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Forest response to chronic hurricane disturbance in coastal New England

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Abstract

Question: Hurricanes and cyclones cause a wide range of damage to coastal forests worldwide. Most of these storms are not catastrophic in ecological terms, but forest responses to storms of moderate intensities are poorly understood. In regions with a high frequency of moderate hurricanes, how does variation in disturbance intensity affect the magnitude of ecological responses?

Location: Naushon Island, Massachusetts, USA.

Methods: We use historical records and dendroecological methods to characterize establishment and growth of *Fagus grandifolia*, *Quercus alba*, and *Quercus velutina* in response to seven non-catastrophic hurricanes of varying intensity, and a major logging event, relative to baseline conditions, over the past 150 years. Our aim was to document variation in the magnitude of responses to known disturbance events of varying intensity, and to determine whether tree growth after moderate hurricanes differs from growth during periods of no disturbance.

Results: Forest harvesting in 1824-1827 had a strong impact on forest composition and growth. Since then, the study region has been characterized by little harvesting but frequent hurricanes. However, only one of the seven storms examined caused substantial increases in growth and new establishment for the dominant species; most moderate disturbances had minimal impact on growth and regeneration dynamics. We also document highly variable responses among species to individual storms, including substantial growth decreases that may not be detected by standard analytical approaches.

Conclusions: Our results caution against the use of simple metrics such as wind speed to predict forest response to specific hurricanes, and highlight the importance of individual disturbance events in controlling long-term forest dynamics, even in regions characterized by high disturbance frequency. In addition, we show that standard approaches to reconstructing disturbance history based on increases in radial growth and pulses of tree establishment are likely to underestimate the frequency of moderate disturbances.

Keywords: Beech; Coastal forest; Dendroecology; *Fagus grandifolia*; Hurricane; Moderate disturbance; Oak; Quercus; Release; Windthrow.

Introduction

Wind storms, including hurricanes, extra-tropical cyclones, tornados, and thunderstorms, cause a wide range of damage to forests worldwide. Previous studies have focused on forest response to individual wind storms at the ends of a spectrum of disturbance severity (i.e., catastrophic wind storms or individual tree-fall gaps). In contrast, the range of forest responses to wind storms of moderate intensities, including most hurricanes, is poorly understood (but see Batista & Platt 2003; Woods 2004; Nagel & Diaci 2006). Given the potential for increased hurricane intensity and/or frequency under future climate scenarios (Emanuel 2005; Webster et al. 2005), characterizing the range of forest responses to past hurricanes is an important first step to understanding how changing wind disturbance regimes may affect forest composition and dynamics.

Most hurricanes are moderate in intensity, causing intermediate levels of tree uprooting, crown damage, and growth change among surviving individuals, with the forest response determined in part by differences in wind resistance, growth, and establishment among species (Brokaw & Walker 1991; Bellingham et al. 1995; Batista & Platt 2003). However, because response to wind disturbance is further conditioned by stand structure and composition, and environmental, meteorological, topographic, and historical factors (Webb 1989; Foster & Boose 1992; Boose et al. 1994; Canham et al. 2001), responses to storms of any intensity can be highly variable.

Studies of forest response to disturbance have been hampered by the difficulty in determining the timing, intensity, and characteristics of disturbance events over long periods. Much of the literature characterizing moderate and high-intensity disturbances has thus been based on indirect reconstructions that infer disturbance events from patterns of change in tree growth (particularly distinct 'releases' in radial growth) and pulses of tree establishment (e.g., Henry & Swan 1974; Lorimer & Frelich 1989). This approach assumes a direct relationship between disturbance intensity, a measure of wind strength, and the magnitude of response, with more intense events eliciting more abundant release and establishment (Lorimer 1980; Frelich & Lorimer 1991). However, because this indirect approach examines only disturbances eliciting abundant release and establishment, it fails to characterize how a broader range of disturbance intensities affects growth and regeneration dynamics relative to baseline conditions.

In this study, we avoid the potential limitations of using patterns of growth responses to infer the timing and intensity of disturbance events by examining variation in the response of coastal forests in the northeastern USA to known hurricanes of a range of intensities over the past 150 years. We assess the magnitude of the storms by explicitly comparing hurricane responses to growth and establishment during periods without disturbance, and to the response to a major logging event. Historical sources and a meteorological model allowed us to construct a detailed, independent record of hurricane frequency and intensity for the study area since European colonization. These conditions present a rare opportunity to examine variation in population and species-level responses to hurricanes of varying intensities in a region characterized by frequent hurricanes.

Methods

Study site

Naushon Island (12 km×2 km), located off the coast of Massachusetts, USA, was chosen for study because hurricanes are the dominant form of natural disturbance, and human land use and other natural disturbances have been minimal for the past 150 years (Busby et al. 2008b). The island is morainal, with medium-to-coarse sandy soils (Fletcher and Roffinoli 1986). The last major logging event occurred in 1824-1827 and strongly affected forests in the western end of the island, as well as portions at the eastern end (Busby et al. 2008b). Native deer have been a significant source of herbivory in forested areas throughout the historical period; however, population estimates at the time of individual hurricanes are not available.

A detailed series of maps depicting land-cover change since 1780 (Des Barres) was used to identify areas of the island that have remained continuously forested. Today, *Fagus grandifolia* dominates all such areas, along with scattered large *Quercus alba* and *Quercus velutina*. Current stand structure varies from lower slopes of ice block depressions dominated by *Fagus* trees 40-70 cm in diameter at breast height (dbh) and 20-30 m tall, to exposed ridges dominated by *Fagus* trees <5 m tall and <25 cm dbh. Beech bark disease (BBD), a scale insect-fungus complex, has been present on the island for >30 years but has resulted in little mortality (D. Houston pers. comm.), in contrast with high mortality rates throughout the northeastern USA (Twery & Patterson 1984; Morin et al. 2006).

Field data

To characterize variation in growth and regeneration responses to specific hurricanes, we sampled vegetation in fixed-area plots (400 m^2), subjectively located in representative examples of the dominant structural types across the island. Within plots ($N = 29$), species and dbh were recorded for all trees >10 cm dbh, and increment cores were taken from 15 to 20 trees >7 cm dbh for age determination and radial growth analysis. Because of the low density of *Quercus* spp. species in study plots, additional *Quercus* trees outside of the study plots were also cored.

Sound tree cores were collected from the base (30-40 cm above the ground) of 647 trees: 433 *Fagus*, 146 *Q. alba*, and 68 *Q. velutina*. Cores were dried, mounted, and sanded to reveal the cellular structure. Tree rings were measured to the nearest 0.01 mm using a Velmex measuring system (East Bloomfield, NY, USA). Cores were used to determine stand age structure for modern forests (excluding rotten cores and cores that substantially missed the pith), and to examine growth dynamics in hurricane and non-hurricane years. Sub-samples of *Fagus* ($N = 92$), *Q. alba* ($N = 58$), and *Q. velutina* ($N = 25$) were cross-dated (COFECHA, Holmes 1983) and used to verify results obtained using the entire sample (data not shown; Busby 2006).

Hurricane regime reconstruction

We used the HURRECON model (see Boose et al. 1994, 2001 for details of HURRECON) to reconstruct hurricane frequency and intensity (maximum sustained wind speed) for Naushon Island for 1620-1997. Wind speeds were then translated into a Fujita scale rating reflecting both wind speed and estimated structural and forest damage (see Fig. 1). While actual damage assessments (e.g., for tornadoes) are typically estimated to the nearest whole Fujita value, fractional Fujita values allow for a continuous function relating wind speed and Fujita value and are useful in cases where there is a good measure or estimate of wind speed (Fujita 1985). Detailed local documentary sources also provided independent information on the extent and severity of damage to forests and structures. Based on these hurricane records, we selected six storms to examine that: (1) were characterized by Fujita scale ratings (F) (1.4-2.2) greater than the median rating for all hurricanes (1.3), and (2) were not preceded or followed (within 6 years) by another hurricane (Fujita scale rating > 1.0). For five of the six storms, written historical records document the impact of the storms in the study area. Less intense hurricanes were not included because these events were typically not recorded in historical documents, and were unlikely to have had observable effects on population-level growth dynamics. We selected hurricanes not preceded or followed by another hurricane to determine growth response to a specific event, recognizing, however, that the effects of a previous hurricane may persist longer than 6 years and may influence wind damage from, and 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 (1869, 1888, 1924, 1944, 1960, and 1991) had reconstructed Fujita scale ratings of 2.2, 1.4, 1.5, 1.9, 1.8, and 1.9, respectively (Fig. 1). An earlier hurricane (1841, 1.8) was also evaluated for *Q. alba*, which was the only species that had sufficient numbers of stems predating this event.

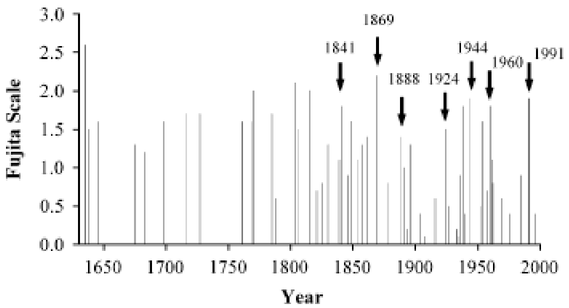

Fig. 1. HURRECON reconstruction of hurricanes affecting the study area (1620-1997). Arrows indicate hurricanes examined using the growth change (GC) frequency distribution analysis. F0 = wind speeds 18–25 m s^{-1}, minor damage to buildings and broken branches, and shallow-rooted trees uprooted; F1 = 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).

Growth changes in hurricane versus non-event years

We developed an analysis that explicitly compares intraspecific variation in growth response following a hurricane to growth in non-event years. We distinguish between two types of non-event years: non-hurricane years, i.e., those that do not fall in a hurricane year, and quiet years, i.e., those that are not preceded or followed (within 6 years) by a hurricane with severity > F1.0. Because of the high frequency of hurricanes, quiet years were regularly distributed within periods that met these criteria; a greater separation between quiet years and hurricanes was not possible. We examined the same number of quiet and non-hurricane years as the number of hurricane years examined ($N = 6$ for each of the three categories). We also examined the effect of the 1824-1827 harvesting event on *Q. alba* growth. For all analyses, data from all stands were pooled by species.

For each core, percentage growth change (GC) was calculated for each hurricane and non-event year (t) using prior (M_p) and subsequent (M_s) 10-year growth means: $GC = [(M_s - M_p)/M_p] \times 100$ (Nowacki & Abrams 1997). We used 10-year averages to filter out short-term growth responses to climate, while detecting sustained growth responses caused by disturbance (Lorimer & Frelich 1989; Nowacki & Abrams 1997). GC values were correlated with tree size in *Fagus*, with smaller trees showing greater GC. Thus, we relativized GC to account for allometric changes in growth with respect to size by multiplying GC by the diameter at year t. GC was not correlated with tree size for *Quercus* spp., and thus was not relativized for those two species.

We generated GC frequency distributions for *Fagus* and *Quercus* spp. for the seven selected hurricane years, the two different sets of non-event years, and the 1824-1827 logging event (*Q. alba* only).

Differences among GC frequency distributions following hurricane years and differences between hurricane years and non-event years are interpreted as resulting from the differential responses of trees to different storms. We report standard descriptive statistics characterizing differences in GC among hurricanes, between hurricane and non-event years, and for the logging event, including: minimum and maximum, 10%, 25%, 75%, and 90% quartiles, mean, median, variance, standard deviation, and skewness. The Kruskal-Wallis rank sum test and Dunn's post hoc test were used to compare these values for the three categories of storm years (hurricane, non-hurricane, and quiet).

In non-event years, we 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 experience growth release (Nowacki & Abrams 1997), we expected distributions to be more varied, with long right tails and significantly higher third quartile values relative to non-event years.

Results

Hurricane regime reconstruction

The HURRECON model identified 58 storms with landfall within the study area from 1620 to 1997 (Fig. 1). An average of 6.5 years elapsed between hurricane strikes (frequency = 0.15/year): 16 years between storms resulting in F0 damage, 13 years between F1 damage, and 75 years between F2 damage. The higher frequency of hurricanes in the last century is most likely the result of increased historical and meteorological data, and is not thought to represent a real change in hurricane frequency (Boose et al. 2001). We found local historical descriptions of only 16 hurricanes affecting Naushon Island (beginning with the 1815 hurricane), including four not identified in the historical research utilized in the HURRECON reconstructions (1928, 1954, and two storms in 1955) (Supporting Information, Appendix S1). The range (0.8-2.2) and median (1.8) of reconstructed intensities for the storms for which we found written documentation suggest a bias toward historical documentation of higher severity storms.

Historical descriptions suggest high variability in forest damage among storms (Appendix S1). Descriptions of the 1944 hurricane (F1.9) indicate that it caused far more damage to forests than other storms with similar reconstructed intensities. The 1960 and 1991 storms, for example, were reconstructed as F1.8 and F1.9, but historical descriptions and field observations indicate that major damage did not occur (Appendix S1).

Population age structure

Fagus trees ranged in age from 26 to 204 years (median = 61 years; $N = 433$). *Fagus* establishment was characterized by two major pulses – one beginning in the 1820s that persisted for > 50 years, and a second following the 1944 hurricane (Fig. 2). The oldest trees in the study area were *Q. alba*, which ranged from 59 to 351 years (median = 181 years; $N = 146$) (Fig. 2). *Q. alba* establishment began in the late 1700s, followed by a four-decade period of increased establishment beginning in the 1820s. *Q. velutina* establishment occurred from 1820 to 1860. *Q. velutina* trees ranged in age from 108 to 196 years (median = 152 years; $N = 68$) (Fig. 2).

Analysis of growth change frequency distributions

To illustrate expected differences in GC frequency distributions among hurricane and non-event years, Fig. 3 compares GC frequencies in 1944 with a strongly contrasting non-event year (1934). For *Fagus* and *Q. alba*, the 1944 distributions have longer right tails than the 1934 distributions (Fig. 3a and b); however, the maximum GC for *Fagus* in 1944 was ten-times greater than for *Q. alba*. In 1944,

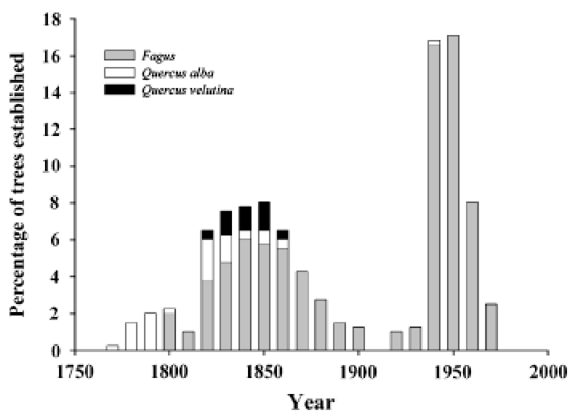

Fig. 2. Age structure of trees located in study plots (*Fagus* $N = 339$, *Quercus alba* $N = 39$, *Quercus velutina* $N = 20$). *Quercus* spp. cored outside of study plots, and trees with rotten cores and cores that substantially missed the pith, are excluded. Tree establishment dates are binned by decade.

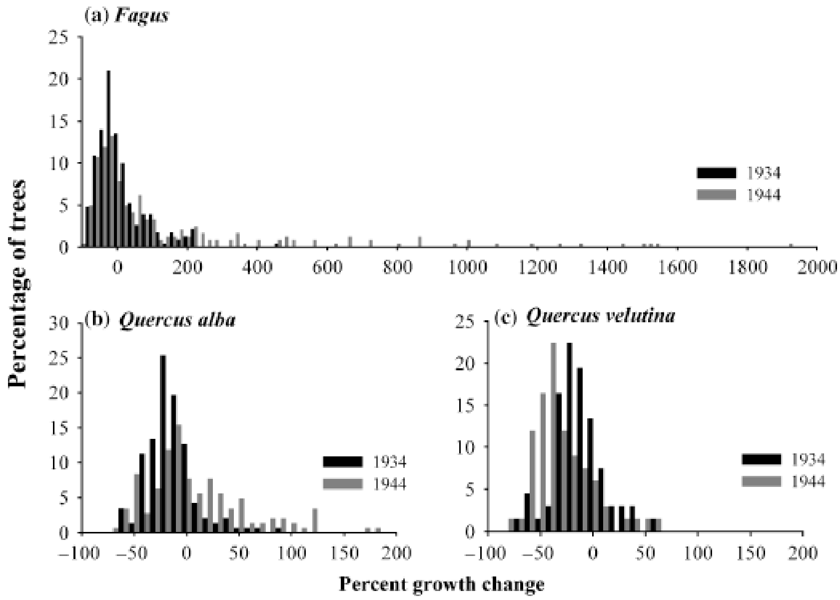

Fig. 3. Growth change (GC) frequency distributions for *Fagus* (1934 $N = 230$, 1944 $N = 246$), *Quercus alba* (1934 $N = 142$, 1944 $N = 143$), and *Quercus velutina* (1934 $N = 67$, 1944 $N = 68$) for a hurricane (1944) and a strongly contrasting non-event year (1934). Although percentage growth change for *Fagus* was standardized for the analysis (Appendix S2), it is not standardized for this figure to allow a comparison of the range in percentage growth change among species.

Table 1. Kruskal-Wallis results comparing GC frequency summary statistics for hurricane (H), non-hurricane (NH), and quiet years (Q).

	Fagus		*Quercus alba*			*Quercus velutina*		
	Kruskal-Wallis statistic	*P*	Kruskal-Wallis statistic	*P*	Dunn's post hoc test $P<0.05$	Kruskal-Wallis statistic	*P*	Dunn's post hoc test $P<0.05$
Minimum	1.21	0.548	1.99	0.368		4.43	0.109	
10% Quartile	2.39	0.302	1.22	0.544		7.29	0.026*	H & Q
25% Quartile	1.56	0.459	1.73	0.421		7.63	0.022*	H & Q
75% Quartile	0.328	0.849	1.07	0.586		7.4	0.025*	H & Q
90% Quartile	0.784	0.676	3.25	0.197		2.85	0.24	
Maximum	1.21	0.548	6.45	0.039*	H & Q	3.87	0.144	
Mean	1.06	0.587	1.02	0.599		5.19	0.075	
Median	2.21	0.331	0.516	0.773		6.63	0.036*	H & Q
Variance	4.29	0.117	7.48	0.024*	H & Q	1.26	0.532	
Standard deviation	3.24	0.198	7.17	0.028*	H & Q	1.28	0.529	
Skewness	0.737	0.692	3.02	0.221		3.17	0.205	

most *Q. velutina* exhibited negative growth responses relative to growth in 1934 (Fig. 3c).

The Kruskal-Wallis rank sum test detected no significant differences overall in the *Fagus* GC frequency distributions for hurricane, non-hurricane, and quiet years (Table 1, Appendix S2). However, for *Fagus*, two hurricanes (1924 and 1944) had substantially higher mean, median, and maximum variance, and 75% and 90% quartile values than non-event years (Fig. 4a and b). The 1960 hurricane had maximum skewness and variance values greater than non-event years, and the 1869 hurricane had greater GC variance than non-event years (Fig. 4b).

The variance, maximum, and standard deviations for *Q. alba* were significantly greater in hurricane years than in non-event years (Table 1, Appendix S2). Like *Fagus*, the *Q. alba* response to the 1944 storm was characterized by higher mean, median, standard deviation, variance, skewness, and 75% and 90% quartile values than non-event years (Fig. 4a, Appendix S2). The 1924 hurricane was characterized by high mean and third quartile values (Fig. 4a). *Q. velutina* growth following hurricanes was significantly different from non-event years, with hurricanes characterized by the lowest 10%, 25%, and 75% quartiles and median values

(Table 1, Appendix S2). However, when examining individual hurricanes, only 1944 was characterized by median, maximum, variance, and 10%, 25%, and 75% quartile values lower than non-event years (Fig. 4a and c). Thus *Q*. *velutina* behaved differently than *Fagus* and *Q*. *alba*, primarily exhibiting decreased growth following hurricanes.

The logging event (t = 1826) resulted in a higher 75% quartile value for *Q*. *alba* (the only species with sufficient sample size to evaluate) than any of the hurricanes (Fig. 4a). *Q*. *alba* also had high mean, median, and 90% quartile values in response to logging.

Discussion

Although hurricanes are relatively frequent in the study region (frequency = 0.15/year), most storms in the past 150 years had minor impacts on species growth and regeneration. In fact, only one storm (1944) had substantial impacts on both growth and establishment of the dominant species. The single major timber harvest from 1824 to 1827 also had long-lasting effects on species composition and growth. Thus, our results highlight the strong influence of infrequent moderate-high severity disturbances on forest dynamics, even in regions characterized by high frequencies of disturbance. These results are consistent with previous research in temperate and tropical forests, demonstrating relatively minimal response following many individual moderate-intensity hurricanes (Brokaw & Walker 1991; Bellingham et al. 1995; Batista & Platt 2003). In addition, these results underscore the observation that response to wind disturbance is controlled by complex interactions among a wide range of meteorological, biotic, historical, and environmental conditions. Thus, disturbances of comparable intensities may result in highly variable patterns of damage and response.

Dissimilarity in growth response to hurricanes

For the dominant tree species, growth change for the seven hurricanes, as a group, was not significantly different from non-event years. Rather, third quartile values identified only two storms

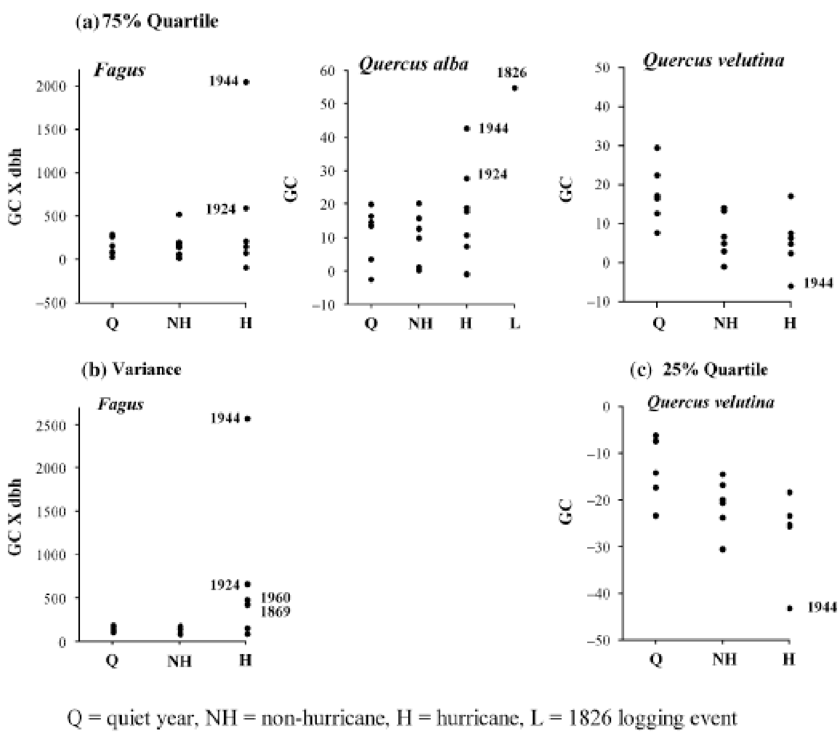

Fig. 4. Third quartile values for *Fagus*, *Quercus alba*, and *Quercus velutina* generated in the growth change (GC) analysis. First quartile values are also shown for *Quercus velutina*, and variance is shown for *Fagus*. Categories shown on the x-axis include: quiet years (Q), non-hurricane years (NH), and hurricanes (H). A third-quartile value for the 1824-1827 (t = 1826) logging event is shown for *Quercus alba* (L).

(1924 and 1944) and the logging from 1824 to 1827 (for *Q. alba*) as distinctive in their population-level effects (Fig. 4). The absence of strong impacts on tree growth following most hurricanes relative to non-event years strongly suggests that these hurricanes affected only a small percentage of trees. This interpretation is also supported by stand age structure, with establishment occurring only after the 1944 hurricane and after the 1824-1827 timber harvest, and historical documentation of timber salvage following only the 1924 and 1944 hurricanes (Appendix S1). While we suspect that the increased tree establishment that occurred for several decades beginning in the 1820s resulted from logging, it is possible that some trees also established in response to hurricanes in the mid-19th century, especially the 1841 hurricane, which reportedly caused moderate damage on the island (Appendix S1).

Variation in growth response to hurricanes of broadly similar intensities suggests that there is not a simple relationship between hurricane intensity and the magnitude of response. Rather, species composition, stand age and height, meteorological conditions, and the time since the last disturbance strongly influence the extent to which a particular storm may result in substantial damage (Foster 1988; Webb 1989; Foster & Boose 1992; Batista et al. 1998; Papaik & Canham 2006). 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 & Boose 1992; Canham et al. 2001), the population structure in 1944 (many trees 80-120 years of age, having established after the 1826 logging event or other disturbances in the 19th century) may have been particularly vulnerable to storm damage. The opposite effect may have resulted in little response to the 1960 hurricane, which occurred soon after substantial removal of vulnerable overstory trees damaged by the 1944 and 1954 hurricanes. Alternatively, variation in responses may reflect dissimilarity in storm intensities. In particular, the intensity of the 1944 hurricane may have been underestimated, or others overestimated, by HURRECON. Documentation of extensive damage elsewhere in southeastern MA following the 1944 hurricane is consistent with this interpretation (e.g., Dunwiddie 1991; Busby et al. 2008a).

Results of this study challenge estimates of the frequency and intensity of moderate disturbances derived using the standard indirect reconstruction approach (Lorimer & Frelich 1989; Nowacki & Abrams 1997). This approach detects only those disturbances eliciting abundant growth release and tree establishment; four of the six hurricanes examined in this study would not be identified or adequately characterized by this method. Thus, the reconstruction method is likely to underestimate the frequency of moderate disturbances that result in limited growth responses. Identifying such hurricanes is not trivial. Despite limited tree growth response, wind, salt spray, and storm surges associated with these events may have important ecological impacts on soil chemistry (Blood et al. 1991), understory plant communities (Gardner et al. 1991), and animal populations (Spiller et al. 1998).

Our direct comparison of responses to known hurricanes with non-event years identified a range of species-specific responses to hurricane disturbance, including no change in growth or regeneration, greater variance in growth response relative to non-event years, both increases and decreases in growth, and greater establishment. While indirect reconstructions of disturbance history typically emphasize increases in growth of surviving trees as evidence of disturbance (Lorimer & Frelich 1989; Nowacki & Abrams 1997), our results support several studies that have documented the potential for decreased growth in response to hurricanes or other disturbances (Foster 1988; Orwig et al. 2001; Lafon & Speer 2002; Motzkin et al. 2002).

Any method, direct or indirect, that uses tree rings to reconstruct forest disturbance history is subject to inherent limitations, which must be considered when interpreting results. In particular, with age, trees become progressively less representative of the population existing at the time of past disturbance events. Thus, if response (or no response) to past disturbance influences the likelihood of survival to the present, there is a potential for bias in comparisons among storms over long time periods. A second confounding factor is the constantly changing structure of forests. At different times in the past, forests were composed of individuals of differing sizes and ages, whose responses to wind disturbance were likely affected by these demographic parameters (Foster and Boose 1992), potentially confounding comparisons among storms. However, despite these methodological limitations, tree ring analyses are extremely valuable for studies of long-term forest dynamics. In particular, our objective was to characterize tree responses to known hurricanes of varying intensities. In doing so, we show great variability in response, most likely resulting from a combination of variations in storm intensities and stand conditions, which reveal the potential to underestimate the frequency of moderate disturbance using traditional approaches.

Species-specific growth and regeneration responses to disturbance

Growth and regeneration responses to hurricane disturbance are species-specific as a result of differing biological and life-history characteristics. For instance, understory *Fagus* ('advanced regeneration') may respond to canopy gaps with substantial increases in growth, and root sprouts may develop in great abundance following above- or below-ground damage (Jones & Raynal 1986; De Steven & Matthiae 1991; Beaudet et al. 2007). In addition, *Fagus* trees unaffected by BBD, such as those evaluated in this study, are relatively resistant to wind damage (Papaik et al. 2005). This suite of traits may be important for the long-term establishment and persistence of *Fagus* in areas where wind disturbance is important (i.e., Russell 1953).

Fagus demonstrates extremely varied regeneration dynamics across its geographic range (cf. Kitamura & Kawano 2001). *Fagus* is considered a late-successional species in northern hardwood forests, where it regenerates in small canopy gaps and may live for 300 years (Ward 1961; Tubbs & Houston 1990). In much of the northeastern USA, most *Fagus* have been structurally weakened by BBD and are highly susceptible to wind damage; therefore, reduced *Fagus* abundance is predicted following severe wind disturbance (Papaik et al. 2005; Papaik & Canham 2006). In contrast, our results indicate that in coastal southern New England, *Fagus* establishment may occur in pulses following major wind disturbance or logging, and *Fagus* growth increases rapidly in response to severe wind disturbance. In the southeastern USA, *Fagus* persists in an environment characterized by relatively frequent moderate hurricanes, but does not increase after such storms relative to other species (Batista et al. 1998). In that region, *Fagus* does not re-sprout, which may help explain why a positive long-term effect of hurricanes on *Fagus* abundance has not been observed. Thus, the combination of *Fagus*' pronounced shade tolerance and its flexible regeneration strategy (e.g., the ability to reproduce via seeds or root sprouts) apparently enable it to establish and persist under a wide range of site and disturbance conditions. Further studies are needed to improve our understanding of the importance of vegetative reproduction for *Fagus* dynamics throughout its geographic range.

Broadly similar responses to disturbance may occur among different *Fagus* species. In many European forests, *F. sylvatica* abundance has increased over the past few centuries in response to selective logging and heavy browsing of associated species (e.g., *Quercus* spp.). Wind disturbance may accelerate the transition to *F. sylvatica* dominance in such forests by creating small- to medium-sized gaps favoring shade-tolerant species (Pontailler *et al.* 1997), or by removing more susceptible conifer species (Nagel & Diaci 2006). Similarly, *F. grandifolia* in our study area may have benefited from the selective harvesting of *Quercus* spp. in previous centuries, browsing of preferred *Quercus* spp. seedlings, and occasional hurricanes that resulted in increased growth and establishment of *F. grandifolia*.

Quercus spp. responded differently to hurricanes than did *Fagus*. While both *Q. alba* and *Q. velutina* established in the decades after the 19th century logging event, we found no regeneration of either species following subsequent hurricanes. This result is consistent with observations suggesting that moderate wind disturbances advance the rate of succession by removing early or mid-successional canopy trees and releasing surviving shade-tolerant saplings (Webb & Scanga 2001). However, other studies have shown that shade-intolerant species that typically do not establish in individual tree-fall gaps may colonize multiple tree-fall gaps created by moderate wind disturbance (Batista & Platt 2003; Woods 2004). In our study area, the establishment of more shade-intolerant *Quercus* spp. following the 1944 hurricane may have been restricted due to competition with *Fagus* root sprouts (Everham & Brokaw 1996; Cooper-Ellis et al. 1999; Beaudet et al. 2007). Near the northern limit of *Fagus*' range, root sprouts grow faster than associated seedlings, allowing sprouts to exploit gaps created by storms and other disturbances (Beaudet et al. 2007). In addition, preferential herbivory of *Quercus* spp. seedlings by a large deer herd may have prevented *Quercus* spp. establishment (Raup 1945; Peterson & Pickett 1995).

Growth responses to hurricanes also differed among species. The magnitude of positive *Q. alba* GC was less than *Fagus* (1924 and 1944), which is consistent with observations of a greater potential for release among shade-tolerant trees (Lorimer & Frelich 1989; Nowacki & Abrams 1997). Importantly, hurricanes had a significant negative impact on *Q. velutina* growth (and some *Q. alba*), with periods of suppression apparently triggered by crown damage. Because, *Q. alba* and *Q. velutina* trees in modern forests were larger in 1944 than *Fagus* trees, averaging 36.7 and 40 cm dbh, versus 15.7 cm dbh for *Fagus* (data not shown), it is likely that the *Quercus* trees we sampled were in the overstory at the time of the 1944 hurricane and would have been more susceptible to crown damage than *Fagus*, which were likely in the understory at that time.

Conclusions

Results of this study support the notion that most hurricanes cause minimal mortality, growth change, and establishment among species (Brokaw & Walker 1991; Bellingham et al. 1995; Batista & Platt 2003). Only a single storm over the past 150 years caused dramatic changes in growth and establishment for the dominant species at our study sites. Intensive logging in the early 19th century resulted in substantial regeneration of *Quercus* spp. and *Fagus*, and a greater increase in growth of *Q. alba* than we observed following any of the hurricanes that we investigated. This result underscores the importance of individual disturbance events for long-term forest dynamics, even in an area characterized by frequent disturbance. Given the overriding importance of severe disturbances, anticipated increases in the intensity of hurricanes in the North Atlantic (Emanuel 2005; Webster et al. 2005) may be expected to result in significant impacts on forest conditions and long-term dynamics.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Documentary sources describing hurricane impacts for storms selected for growth change analysis.

Appendix S2. First- and third-quartiles and median values derived from beech, white and black oak growth change frequency distributions. Quiet years are distributed in the only two 'quiet periods' that occurred in the study period: 1904-1916 and 1969-1983.

Supporting Information may be found in the online version of this article.

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