Landscape-level variation in forest response to hurricane disturbance across a storm track

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Abstract: Hurricane wind speeds at a given site are related to the intensity of the storm and the distance and direction from the storm center. As a result, forest damage is expected to vary predictably with respect to location relative to the storm track. To determine whether patterns of forest response along the track of a major hurricane in coastal New England were consistent with the expected patterns of wind damage, we investigated tree growth responses to the storm in several study sites that are similar with respect to site conditions, vegetation, and disturbance history. Growth responses to a severe hurricane in 1944 varied predictably among study sites with respect to distance from the storm track. Sites closest to the storm track experienced lesser wind damage and exhibited minimal growth responses, whereas sites farther east of the storm track and closer to the area of maximum estimated wind speed were characterized by greater wind damage and growth changes. Variation in estimated wind speed among our study sites (5–10 m/s) is not much greater than anticipated increases in hurricane intensity predicted under future climate scenarios (3–7 m/s). Thus, our results suggest that the magnitude of anticipated increases in wind speeds associated with Atlantic hurricanes may be sufficient to cause changes in forest response.

Résumé : À un endroit donné, la vitesse du vent associé à un ouragan est reliée à l'intensité de la tempête ainsi qu'à la distance et à la direction de cet endroit par rapport au centre de la tempête. En forêt par conséquent, les dommages devraient varier de façon prévisible en fonction la position par rapport à la trajectoire d'une tempête. Dans le but de déterminer si la réaction de la forêt le long de la trajectoire d'un ouragan majeur dans la région côtière de la Nouvelle-Angleterre était cohérente avec la répartition attendue des dommages causés par le vent, nous avons étudié la réaction en croissance des arbres à la tempête dans plusieurs stations où les conditions, la végétation et l'historique des perturbations étaient semblables. La réaction en croissance à un violent ouragan survenu en 1944 variait de façon prévisible parmi les stations étudiées en fonction de leur distance de la trajectoire de la tempête. Il y avait moins de dommages causés par le vent et la réaction en croissance était minimale dans les stations situées le plus près de la trajectoire de la tempête tandis que les variations de croissance et les dommages causés par le vent étaient plus importants dans les stations situées plus loin à l'est de la trajectoire de la tempête et plus près de la région où l'on estime que la vitesse du vent était maximale. La variation de la vitesse du vent estimée parmi les stations étudiées (5–10 m/s) n'est pas beaucoup plus grande que les augmentations anticipées de l'intensité des ouragans prédites par les scénarios climatiques futures (3–7 m/s). Par conséquent, nos résultats indiquent que l'ampleur de l'augmentation anticipée de la vitesse des vents associés aux ouragans dans l'Atlantique pourrait être suffisante pour entraîner des changements dans la réaction de la forêt.

[Traduit par la Rédaction]

Introduction

Spatial variation in forest response to disturbance is largely determined by the interaction between landscape heterogeneity — including geography, vegetation, and historical factors — and variation in disturbance characteristics (Romme 1982; Foster et al. 1998). For "nondirectional" disturbances, landscape heterogeneity may not influence spatial pattern in forest response. For example, in forests in which individual tree-fall gaps are the primary disturbance, variation in slope and aspect may not affect the spatial pattern of gap formation (Frelich and Lorimer 1991). However, for many disturbances, landscape characteristics can create gradients in disturbance frequency and intensity from "exposed" to "protected" sites, resulting in spatial variation in forest damage and response (e.g., Turner et al. 1989; Foster and Boose 1992; Jules et al. 2002). Some disturbance agents also have characteristic spatial patterning of their own that may directly affect spatial variation in forest damage. For instance, the surface wind fields of most hurricanes are similar, resulting in relatively consistent gradients of wind speed that are related to distance and direction from the storm center (Boose et al. 1994). Thus, the likelihood of forest damage is expected to vary predictably with respect to location relative to the storm track (Boose et al. 1994, 2001; Johnson and Miyanishi 2007).

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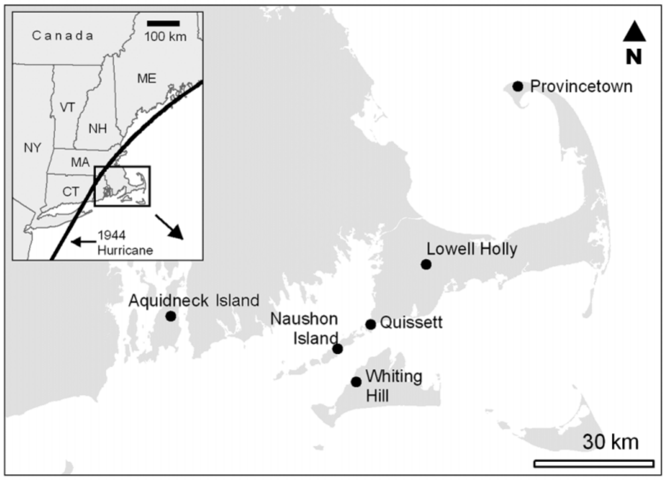
Although the importance of heterogeneity in disturbance characteristics for forest response is generally recognized, the scale at which it becomes important for different landscapes and different disturbance regimes remains poorly understood. At local scales (approximately 1 km), spatial patterns of disturbance are frequently highly variable for all but the most severe disturbances (Canham et al. 2001). At much coarser regional scales (hundreds of kilometres), relative gradients of disturbance frequency and intensity may be stable over long time periods and thus may have substantial influence on broad vegetation patterns. Such spatial variation in forest response to regional patterns in disturbance severity is likely affected by gap size. For example, small gaps created in regions characterized by low severity wind disturbance and the loss of individual trees will likely be filled with existing vegetation (Webb 1999; Brokaw and Bushing 2000). Larger gaps created in areas affected by more severe storms may result in the new establishment of shade-intolerant species (Runkle 1982). Whether such variation in forest response exists at the landscape scale (approximately 10–100 km; Johnson and Miyanishi 2007) is not known. An understanding of landscape-level variation in forest response to disturbance has been hampered by the difficulty of separating the direct effects of variation in disturbance characteristics from the confounding effects of site, vegetation, and historical factors. In heterogeneous landscapes with complex histories of natural and human disturbance, it is rarely possible to fully control for landscape variation in vegetation and site history to isolate the direct influence of variation in disturbance characteristics. Thus, studies that minimize landscape variation among sites are useful for determining how spatial variation in disturbance characteristics may influence forest disturbance and subsequent response.

In this study, our objective was to determine whether it is possible to detect landscape-level variation in forest response to hurricane disturbance relating directly to location relative to a known storm track. Specifically, our analyses examine spatial variation in forest response to hurricane wind, but not variation in disturbance severity or gap size. To minimize the potential confounding effects of landscape heterogeneity, we investigated several study sites in coastal New England that have broadly similar site conditions, vegetation, and disturbance histories. Mild topography and relatively homogeneous stand characteristics among sites enabled us to determine whether observed patterns of forest response to disturbance are consistent with those expected from spatial variation in hurricane characteristics. We used several analyses to characterize forest responses, assuming that if spatial location across the storm track is important, different tree growth response analyses should be spatially consistent.

Hurricane meteorology and the Great Atlantic Hurricane of 1944

Hurricanes have predictable meteorological characteristics that result in spatial gradients of wind speed and disturbance intensity. Although hurricanes may be quite large (radius >1000 km), the radius of sustained hurricane-force winds is often <100 km (Boose et al. 1994). Within that zone, the strongest winds are expected to the right of the storm track in the northern hemisphere, where the forward motion of the storm coincides with the rotational motion of the wind around the storm center. This is particularly important in New England, where hurricanes are typically fast moving (Boose et al. 2001). Maximum wind speeds generally occur in the hurricane eyewall, approximately 30 km from the storm center in tropical regions and 50–100 km from the storm center for late-stage hurricanes in New England (Boose et al. 1994, 2001). As a result of steep gradients of pressure and wind velocity near the storm center, forest damage and response may be expected to vary with distance from the storm track (Boose et al. 1994; Quine and Gardiner 2007).

Fig. 1. Map showing study sites in southern New England. Track of the Great Atlantic Hurricane of September 1944 (hereinafter referred to as the 1944 hurricane) is delineated by the solid line in the inset.



Atlantic hurricanes derive their energy from warm ocean waters in tropical and subtropical regions and lose strength as they travel north over land and cold ocean water. In New England, hurricane frequency and intensity are defined by consistent storm paths, the shape of the coastline, and the weakening of storms as they travel north (Boose et al. 2001). Hurricane frequency and intensity in the region decrease from southeast to northwest, with hurricanes occurring fairly frequently in coastal New England (0.15 per year). However, severe hurricanes are rare, and our previous studies determined that only the single most severe storm in the past 150 years was important for forest development on an offshore island (Busby et al. 2009*a*). The Great Atlantic Hurricane of September 1944 (hereinafter referred to as the 1944 hurricane) made landfall on Long Island, New York, and subsequently passed over Rhode Island and coastal Massachusetts with recorded wind speeds >44 m/s (100 mph) before traveling northeast out to sea. The storm traveled 108 km from Point Judith, Rhode Island, to South Weymouth, Massachusetts, in 110 min, indicating a forward motion of 16 m/s (37 mph) (Ludlum 1976). Numerous historical accounts suggest that this storm was more destructive to the forests of the coastal study region than the 1938 New England Hurricane that affected much of central New England (Foster 1988; Dunwiddie 1991). A comprehensive review of records of storm damage throughout New England

Table 1. Stand characteristics for study sites.

Site	Plots (*N*)	Substrate	Dominant tree species*	Approximate size of stand (ha)	Fagr Basal area (m^2/ha)	Fagr Relative basal area (%)	Fagr Density (stems/ha)
Provincetown, Massachusetts	2	Dune	Fagr, Acru, Nysy, Piri	3	18.8	66.1	525
Lowell Holly, Massachusetts	3	Outwash	Fagr, Quve, Piri, Qual	26	28.2	85.4	642
Quissett, Massachusetts	3	Moraine	Fagr, Quve, Qual, Acru	17	15.9	66.2	325
Whiting Hill, Massachusetts	2	Moraine	Fagr, Cato, Quve, Osvi	11	19.3	64.0	650
Naushon Island, Massachusetts	18	Moraine	Fagr, Qual, Quve, Acru	980	30.8	95.3	668
Aquidneck Island, Rhode Island	2	Till	Fagr, Qual, Acru	4	30.3	86.4	563

Note: Elevation at all sites is <30 m a.s.l. Fagr, *Fagus grandifolia*; Acru, *Acer rubrum*; Nysy, *Nyssa sylvatica*; Piri, *Pinus rigida*; Quve, *Quercus velutina*; Qual, *Quercus alba*; Cato, *Carya tomentosa* (L.) Nutt.; Osvi, *Ostrya virginiana* Mill. (K.) Koch.

*Four tree species with greatest relative basal area, listed in decreasing importance.

in combination with meteorological data was used to reconstruct the gradient in wind speed across the region (Boose et al. 2001; see also harvardforest.fas.harvard.edu/data/p01/hf011/hf011.html [accessed 15 January 2008]).

Methods

Study area

Study sites are located along the southern New England coastline, on Cape Cod, Aquidneck Island, Martha's Vineyard, and Naushon Island (Fig. 1). This region is characterized by glacial deposits of Wisconsinan origin, with extensive outwash plains, moraines, dunes, and glacial lake deposits (Oldale 1992). Broadscale patterns of vegetation have been shaped by variation in geography, environment, and site history (Motzkin et al. 2002; Foster et al. 2002). Pitch pine – scrub oak (*Pinus rigida* Mill. – *Quercus ilicifolia* Wangenh.) vegetation occurs primarily on outwash sites that were continuously wooded and heavily influenced by fire; forests dominated by black and white oak (*Quercus velutina* Lam. and *Quercus alba* L.) and mixed pine–oak forests are found on both outwash plains and on moraines; American beech (*Fagus grandifolia* Ehrh.; hereinafter referred to as beech) is locally important on mesic sites on moraine, outwash, and dune deposits (Busby et al. 2009*b*).

We investigated six compositionally similar beech–oak forests in the study region: Aquidneck Island (Rhode Island), Lowell Holly (Cape Cod), Provincetown (Cape Cod), Quissett (Cape Cod), Whiting Hill (Martha's Vineyard), and Naushon Island (Elizabeth Islands) (Fig. 1). Three of the six study areas (Naushon Island, Whiting Hill, and Quissett) are located on moraine deposits; Aquidneck Island is located on till, Provincetown is on dune deposits, and Lowell Holly is on outwash. Beech dominates all study sites, ranging from 64% relative basal area on Whiting Hill to 95.3% on Naushon Island (Table 1). Oak species, hickory (*Carya* spp.), pitch pine, red maple (*Acer rubrum* L.), birch (*Betula* spp.), and black-gum (*Nyssa sylvatica* Marsh.) account for the remaining stems. For modern beech trees that survived the 1944 hurricane, size structure at the time of the hurricane did not differ significantly among sites (Kruskal–Wallis rank-sum test, $F = 8.001$, $p = 0.156$); oak size differed for Naushon Island only ($F = 48.25$, $p < 0.0001$, excluding Naushon $F = 4.053$, $p = 0.399$). Thus, modern stands comprise stems that were broadly similar in composition and size structure at the time of the 1944 hurricane. We have no data on the size distribution of stems blown down in the storm. In addition, although much of the region was cleared in the 19th century for agriculture (Hall et al. 2002), detailed historical maps and age structure reconstructions indicate that all study sites were wooded in the mid-19th century and thus share broadly similar land use histories (Hall et al. 2002; Motzkin et al. 2002; Busby et al. 2009*b*).

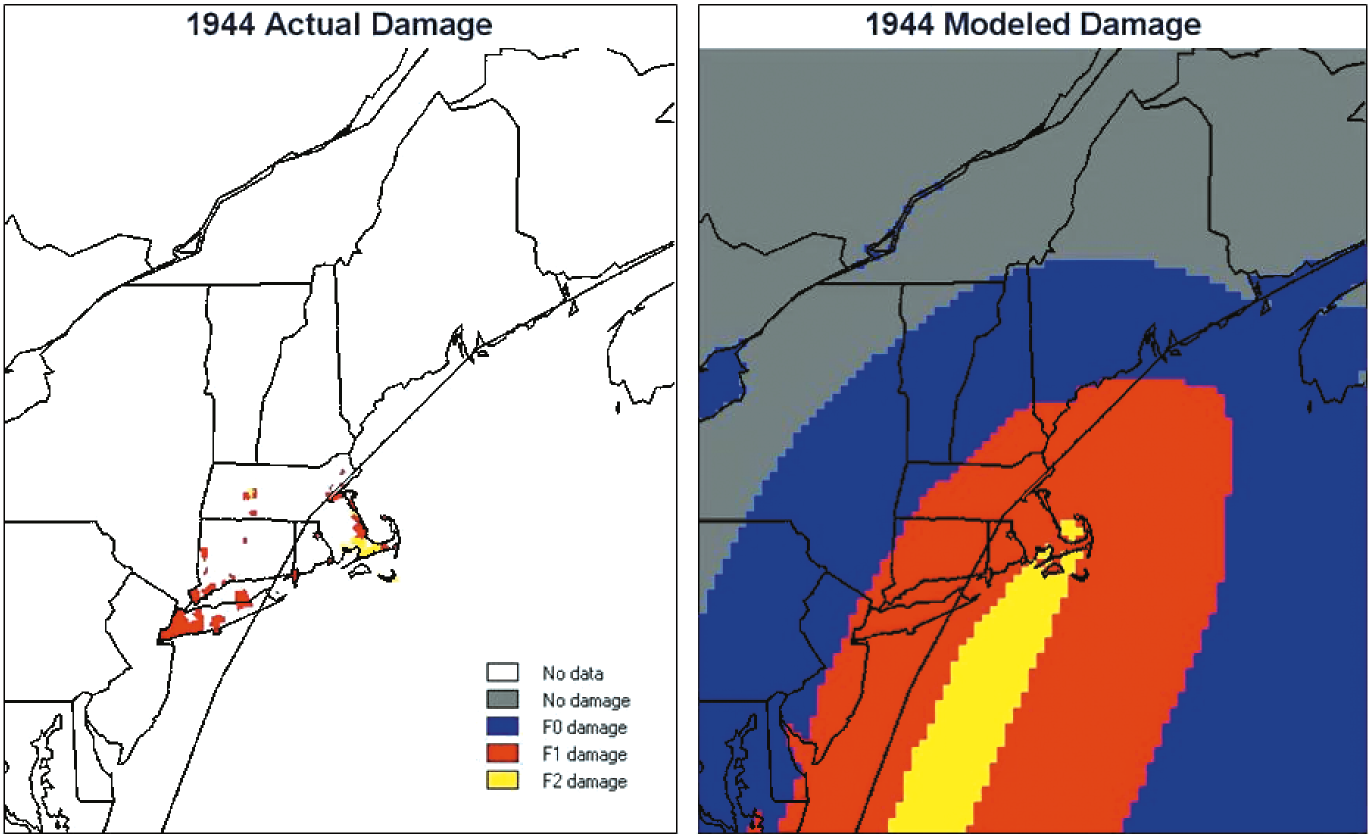
The 1944 hurricane traveled northeast through the study area (Fig. 1). Actual damage in the region was greatest at the base of Cape Cod and on nearby islands (approximately 100 km from the storm track), where hurricane winds >44 m/s (100 mph) were recorded (Fig. 2). Reports from this area indicate F2 damage on the Fujita scale, with houses unroofed or destroyed and extensive tree blowdowns (see Fig. 2 for description of Fujita scale). Along coastal Rhode Island and outer Cape Cod, reports indicate somewhat slower wind speeds and damage consistent with F1 on the Fujita scale, with houses damaged and scattered tree blowdowns. Both damage reports from the surrounding area and meteorological model estimates suggest that the study sites, although separated by approximately 10–75 km, experienced a range of wind damage from F1 (Aquidneck Island and Provincetown) to F2 (Naushon Island, Whiting Hill, Quissett, and Lowell Holly) (Fig. 2). Our analyses were aimed at determining whether we could detect forest responses to the 1944 hurricane that were consistent with this apparent variation in the pattern of storm intensity.

Additional study sites located farther west of the storm track would improve our ability to characterize spatial variation in the severity of forest response. However, expanding the study area inland would limit our ability to restrict among-site variation, as topographic relief increases immediately to the west of the study area. In addition, within the coastal region, potential study sites were largely limited to those we sampled because comparable beech–oak forests are rare (Busby et al. 2009*b*).

Growth response to the 1944 hurricane

To characterize spatial variation in response to the 1944 hurricane, we examined tree growth following the storm using increment cores collected from study sites between 2002 and 2004. We collected tree cores from fixed-area plots (400 m^2) subjectively located in areas of representative

Fig. 2. Maps showing spatial patterns of actual wind damage by town (for towns with available data) and HURRECON-modeled wind damage for the entire region. Track of the 1944 hurricane is delineated by the solid line. Fujita scale: F0, sustained wind speeds 18–25 m/s, minor damage to buildings and trees; F1, 26–35 m/s, houses damaged and single or isolated groups of trees blown down; F2, 36–47 m/s, houses unroofed or destroyed and extensive tree blowdowns (Boose et al. 1994, 2001).



vegetation. For study areas <15 ha we sampled two plots per site (Provincetown, Whiting Hill, and Aquidneck Island), and for areas 15–30 ha we sampled three plots (Lowell Holly and Quissett). Naushon Island is the only site in the northeastern coastal region where comparable vegetation occurs across extensive areas (approximately 1000 ha). We established 18 plots on Naushon Island (Busby et al. 2008) and subsampled this larger sample for comparative analyses with other sites. We randomly selected Naushon Island beech and black and white oak cores equal in number to the largest tree core sample size among the other five sites (N = 36 for beech and N = 12 for black and white oak combined).

Within each plot, species and diameter at breast height (dbh) were recorded for all trees >10 cm dbh, and increment cores were taken from 15–20 trees >7 cm dbh for radial growth analysis. Additional trees outside of study plots were cored to increase sample sizes for the dominant species. Cores were collected from the base (30–40 cm) of trees and 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, New York) and cores were visually crossdated.

Data analysis

To determine whether tree growth responses to the 1944 hurricane differed among sites we used three quantitative analyses: (*i*) percent growth change (GC), (*ii*) response index (RI), and (*iii*) transient patterns in growth following the hurricane. For all analyses, only the dominant species for which we had a sufficient sample size — beech and black and white oak species combined — were compared among sites. For each of the six study sites, cores from all plots were pooled.

To determine the impact of the 1944 hurricane on radial growth of surviving beech and oak trees, GC was calculated for 1944 using prior (M_p) and subsequent (M_s) 10 year growth means for each tree:

$$\mathrm{GC} = \left(\frac{M_s - M_p}{M_p}\right) \times 100$$

We examined growth change based on 10 year means 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). GC values were correlated with tree size in beech, 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 *y*. GC was not correlated with tree size in black and white oak and thus was not relativized for those species.

GC is commonly used to detect increases in growth (releases) associated with canopy disturbance (Lorimer and Frelich 1989). We interpret elevated GC in 1944 as growth release, negative GC as hurricane damage, and zero GC as an indication that the hurricane had little impact on the tree sampled. We used the Kruskal–Wallis rank-sum test and Dunn's post-hoc test to determine whether there was significant variation in GC among sites.

Because hurricanes may cause immediate declines in growth (caused by structural damage) followed by increases (in response to the death of neighboring trees), effectively "canceling" GC over a 10 year period, we also used a RI to compare growth change following the 1944 hurricane among sites. The RI sums the absolute value of the difference in growth between M_p and each of the 10 years following the hurricane (rw = ring width):

$$\mathrm{RI} = \left|\frac{1945_{\mathrm{rw}} - M_{\mathrm{p}}}{M_{\mathrm{p}}}\right| + \left|\frac{1946_{\mathrm{rw}} - M_{\mathrm{p}}}{M_{\mathrm{p}}}\right| \cdots \left|\frac{1954_{\mathrm{rw}} - M_{\mathrm{p}}}{M_{\mathrm{p}}}\right|$$

An elevated RI suggests high impact (which may be caused by increases or decreases in growth), whereas a low RI indicates the hurricane did not influence tree growth. We compared RI values among sites using the Kruskal–Wallis rank-sum test and Dunn's post-hoc test, to determine whether differences are consistent with estimated variation in wind speed across the storm track.

To determine whether year-to-year variation in growth following the storm reveals additional information about the growth response, we compared growth in each of the 10 years following the 1944 hurricane to M_s. Examining transient patterns in growth following the storm relative to mean growth following the storm illustrates the nature and time course of growth change (regardless of release or suppression). For example, in the years immediately following the hurricane, positive growth relative to the posthurricane mean indicates rapid attainment of maximum release, whereas negative growth followed by positive growth would indicate gradual release or damage followed by recovery. In addition, variation in annual growth relative to the posthurricane mean is a measure of the magnitude of the response.

The year-to-year residuals (R_y), the difference between a measured annual ring width (W_y) and M_s, were calculated for beech and for black and white oak species combined, for years 1 to 10 following the 1944 hurricane:

$$R_y = W_y - M_s$$

To compare the range of responses among trees of differing life stages and sizes, we standardized residuals by dividing R_y by M_s.

For beech, and for black and white oak combined, we used linear regression to fit a line to the residuals for each site for years 1–10. If the slope of the regression line for a site did not differ significantly from zero, we concluded the hurricane did not impact growth at the site. We interpret a positive or negative slope as a hurricane response, with a greater slope indicative of greater magnitude of GC over the 10 year period. Analysis of covariance was used to determine whether the slopes of linear regression lines differed among sites. To gauge the impact of climatic conditions on observed year-to-year patterns in growth, we examined the relationship between residuals and the Palmer Drought Severity Index (PDSI) for the Massachusetts NCDC Climate Division 3 (NOAA CLIMVIS). Monthly PDSI values were averaged to generate a yearly signal for the period 1944–1954. Multivariate linear regression was used to determine whether there was a correlation between PDSI values and residuals.

Table 2. Results for percent growth change (GC) and response index (RI) analyses.

Site	Beech	Oak
GC		
Kruskal–Wallis rank-sum test statistic	13.72	20.8
p	0.0175	0.0009
Dunn's post-hoc		
Aquidneck Island	516.6ab	59.2b
Lowell Holly	1166.0a	245.1a
Provincetown	25.9b	–20.5b
Quissett	544.8ab	51.7b
Whiting Hill	769.7ab	35.7b
Naushon Island	2523.3ab	–13.0b
RI		
Kruskal–Wallis rank-sum test statistic	27.61	22.4
p	<0.0001	0.0004
Dunn's post-hoc		
Aquidneck Island	5.0b	7.0b
Lowell Holly	10.8a	25.1a
Provincetown	9.3b	2.6b
Quissett	11.9ab	9.8ab
Whiting Hill	29.1a	10.7ab
Naushon Island	36.6a	4.5b

Note: Mean values are reported. Lowercase letters indicate significant and nonsignificant differences among sites (letters should be compared down each column). Note that beech GC was relativized to account for allometric changes in growth with respect to size by multiplying GC by the diameter at year *y*. GC was not correlated with tree size in black and white oak and thus was not relativized for those species.

Results

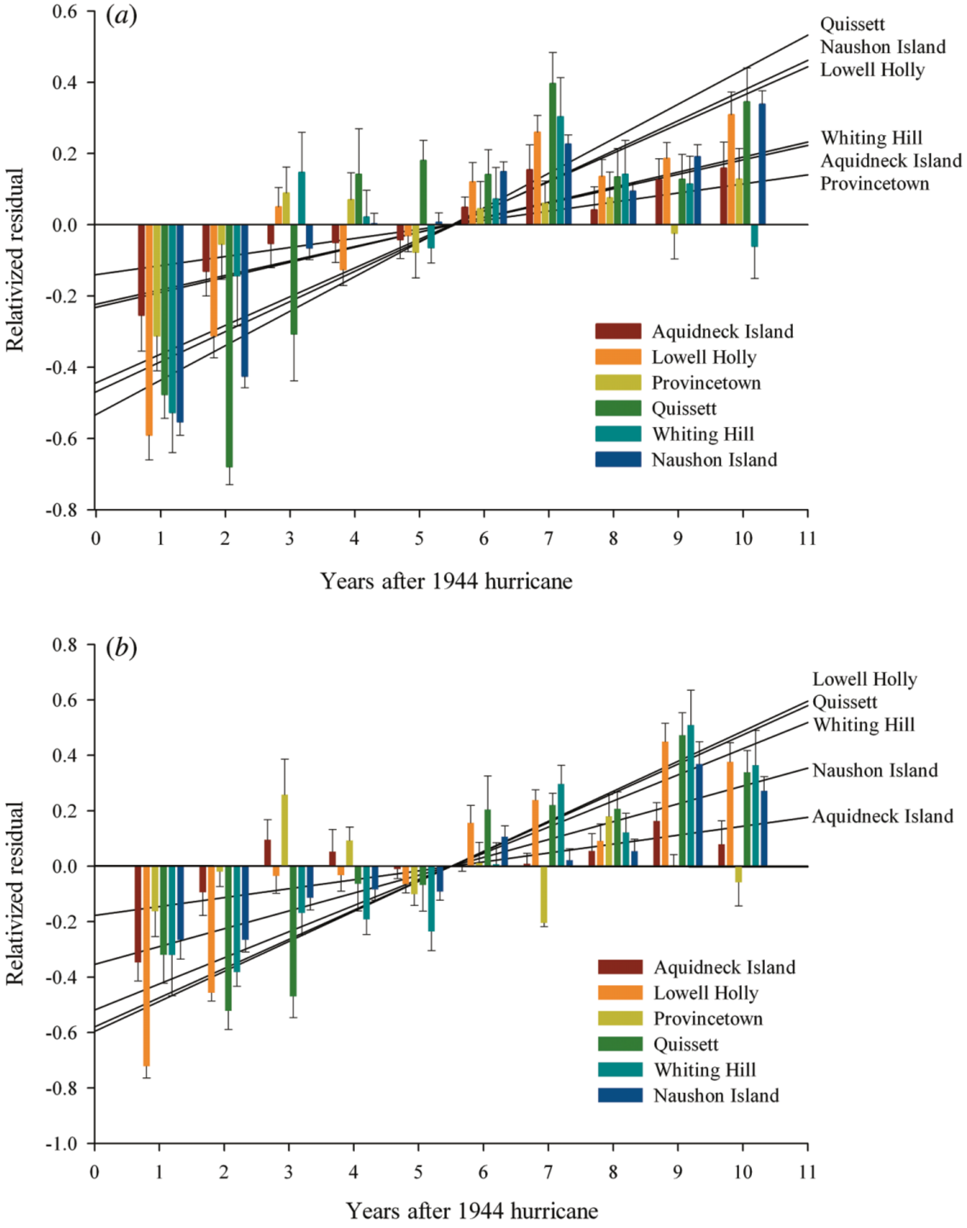
Growth response to the 1944 hurricane

GC following the 1944 hurricane differed among sites for both beech (p = 0.02) and black and white oak species combined (p = 0.0009; Table 2). For beech, this difference was significant for Lowell Holly and Provincetown only, with Lowell Holly exhibiting elevated growth and Provincetown showing minimal response (Table 2). Oak in Lowell Holly also exhibited significantly positive growth change (Table 2).

The RI for beech and black and white oak species combined also differed among sites ($p < 0.0001$ and $p = 0.0004$; Table 2). For beech, Whiting Hill, Naushon Island, and Lowell Holly were characterized by greater growth responses than Provincetown and Aquidneck Island (Table 2). The RI for oak at Lowell Holly was greater than at Aquidneck Island, Provincetown, and Naushon Island (Table 2).

Transient patterns in growth over the 10 years following the 1944 hurricane illustrate variation in the strength of

Fig. 3. Mean residuals for beech (*a*) and black and white oak species (*b*) showing transient patterns of growth in the 10 years following the 1944 hurricane. Provincetown is not shown for oak because the slope did not differ from zero. Error bars indicate the standard error of the mean.



response among sites and were not correlated with PDSI values (*p* values for multivariate regression model for each site = 0.27, 0.093, 0.15, 0.49, 0.22, and 0.16). Comparing beech growth in the 10 years following the storm to mean growth following the storm, all sites exhibited a significantly positive trend except Provincetown and Whiting Hill, whose slopes did not differ from zero (Fig. 3, Table 3). Lowell Holly, Naushon Island, and Quissett were all characterized by greater slopes than Aquidneck Island and Provincetown (Fig. 3, Table 3).

For oak, all sites excluding Provincetown exhibited a positive growth trend over the 10 years following the storm (Fig. 3, Table 3). Thus for beech and oak, the slopes for Provincetown residuals did not differ from zero. Lowell Holly, Quissett, Whiting Hill, and Naushon Island all exhibited greater slopes than Aquidneck Island. In addition, Lowell Holly and Quissett had greater slopes than Naushon Island (Fig. 3, Table 3).

To summarize, despite some variation among analyses and among species, for both beech and for black and white oak species combined, Provincetown and Aquidneck Island show consistently minimal growth responses to the 1944 hurricane, whereas Naushon Island, Lowell Holly, and Whiting Hill show consistently greater responses. Quissett shows high growth response in the residual analysis but not in the GC or RI analyses.

Discussion

The most intense windstorms may result in relatively uni-

Table 3. Residual analysis results for beech and black and white oak species combined.

Linear regression					Analysis of covariance					
P	*F*	r^2	Slope		Aquidneck Island	Lowell Holly	Provincetown	Quissett	Whiting Hill	Naushon Island
Beech										
0.0001*	49.09	0.86	0.041	Aquidneck Island	X	X	X	X	X	X
0.0008*	27.12	0.77	0.081	Lowell Holly	0.027*	X	X	X	X	X
0.065	4.555	0.36	0.025	Provincetown	0.27	0.012*	X	X	X	X
0.0041*	15.75	0.66	0.097	Quissett	0.039*	0.59	0.018*	X	X	X
0.089	3.742	0.32	0.042	Whiting Hill	0.95	0.17	0.51	0.11	X	X
0.0004*	34.99	0.81	0.085	Naushon Island	0.011*	0.86	0.39	0.67	0.12	X
Black and white oak										
0.026*	7.459	0.48	0.032	Aquidneck Island	X	X	X	X	X	X
0.0002*	38.92	0.83	0.11	Lowell Holly	0.0023*	X	X	X	X	X
0.979	0	na	na	Provincetown	0.14	0.00038*	X	X	X	X
0.0001*	46.32	0.85	0.11	Quissett	0.0017*	0.89	0.0003*	X	X	X
0.0002*	44.9	0.85	0.094	Whiting Hill	0.0038*	0.54	0.00055*	0.61	X	X
<0.0001*	53.15	0.87	0.064	Naushon Island	0.044*	0.038*	0.0037*	0.035*	0.09	X

*$p < 0.05$.

form, complete damage, suggesting consistent wind speeds that exceed the resistances of most tree species (Telewski 1995; Canham et al. 2001). For example, intense thunderstorm downbursts or tornados may completely blow down entire forest stands within their paths, with minimal damage to immediately adjacent areas (Fujita 1985). However, moderate windstorms, including most hurricanes, typically result in a much broader range of damage across the landscape (Boose et al. 1994, 2001). This variation is heavily influenced by individual storm characteristics and the interaction between wind direction and topographic exposure (Boose et al. 1994; Finnigan 2007; Quine and Gardiner 2007). In this study, we minimized potential topographic effects by selecting sites that are relatively flat as a result of common geologic history. We also minimized potential influences of variation in stand composition and structure by selecting sites with similar vegetation. This allowed us to evaluate forest response relative to variation in windstorm intensity across a storm track. Whereas most studies emphasize growth releases of surviving trees as evidence of disturbance (Lorimer and Frelich 1989; Nowacki and Abrams 1997), we utilized both increases and decreases in growth and the nature and time course of these changes to characterize spatial variation in growth responses among sites.

Growth response to the 1944 hurricane

Growth response to the 1944 hurricane varied among sites in a manner that is consistent with the distance and direction from the storm center, with some notable variation. The fastest wind speeds recorded during the storm and damage reports soon after the storm confirm that the storm was most intense approximately 100 km east of the storm track, whereas wind speeds and damage were somewhat lower to the west and closer to the storm track. In combination, growth response variables suggest that response was stronger (indicative of growth releases or suppression) at study sites located near the base of Cape Cod (Naushon Island, Lowell Holly, Quissett, and Whiting Hill), where wind speeds were an estimated 35–40 m/s, than for Aquidneck Island, which was closer to the storm center. Provincetown was most consistent in showing limited response, which would not be expected based solely on the distance to the storm track, as it is approximately the same distance east of the storm track as the base of Cape Cod, where the storm was apparently most intense. Damage reports after the hurricane as well as our analyses suggest that the storm was less intense by the time it reached Provincetown. Such weakening is observed in nearly all New England hurricanes and is caused by the storm’s passing over land or over cold ocean waters north of the Gulf Stream (Boose et al. 2001).

All three growth analyses document relatively similar responses among the four sites that were closest to the base of Cape Cod, where the highest wind speeds apparently occurred. Modest variation detected within this group of sites (i.e., Lowell Holly and Naushon displayed consistently stronger responses to the storm than Quissett and Whiting Hill) may have resulted from minor variation in local meteorological, site, or vegetation characteristics at the time of the storm.

Spatial variation in windstorm intensity

In a relatively “flat” landscape, we have demonstrated landscape-level variation in forest response to a severe hurricane associated with variation in wind speed across a storm track. In Florida, another flat landscape, greater hurricane damage was also reported for sites located closer to the hurricane eye wall than those farther away (Horvitz et al. 1995). However, unlike our study, differences in species composition and forest size structure between sites confounded the comparison of distance to the storm track in Florida.

Most hurricanes and other windstorms impact landscapes where landforms heavily influence wind speed (e.g., Sinton et al. 2000; Kramer et al. 2001). For instance, on Caribbean islands with complex topography, variation in local landforms can enhance or retard wind speed (Bellingham 1991; Brokaw and Walker 1991; Boose et al. 2004). In inland New England, site exposure heavily influenced forest damage in the 1938 hurricane (Foster and Boose 1992). Similarly, in the mountainous terrain of a southern Appalachian watershed, topography plays a major role in determining patterns of moderate hurricane disturbance, with greater damage in basins than highlands (McNab et al. 2004). Thus, while we suspect that variation in wind patterns and forest damage are generally related to distance and direction from storm centers, caution is necessary in predicting wind speeds and damage patterns in landscapes with complex topography.

Wind speed variation and forest community dynamics

In this study, sites affected by wind speeds associated with F2-level damage (36–47 m/s) were characterized by significantly greater growth responses than sites experiencing F1-level wind speeds (26–35 m/s). Greater growth responses likely reflect more severe damage and blowdowns and larger gap size. It is well-established that larger gaps created by greater wind speeds differ in ecologically meaningful ways from small gaps created by the loss of individual trees or small groups of trees as a result of low-intensity wind disturbance or natural tree mortality (e.g., Runkle 1982; Woods 2004). In particular, whereas individual treefall gaps are typically filled within a decade by existing vegetation, larger gaps may result in the establishment of new shade-intolerant species or other species capable of rapid regeneration responses to large gaps. Thus, spatial variation in wind speed over relatively short distances may have dramatically different effects on forest community dynamics. Similarly, our previous research on Naushon Island demonstrated that temporal variation in hurricane severity resulted in major differences in community response. While moderate hurricanes occurred frequently on Naushon Island over the past 150 years (0.15 per year, mostly F1), only the 1944 hurricane resulted in significant impacts on forest growth and regeneration for the dominant species (Busby et al. 2009*a*). However, on Naushon Island, shade-tolerant beech, but not shade-intolerant oak species, benefitted from large gaps by producing vegetative sprouts (Busby et al. 2008).

Potential impact of greater hurricane wind speeds under climate change

In a relatively homogeneous landscape and among sites with similar vegetation and histories, we detected variation in growth responses to a severe hurricane in coastal New England among sites that were separated by only 10–75 km. Variation in growth response was generally consistent with expectations based on estimated wind speed and distance to the storm center. Of particular interest is the fact that we were able to detect significant variation in forest response resulting from only moderate differences in estimated wind speeds (5–10 m/s). Such differences are not much greater than increases in Atlantic hurricane intensity (3–7 m/s) anticipated in the coming decades as a result of climate change (Knutson et al. 1998; Webster et al. 2005). Even modest changes in the intensity of wind disturbance, comparable to the gradient in wind speeds investigated in this study, may alter disturbance dynamics enough to cause long-term changes in community dynamics (Woods 2004). If growth responses observed in this study are indicative of larger gap size, we expect anticipated increases in Atlantic hurricane wind speed may result in larger gaps, potentially benefitting shade-intolerant species or other species such as beech that are capable of rapid vegetative regeneration in response to large gaps.

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