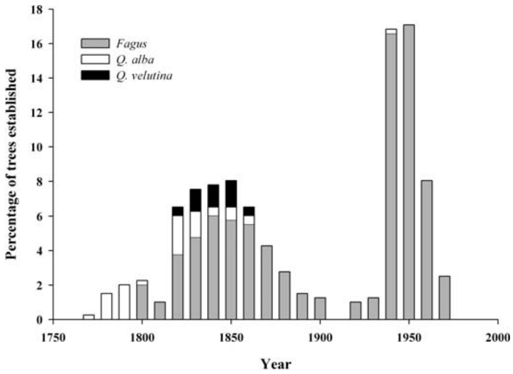


FIG. 5. Tree establishment (binned by decades) for *Fagus* and *Quercus* spp. on Naushon Island. *Quercus* spp. sampled outside of study plots are not included.

hornbeam, maple and black gum" (Fogg 1930).

MODERN FOREST CONDITIONS. *Fagus* trees dominated all study plots, accounting for > 96% of stems. *Quercus* spp. accounted for the remaining stems; other species (*Acer rubrum* L. and *Ostrya virginiana* Mill.) made up < 1% of stems and were excluded from age structure and growth analyses. *Fagus* trees ranged in age from 26 to 204 years (median = 61 years, N = 433). Two major pulses of *Fagus* establishment occurred in the past 200 years—one following the logging in 1824–1827 that persisted for > 50 years and a second following the 1944 hurricane (Fig. 5). In addition, with the exception of 1910–1920, some *Fagus* established in every decade since 1800. The oldest trees in the study area were *Q. alba*, which ranged from 59 to 351 years (median = 181 years, N = 146) (Fig. 5). *Q. alba* establishment occurred in the late 1700s, followed by a period of increased establishment beginning in the 1820s. *Q. velutina* establishment occurred from 1820–1860, synchronous with the second period of *Q. alba* establishment. *Q. velutina* ranged in age from 108 to 196 years, with a median age of 152 years (N = 68) (Fig. 5).

GROWTH DYNAMICS. Greater than 25% of *Fagus* trees were released in the 1920s (28% of trees) and 1940s (37%) (Fig. 6a). Excluding these decades, 13% of *Fagus* trees experienced moderate or major release each decade (Fig. 6a). An average of 10% of *Fagus* trees showed suppression every decade. Decades with > 25% moderate and major releases in

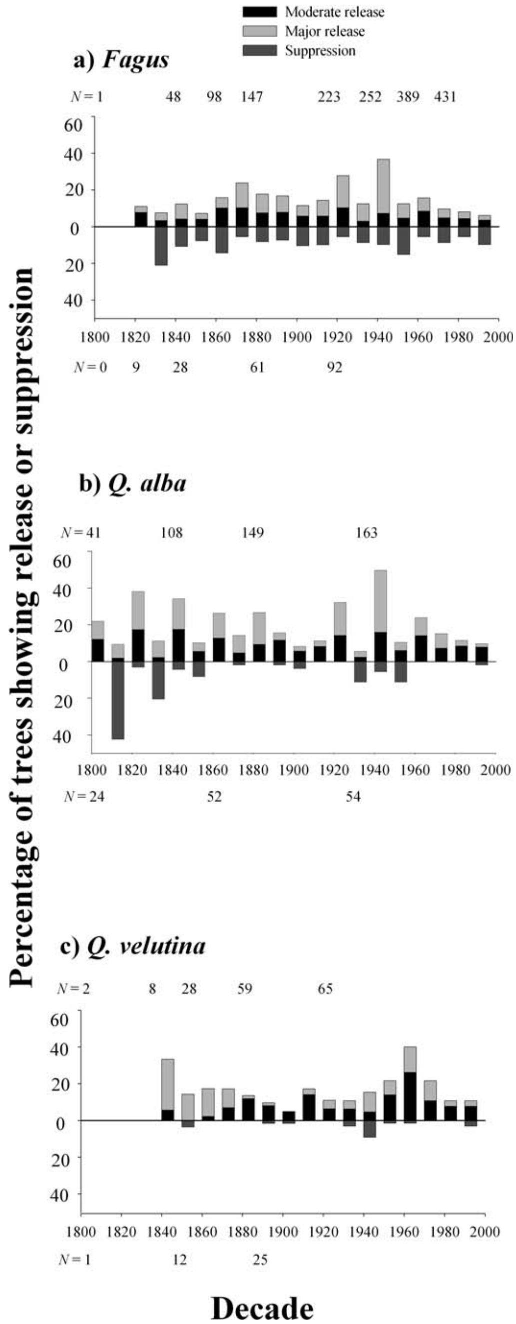


FIG. 6. Disturbance chronologies for *Fagus grandifolia*, *Quercus alba*, and *Q. velutina*. Bars above the x-axis indicate the percentage of released stems (moderate and major); bars below the x-axis represent the percentage of suppressed stems. The sample size of trees used in the release analysis is shown above the panels; the size of the sub-sample used for the suppression analysis is shown below. We report the percentage of stems showing release or suppression only for $N > 10$.

the *Q. alba* chronology were: 1820 (38% of trees), 1840 (35%), 1860 (27%), 1880 (27%), 1920 (32%), and 1940 (50%) (Fig. 6b). Excluding these decades, the average level of *Quercus alba* release per decade was 13%. Abundant *Q. alba* suppression occurred in two decades (1810, 1830) which were also characterized by low levels of release (Fig. 6b). Two decades were characterized by > 25% *Q. velutina* release: 1840s (33% of trees) and 1960s (40%) (Fig. 6c). Excluding these decades, the average decadal moderate and major *Q. velutina* release was 14%. Major *Q. velutina* release events occurred when the even-aged cohort was young (1840–1870), while varying levels of moderate release occurred thereafter (Fig. 6c). *Q. velutina* suppression occurred in the 1940s (9% of trees) (Fig. 6c).

**Discussion.** Temperate forests across the eastern U.S. are characterized by complex histories of natural and anthropogenic disturbances (Williams 1989, Whitney 1994, Foster and Aber 2004). However, attempts to evaluate the influence of such complex histories on forest composition and dynamics are frequently limited by the lack of detailed information on both disturbance history and changes in forest composition over time. On Naushon Island, detailed historical records for the past > 300 years, in combination with dendroecological analyses, provided an unusual opportunity to document disturbance history and historical changes in forest composition. Our results suggest that modern *Fagus*-dominated forests developed as a result of species-specific responses to multiple disturbances through the historical period, including forest harvesting, hurricanes, and deer herbivory, and the absence of fire. Thus, our results support a growing body of literature that highlights the importance of disturbance interactions in shaping long-term forest structure and composition (e.g., Veblen et al. 1994, Pickett and Peterson 1995, Bigler et al. 2005, Cowell and Hayes 2007).

Stand Development. Early historical descriptions and paleoecological data indicate that mixed forests of *Quercus* spp. and *Fagus*, along with several less abundant species, were widespread at the time of European settlement. Several factors apparently contributed to the decline in *Quercus* spp., and an increase in the relative importance of *Fagus* in the past 200 years. Selective logging of highly valued *Quercus* spp. may have reduced their abundance, as has occurred elsewhere in the eastern U.S. and in Europe (Vera 2000, Cogbill et al. 2002, Abrams 2003). However, a large clearcut in the 1820s initiated abundant *Q. alba* and *Q. velutina* (and *Fagus*) establishment and the second biggest pulse of *Q. alba* release in the study period. Following heavy cutting, *Quercus* spp. may re-sprout from the root collar or establish from seed, with sprouts and seedlings thriving in open conditions (Roberts 1990, Sander 1990, Abrams 2003). However, a lack of substantial cutting in the past > 150 years has resulted in little further establishment by *Quercus* spp. (Abrams 2003).

In the eastern U.S., fire-adapted ecosystems often contain *Quercus* spp. capable of surviving fires or establishing from seed or sprouts after fires. Fire suppression, in combination with selective cutting, has contributed to a regional decline in *Quercus* regeneration (Abrams 2003). The lack of fire in the study area during the historical period has presumably contributed to *Quercus* declines by maintaining conditions unfavorable for *Quercus* establishment, while allowing for an increase in fire-intolerant *Fagus* (Tubbs and Houston 1990).

Hurricane history has apparently also contributed to the increase in *Fagus* over the past > 150 years. *Fagus* in the study area have higher rates of average decadal release than those in inland forests (Lorimer 1980, Lorimer and Frelich 1989). We suspect that this results from the high frequency of low-moderate intensity hurricanes on the coast, which create scattered canopy gaps that initiate growth release among understory *Fagus* (Busby 2006). While most such hurricanes have not resulted in substantial establishment of *Fagus* or *Quercus* spp., they provide a mechanism for *Fagus* seedlings and saplings to reach the canopy, and thus contribute to an increase in *Fagus* abundance relative to less shade-tolerant *Quercus* species (Canham 1990).

Results of our dendroecological analyses indicate that, in addition to frequent low-moderate intensity hurricanes, a major disturbance affected the study area in the 1940s. We interpret this event as the 1944 hurricane based on documentation of severe damage (~1/5 of trees island-wide were reported to have been uprooted) and subsequent salvage operations (Appendix). Although the proportions of *Fa-*

*gus*, *Quercus alba* and *Q. velutina* uprooted by the hurricane are unknown, all were in the overstory at the time and were susceptible to damage and blowdown (Busby 2006). A high percentage of *Fagus* present in the understory experienced substantial growth releases, and *Fagus* established abundantly following the 1944 hurricane. Unlike *Fagus*, we observed no *Quercus* spp. regeneration in response to the 1944 hurricane. As *Fagus*, *Q. alba*, and *Q. velutina* were all previously common and were blown down by the storm, but only *Fagus* successfully established, the 1944 hurricane apparently resulted in a substantial increase in the proportion of *Fagus* relative to *Quercus* spp.

High levels of herbivory undoubtedly also contributed to the relative increase in *Fagus* versus *Quercus* over time. *Quercus* spp. are more palatable to deer than *Fagus* and may decline in response to high browsing pressure (Tubbs and Houston 1990, Vera 2000, Tripler et al. 2005). Through the historical period, deer densities on Naushon ranged from 2–22 deer/km$^2$, with substantially higher densities when expressed relative to the area of woodlands. Elsewhere in the Northeast, deer densities $> 10$ per km$^2$ have reduced *Quercus rubra* L. sapling abundance and overall sapling species richness (Healy 1997). Following the 1944 hurricane on Naushon, H. M. Raup observed that deer browsing in forested areas restricted *Quercus* and *Carya* regeneration, while *Fagus* reproduction was abundant (Raup 1945; Appendix).

We suspect that deer herbivory favored *Fagus* over *Quercus*. spp. through the historical period, and that this was particularly important following the 1944 hurricane. However, if herbivory alone prohibited *Quercus* spp. establishment, *Quercus* regeneration would have been expected to increase following a drastic reduction in the sheep and deer populations in the 1980s; this did not occur. Thus, selective herbivory is not the only mechanism responsible for *Fagus* dominance (Gross et al. 2000). Rather, *Quercus* spp. regeneration requires not only release from herbivore pressure but also open canopy conditions created by fire, heavy cutting, or other disturbances (Abrams 2003).

To summarize, several interacting factors resulted in the rise in *Fagus* dominance over the past $> 300$ years. Early selective harvesting of *Quercus* spp. accompanied by intense herbivory and frequent, low-moderate intensity hurricanes favored *Fagus* over *Quercus* spp. Although a large clear-cut operation in the early 19$^{th}$ century resulted in both *Quercus* spp. and *Fagus* establishment, thereafter, a century of limited harvesting but frequent low-moderate hurricanes encouraged *Fagus* but little *Quercus* spp. regeneration. A severe hurricane in 1944, accompanied by selective herbivory of *Quercus* seedlings, accelerated the development of *Fagus* monodominance by releasing *Fagus* saplings and initiating abundant *Fagus* establishment. In the absence of severe disturbance that may allow *Quercus* spp. to regenerate, we expect the relative importance of *Fagus* to continue to increase as mature *Quercus* spp. begin to die off.

GEOGRAPHIC VARIATION IN BEECH STAND DYNAMICS. Unlike the gap dynamics model of beech regeneration that has been described throughout much of 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 (e.g., after the early 19$^{th}$ century cutting event and the 1944 hurricane). Importantly, our results confirm the importance of wind disturbance for the establishment and persistence of beech (Russell 1953). The ability of beech to develop abundant root-sprouts in response to crown, stem or root damage contributes to successful regeneration after wind disturbance (Putz and Sharitz 1991, Cooper-Ellis et al. 1999). For example, following a catastrophic tornado in northern Pennsylvania, Peterson and Pickett (1995) reported that 66% of beech stems originated from sprouts and 33% from seed. We suspect that root sprouting 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 wind disturbance may be important for the establishment and persistence of beech. The high frequency of substantial growth increases among understory trees 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). This behavior is similar to beech growth following the severe hurricane that struck central New England in 1938 (Merrens and Peart 1992), and following a moderate hurricane 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 apparently do not develop root sprouts, which may help explain why a positive long term effect of hurricanes on the beech population was not observed. In central New England, where hurricanes occur less frequently than along the coast, a single hurricane may release beech or initiate sprouting, but beech may be subsequently 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 requires several periods of release before reaching the canopy (Canham 1990, Poage and Peart 1993).

**Conclusion.** Numerous prior studies attempting to relate disturbance history to changes in species composition and richness over time have focused on simple systems characterized by disturbances of a single type, assuming that 'pioneer' species are favored by frequent disturbance, whereas superior competitors are favored in the absence of disturbance (e.g., Connell 1978). Results of this study, and others (e.g., Collins et al. 1995), do not support such a trade-off between the ability to withstand disturbance and competitive ability. In coastal environments characterized by complex disturbance history, *Fagus* has both a superior competitive ability (pronounced shade tolerance) and a superior ability to tolerate disturbance (through advanced regeneration and sprouting). Thus, rather than following generalized models relating species composition or richness to disturbance frequency or intensity, our results highlight the importance of individual species responses to complex and interacting disturbances in controlling changes in forest composition over time (Veblen et al. 1994, Pickett and Peterson 1995, Bigler et al. 2005, Cowell and Hayes 2007). In our coastal study area, modern *Fagus* dominance developed in response to such a complex history of natural and human disturbance over several centuries. Interestingly, *Fagus* was apparently equally abundant in the study area and other coastal sites at various times before European colonization (Foster et al. 2002, Foster et al. 2006), having undoubtedly developed in response to differing disturbance regimes. Our results suggest that detailed information on both long-term history and species biology are necessary for understanding changes in forest composition over time, and for evaluating the range of conditions under which species-poor forests may be expected to replace more species-rich systems, or the reverse.

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## Appendix.

### 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 in Quinn and Quinn 1983). ‘‘[Cuttyhunk]…is overgrown with wood and rubbish, viz. oaks, ashes, beech, walnut, witch-hazel, sassafras and cedars…’’ (Archer in 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" (Winthrop in 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" (Towne in 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"[2] (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).

**1841** Oct. 3 1841 "A gale from the north-east commenced in the morning and in the course of the

[2] 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).

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 beech 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).

**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 beech 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 in Torrey and Allen 1962).

**1860** John Gifford sold $84.13 worth of wood in 1860, $65.39 in 1861, and $13.90 in 1862 (Forbes and Gregg 1979).

**1869** ''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).

**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).

**1875** Thinning along roads, for example: ''I have this marked for culling about 100 old trees on Main Road between Grapevine Walk and Yellow Gate, and about 100 more from Red Gate (at Trotting Course) along Ridge Road as far as Amphitheatre Path, including 100 yards or so on said path – also including some on the south ridge of the valley where Robert's grave stands'' (Emerson and Leon 2003). Additional thinning along South Bluff road: ''Along the ridge from the Cove to the Black Woods seems to have been left a strip of the original forest now chiefly fine old oaks and beech. I have, along the wood road, tried…thinning out the beech saplings and sprouts around any good oaks and I mean to extend this plan'' (Emerson and Leon 2003). Very few descriptions of thinning in continuously forested areas were found: ''The Black Woods and beech woods are fine bodies of wood with many old trees which we gradually thin for fuel'' (Emerson and Leon 2003).

**1882** Thinning along roads: ''They have made quite a show in thinning along the Gap in the Wall Road to the north end of Painted Path, and some on the Cove Road. I have marked some 80 trees with O with a limit of 12 ft. to be cleared around each'' (Emerson and Leon 2003).

**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 shorter 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'' (Hollick 1901).

**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 in Dunwiddie and Adams 1994).

**1916** ''Trees, in stretches of miles; beech, 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 1919).

**1924** ''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).

**1928** ''The hurricane which hit Florida on Sept 6 reached Naushon on the 9th [September] with gale winds and torrential rains. Cellars were flooded and trees were down, 28 on Lackey's Bay Road alone.

Except for the uprooting of trees no great damage was done'' (Emerson and Leon 2003).

**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).

**1938** Sept. 21. ''Terribly destructive hurricane hit the Island at extreme high tide. Pine Island was swept clean of its age-old cedars and all but washed away. At the Blue Hills Observatory the wind reached 186 mph'' (Emerson and Leon 2003). ''A great many of the noblest trees on the island were blown down….Most of the trees on Cedar Island were blown down'' (Forbes 1964). ''The storm, by far the worst in many years, blew down thousands of trees, some of magnitude and beauty, but fortunately most of those blown down showed that they had been defective in sundry respects, and once they had fallen and were cleared away, there were enough fine trees left so that the grandeur of the forest will be in no way impaired'' (Annual Report 1939).

**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). Post-hurricane timber salvage (1946–48): ''So far the total amount removed is a little under 1,000 cords or less than 10% of the estimated total'' (Annual Report, 1946). ''To date Smith has sawed up about 330,000 feet of lumber, 90% of which is oak.'' (Annual Report 1947) ''H.D. Smith sawed over 200,000 board feet, chiefly oak, most of which remains unsold'' (Annual Report 1948).

**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). ''In spite of the fact that they [deer] do not eat it [*Fagus*] if other browse is available, many of the young beech sprouts in the east end have been severely nibbled back. Further more numerous oak seedlings have been reported early in the year but no young oaks are to be found. Also a place that was wired in by D.C. Forbes to keep deer and sheep out did show a good growth of oak as well as other young trees that he planted there'' (Raup 1945).

**1954** Aug. 31 ''[Hurricane] Carol, with winds of 135 mph, struck Naushon at high tide. All bridges to Nonamesset were carried away and the Monsod boat house landed upside down in the swamp across the road at the head of Lackey's Bay'' (Emerson and Leon 2003). ''Hurricane Carol turned most of the leaves grayish-brown so that it looked like winter'' (Forbes 1964).

**1954** Sept. 11 ''[Hurricane] Edna, with winds of almost 100 mph, did some damage to already weakened trees and structures but far less than 'Carol,' as the tide was low when it hit the island'' (Emerson and Leon 2003). ''Hurricane Edna blew leaves off the trees that had been recently damaged by Carol'' (Forbes 1964).

**1954** Oct. 16 ''[Hurricane] Hazel, the third hurricane to strike the islands this autumn, did immense damage to the trees. Clouds of wind-swept spray were driven right across Naushon. This final blast denuded the forest, already weakened by the previous storms, and actually killed great numbers of trees, especially on the south side of the Island. The forest has never recovered'' (Emerson and Leon 2003).

**1955** Aug. 13 ''[Hurricane] Connie did not do much harm at Naushon'' (Emerson and Leon 2003).

**1955** Aug. 19 ''[Hurricane] Diane, with winds reported at 74 mph, struck the Island hard, also at high tide. Tremendous rain (16 inches reported at Hartford) and heavy seas washed out the beaches and banks along the shores. Cedar Island lost all its cedar trees and Fisherman's Island was badly denuded of trees and badly washed away in places'' (Emerson and Leon 2003).

**1960** Sept. ''[Hurricane] Donna again washed away the shores…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 blowdowns and areas of thickly crowded new growth, the forest has come back and regained much of its former beauty'' (Emerson and Leon 2003).

**1985** ''[Hurricane] Gloria hit with winds of 70 mph'' (Emerson and Leon 2003).

**1991** ''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).

**2005** *Fagus grandifolia* dominates areas continuously forested throughout the historical period. In plots in dwarf *Fagus* stands, 96% of stems are *Fagus* and 4% are oak species. In intermediate sites, 98% are *Fagus* and 1% *Quercus* spp., and in tall plots 93% are *Fagus* and 6% *Quercus* spp. Other species found in study plots, but not used for age or growth analysis, included *Acer rubrum* and *Ostrya virginiana*. No *Quercus* spp. regeneration was observed in continuously wooded area, although oak have established in open areas.