Dwarf Beech Forests in Coastal New England: Topographic and Edaphic Controls on Variation in Forest Structure

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ABSTRACT.—We characterize structural variation of forests dominated by American beech (*Fagus grandifolia*) on Naushon Island, Massachusetts with respect to edaphic and environmental conditions, and describe dwarf beech forests that are rare throughout the eastern U.S. Age structure reconstructions and historical references confirm that dwarf beech stands have persisted in the study area for >100 y. Dwarf beech are characterized by extremely slow radial growth rates, with some individuals growing <0.1 mm per year for >25 y, and ages up to 200 y. In the most severely stunted stands, all beech stems are <2 m tall and <8 cm basal diameter. In contrast, adjacent tall-stature forests support beech trees of similar age that are 20–30 m tall and up to 70 cm diameter (at 1.4 m). Variation in vegetation structure is strongly related to topographic position and edaphic conditions. Dwarf stands occur on morainal knobs and ridges characterized by excessively-drained sandy soils and well-developed E-horizons; soil organic horizons are absent or minimal as a result of chronic wind-removal of leaf litter. Tall-stature beech stands occur in nearby topographic depressions characterized by finer-textured soils, greater soil fertility and protection from chronic wind disturbance. Dendroecological analyses document differential tree growth and establishment responses to severe disturbances among structural types. However, individual disturbance events do not appear to contribute significantly to forest structure. Instead, dwarf growth forms apparently develop in response to harsh edaphic conditions, including chronic nutrient depletion, drought stress and wind exposure.

INTRODUCTION

Dwarf or 'pygmy' forests comprised of stunted, short-stature trees occur worldwide near treeline (*i.e.*, krummholz), but are rare in climatic regions that otherwise support tall-stature forests (Reich and Hinckley, 1980; Cairns, 2005). Tree growth forms in dwarf forests below treeline are characterized by gnarled branches, canopy die-back, and in some species, early loss of apical dominance and an increase in the importance of vegetative sprouting (Fang *et al.*, 2006). Such dwarf forests have been documented on xeric or nutrient poor soils, sites with high levels of aluminum, nickel, chromium or other elements that may be toxic to trees (Walker, 1954; Westman, 1975; Reich and Hinckley, 1980; Feller *et al.*, 2003), and on frequently or chronically disturbed sites (Andresen, 1959; Good and Good, 1975; Motzkin *et al.*, 2002). In North America, naturally occurring dwarf trees are apparently most common among conifers, although some hardwoods are known to develop dwarf forms, particularly in taxa such as oaks (*Quercus* spp.) where shrubby species are common (Reich and Hinckley, 1980).

American beech (*Fagus grandifolia*) is a common and ecologically important species throughout the eastern United States, occurring in a wide range of forest types under varied site conditions (Braun, 1950; Tubbs and Houston, 1990; Cogbill, 2005). Across much of its range, beech attains average heights of 18–24 m in mixed stands with a range of associated species (Tubbs and Houston, 1990). In contrast, in coastal New England beech occasionally

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forms nearly pure stands in areas that are protected from fire but where hurricanes are common (Busby *et al.*, 2008a, b). The largest known coastal beech forest in the eastern U.S. is on Naushon Island, Massachusetts. Monodominant beech stands occupy approximately 1000 ha on the island and are characterized by substantial variation in forest structure (Busby, 2006). Unusual dwarf beech forests occur in close proximity to tall-stature stands. In this study, we characterize this structural variation, and evaluate the extent to which structural variation corresponds with topographic and edaphic gradients. In addition, we use dendroecological analyses to compare age structure and long-term growth and regeneration dynamics among structural types. The specific objectives of this study are to: (1) characterize structural variation in the study area, comparing dwarf beech forests with nearby tall-stature forests; (2) compare age structure and growth responses to disturbance among structural types; (3) evaluate the extent to which structural variation corresponds with topographic and edaphic gradients.

METHODS

STUDY AREA

Study sites are located on Naushon Island (12 km × 2 km), the largest of the Elizabeth Islands which are located southwest of Cape Cod, MA. The island is part of an end moraine that was formed during the late-Wisconsinan glaciation, when the Buzzard's Bay ice lobe re-advanced in its long-term retreat, thrusting and folding glacial deposits into a complex topography characterized by numerous ridges (the highest ranging from 30–50 m asl) and depressions of varying sizes (Woodworth and Wigglesworth, 1934; Oldale, 1992). Soils are primarily medium-to-coarse sandy loams, with abundant surface stones and boulders (Fletcher and Roffinoli, 1986).

Two large areas on the island, hereafter referred to as the East and West end forests, are approximately equal in size and cover 1052 ha (47%) of the 2226 ha island. Beech dominates nearly all of these forests, with scattered large white oak (*Quercus alba*) and black oak (*Quercus velutina*) occurring at low densities. Beech bark disease, an introduced scale insect-fungus complex, has been present on the island for >30 y (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).

Three common and distinct structural stand types occur on Naushon Island; we refer to these as: dwarf, intermediate and tall types (Fig. 1). Dwarf types are located on knobs or ridges with exposed, sandy or rocky soils and are dominated by short stature beech trees 1–5 m tall and <25 cm in diameter. Scattered oak trees occur at very low densities in dwarf types and are 30–40 cm in diameter and 5–10 m tall, rising above the stunted beech canopy. Intermediate types are found in mid-slope positions and in areas with little topographic variation. Many of these stands support dense pole-sized beech trees, while others contain beech trees in all size classes up to 40 cm in diameter and 20 m tall. Tall stand types occur at the bottom and lower slopes of ice-block depressions ('hollows') and other lowlands. Beech trees 40–70 cm in diameter and 20–30 m tall dominate the canopy, and beech are present in all smaller size classes. Surface soils in structural forest types follow the topographic gradient, with a deepening and darkening of the A horizon and a shallowing of the E horizon from knobs to hollow bottoms.

Hurricanes occur frequently in the study area (frequency = 0.15/year; Busby, 2006) and cause a range of damage to forests, including defoliation, salt spray damage, crown damage, bole snap and the uprooting of trees (Boose *et al.*, 1994, 2001). While most hurricanes over the past 150 y have had minor impacts on beech and oak growth and regeneration in the
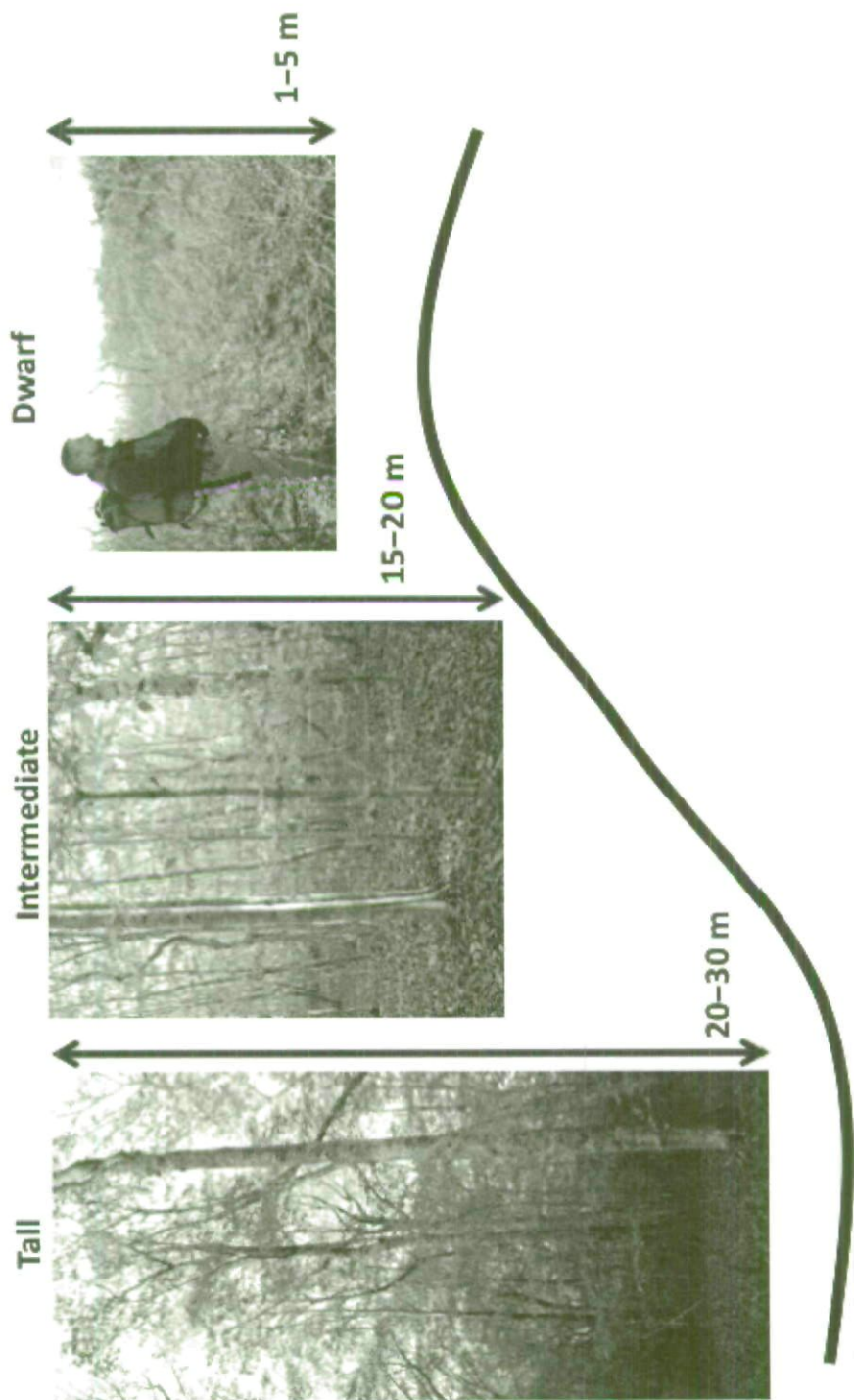
Fig. 1.—Schematic depicting topographic gradient with photographs of representative structural types on Naushon Island, MA. Oak trees emerge above the beech canopy in dwarf types

study area, a severe hurricane in 1944 led to abundant beech growth release and establishment (Busby *et al.*, 2009). Winter storms ('nor-easters') are also frequent, but likely cause less severe damage because they occur after leaf-fall when deciduous species may be less susceptible to crown damage and blowdown.

The last major logging event in the study area was an extensive clear-cut in 1824–1827 that affected both the East and West end forests (Busby *et al.*, 2008a). Detailed historical records confirm that there has been minimal cutting since that time, with the exception of salvage operations immediately following storms in 1898, 1924 and 1944. High native deer populations have been a significant source of herbivory in forested areas throughout the historical period.

GROWTH AND REGENERATION DYNAMICS

To characterize forest structure and dynamics along a topographic gradient, we sampled vegetation in 24 fixed-area square plots (400 m^2) subjectively located within representative forest structural types in both the East and West end forests (dwarf n = 6, intermediate n = 12 and tall n = 6). Whenever possible, dwarf, intermediate and tall stands were selected in close proximity to document variation across a topographic gradient. In each plot, we recorded average tree height, slope, aspect and the presence and orientation of tip up mounds. Species and diameter at breast height (dbh = 1.4 m) 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 analyses. Cored trees were selected to represent the range of tree species and tree sizes in structural types. Because of the low density of oak species in study plots, and their greater age than the more abundant beech, additional oak trees located outside of plots were cored to facilitate analysis of long-term growth dynamics. Oak trees sampled outside of plots were not used for age structure analysis.

Tree cores were dried, mounted and sanded before tree rings were counted and measured to the nearest 0.01 mm using a Velmex measuring system (East Bloomfield, New York). Because our analyses did not require precise chronologies, we did not cross-date the complete sample. A sub-sample of beech cores (n = 92) was crossdated using the program COFECHA (series intercorrelation = 0.445, average mean sensitivity = 0.279; Holmes, 1983) and used to validate results obtained using the complete sample. Seven of the 92 crossdated tree cores exhibited a single missing ring (1945 in each case); the frequency of missing rings was 0.05% (7 of 13,247 total rings) (Busby, 2006). Missing rings were extremely uncommon, and thus not significant for our analyses.

All cores were used to determine tree ages and average annual growth for the dominant species (beech and oak spp.), excluding rotten cores and cores that substantially missed the pith. Beech cores only were used to examine radial growth dynamics. In dwarf plots, random samples of 5–10 beech seedlings (stems <10 cm basal diameter and not reaching breast height) and saplings (stems <10 cm dbh and taller than breast height) per plot were cut for age determination.

We used analysis of variance (ANOVA) and Tukey post hoc tests to compare average diameter and average annual growth data among structural types for beech and for oak species combined. Non-parametric tests (Kruskal-Wallis and Dunn's post hoc) were used to compare non-normally distributed structural data among sites (basal area and density). Next, to determine whether observed structural variation is related to disturbance history, we compared stand-level disturbance chronologies for beech structural types. By identifying the percentage of trees that experienced growth releases each decade, a disturbance chronology is used to estimate the average level of decadal release (in the absence of major disturbance), and to approximate the timing of stand-level disturbance events based on

pulses in decadal release. The severity of a disturbance event is estimated by the percentage of trees released, with a stand-level disturbance defined as growth release in a minimum of 25% of stems (Nowacki and Abrams, 1997). Following criteria developed in previous studies of beech growth response to disturbance, moderate and major releases were defined as growth changes of 50–100% and >100% (Lorimer and Frelich, 1989). Using all beech cores, percent growth change (GC) was calculated for all years using prior (M_p) and subsequent (M_s) ten-year annual 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). Growth suppression (GC −50% or less; Foster, 1988) resulting from structural damage to surviving trees was identified using the cross-dated sub-samples.

<center>SOIL PROPERTIES</center>

Composite mineral soil samples (0–15 cm) derived from two samples per study plot were mixed and then analyzed to evaluate the relationship between physical and chemical soil properties and forest structure. Soil samples were oven-dried (105 C for 48 h) and sieved (2 mm) prior to analysis by Brookside Laboratories (New Knoxville, Ohio) to determine soil texture, pH (McLean, 1982), total exchange capacity (TEC), percent organic matter (SOM%; Store, 1984), and exchangeable cation and macronutrient concentrations (ppm) (P, Ca, Mg, K, Na) (Mehlich, 1984). Sub-samples were ground (<250 micro meters) prior to total carbon and nitrogen analysis, which was determined by the Analytical Chemistry Laboratory (University of Georgia) using micro-dumas combustion. ANOVA and Tukey post hoc tests were used to compare soil parameters among structural types.

<center>RESULTS</center>

<center>FOREST COMPOSITION, STRUCTURE AND DYNAMICS ALONG A TOPOGRAPHIC GRADIENT</center>

Beech trees dominated all study plots, accounting for 99% of stems in dwarf and intermediate types and 98% in tall types (Table 1). Oak species accounted for the remaining stems; other species (*Acer rubrum* and *Ostrya virginiana*) accounted for <1% of stems and were excluded from age structure and growth analyses. Beech stem density was greatest in dwarf types and lowest in tall types, whereas beech basal area was greater in tall than dwarf types (Table 1, Fig. 2). Intermediate types had basal area and density values between those of dwarf and tall types (Table 1, Fig. 2). Tree diameter (at 1.4 m) for beech differed among structural types, averaging 10.9 cm for dwarf types, 20.1 cm for intermediate and 33.5 cm for tall (Table 1). Oak diameter differed between dwarf and tall types only, averaging 38.4 and 57.8 cm respectively (Table 1). Average annual radial growth for both beech and oak did not differ among structural types (Table 1). However, excluding one outlier intermediate type plot with radial growth substantially above average, beech growth was greater in tall types than dwarf types (P = 0.023). Radial growth in some dwarf study sites was extremely slow. In one dwarf study plot, annual beech growth averaged only 0.79 mm (mean of 1700 y of ring width data from 13 trees), with some individuals growing <0.1 mm per year for >25 y.

Despite major differences in forest structure, tree ages in tall, intermediate and dwarf types were remarkably similar (Fig. 3). Overall, beech trees ranged from 26 to 204 y, with a median age of 61 y (n = 433). Beech establishment was characterized by two major pulses of

TABLE 1.—Structural characteristics for dwarf, intermediate, and tall forest types on Naushon Island, MA. Mean values are reported with percentages in parentheses. ANOVA and Turkey post hoc tests were used to compare normally distributed data (diameter and annual radial growth); the Kruskal-Wallis test and Dunn's post hoc tests were used to compare non-normally distributed data (basal area and density). Within a row, values labeled with different letters differed significantly

		Dwarf[+] (n = 6)	Intermediate (n = 12)	Tall (n = 6)	p	Test Statistic
Basal area	Beech	14.03 (78) a	28 (95) b	35.5 (96) b	0.0006	KW = 14.83
(m^2/ha)	Oak	4.1 (22)	1.4 (4)	1.3 (3)	0.3	KW = 2.4
Density	Beech	6737.5 (99) a	835.4 (99) a	382.1 (98) b	0.004	KW = 11.05
(stems/ha)	Oak	37.5 (1)	6.3 (1)	7.2 (2)	0.26	KW = 2.7
Diameter (cm)	Beech	10.9 a	20.1 b	33.5 c	<0.0001	F = 28.27
	Oak*	38.4 a	51.7 a,b	57.8 b	0.012	F = 6.208
Annual radial	Beech	0.796	1.13	1.29	0.11	F = 2.43
growth (mm)	Oak*	0.945	1.32	1.28	0.08	F = 3.1
Height (m)	Beech	<5	10–20	20–30		
	Oak	5–10	10–20	20–30		

* Includes trees sampled outside of study plots; [+] for one dwarf study site with all trees <1.4 m, basal diameters were measured and stems <1.4 m were included in density and basal area calculations

establishment—one following the 1824–1827 cutting event that persisted for 50 y and a second following the 1944 hurricane (Fig. 3a, b, c). The percentage of trees that established in the period 1940–1960 was greater in dwarf than intermediate or tall types.

Abundant beech were released in the 1940s in tall and intermediate types (55% and 53% of trees, respectively), but not in dwarf types (Fig. 4a, b, c). Peaks in major release also occurred in the 1920s (41%) and 1870s (31%) in tall types, in the 1840s (30%) in intermediate types, and in the 1870s (43%) in dwarf types. Moderate levels of growth
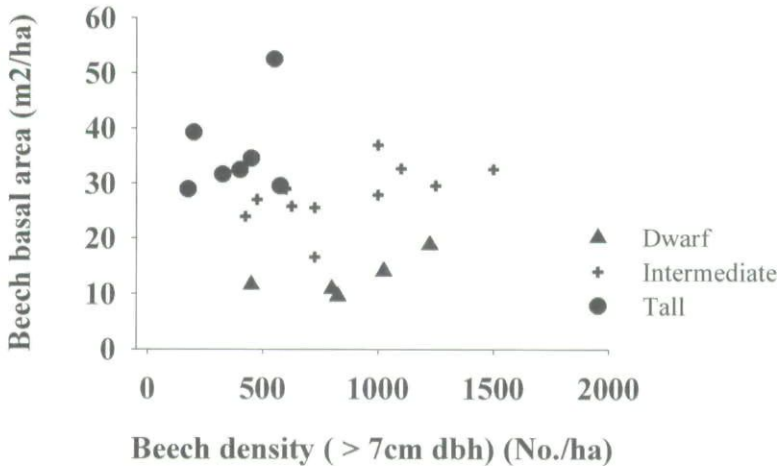

FIG. 2.—Basal area (m^2/ha) and density (stems/ha) of beech trees (>7 cm dbh) in dwarf, intermediate and tall study plots. For one dwarf study plot where all stems were below breast height (1.4 m), total basal area was calculated using basal diameter of stems (basal area = 19.15 m^2/ha, density = 36,000 stems/ha, data point not shown)
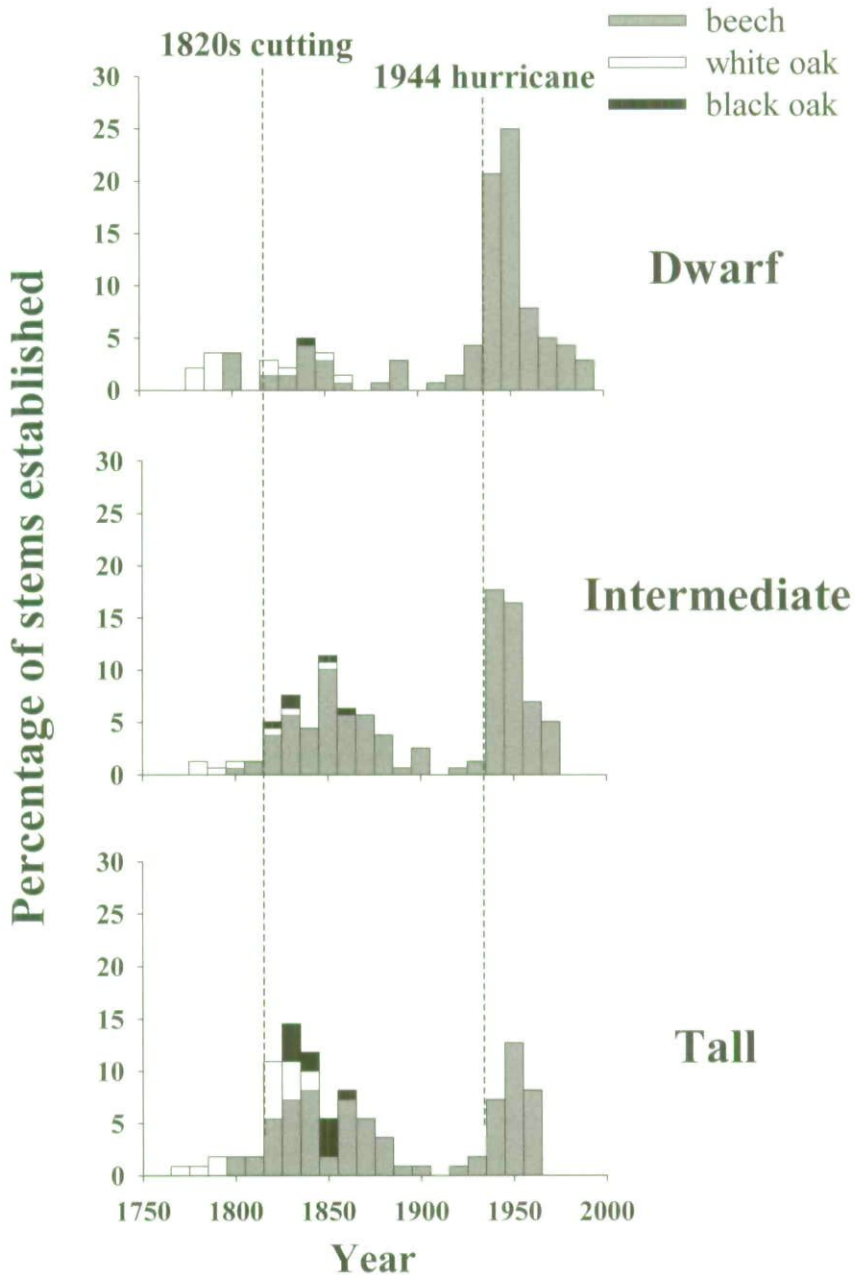
Fig. 3.—Age structure for distinct structural types relative to the 1820s cutting event and the 1944 hurricane. Dwarf sample sizes: beech = 140, white oak = 13, black oak = 1; intermediate sample sizes: beech = 146, white oak = 7, black oak = 5; tall sample sizes: beech = 83, white oak = 16, black oak = 11. Oak trees sampled outside of study plots are not included
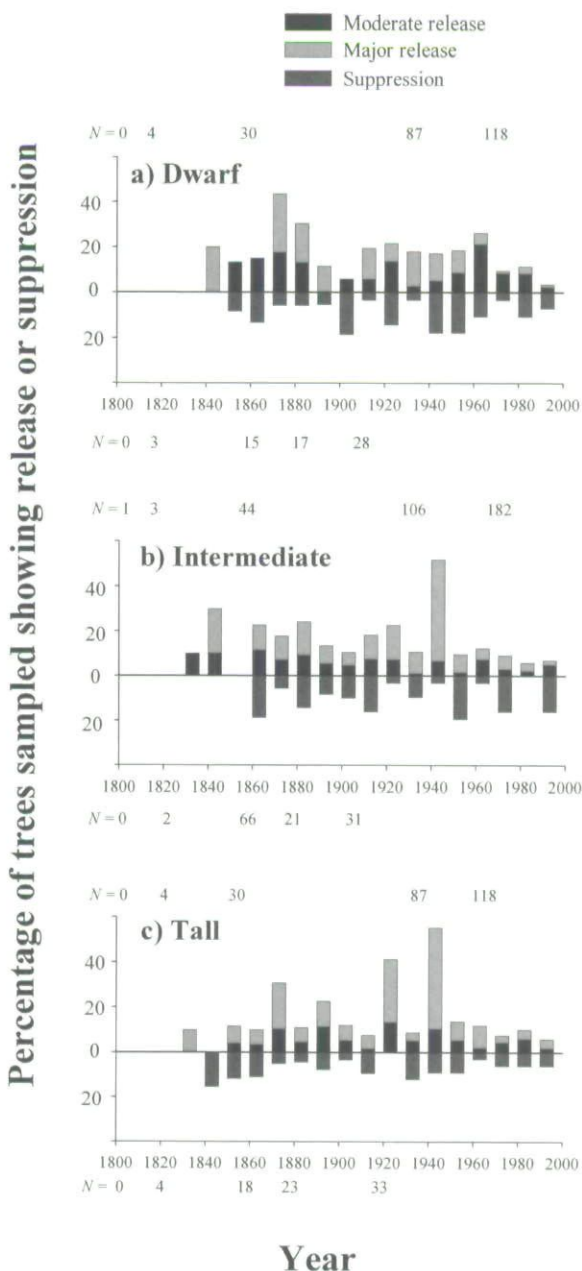
FIG. 4.—Beech disturbance chronologies for distinct structural types. Bars above the x-axis indicate the percentage of released stems; bars below the x-axis represent the percentage of suppressed stems. The sample size of trees used in the release analysis is shown above the panels; the size of the sub-sample used for the suppression analysis is shown below. We report the percentage of stems showing release or suppression only for n > 10

TABLE 2.—Mineral soil properties grouped by structural type. Within a row, values labeled with different letters differed significantly (Turkey post hoc P < 0.05), ANOVA P and F values are also reported

	Dwarf (n = 6)	Intermediate (n = 12)	Tall (n = 6)	P	F
Sand (%)	84.62	73.13	67.32	0.1	2.5
Silt (%)	13.69	22.13	23.53	0.3	1.26
Clay (%)	1.69 (a)	4.74 (a)	9.15 (b)	<0.0001	16.64
Calcium (ppm)	123.6	150.58	132.71	0.79	0.24
Magnesium (ppm)	26.8	35.75	36.29	0.22	1.64
Potassium (ppm)	16.4	25.33	26.57	0.14	2.14
Sodium (ppm)	26.4	28.92	33.29	0.57	0.57
Sulfur (ppm)	24.4	30.08	37.43	0.16	2.03
Total exchange capacity	3.23	4.1	3.51	0.37	1.04
pH	4.22	4.2	4.49	0.13	2.3
Organic matter (%)	1.84 (a)	3.94 (b)	4.12 (b)	0.02	4.7
Phosphorous (ppm)	17 (a)	25.08 (a, b)	28.29 (b)	0.04	3.8
Nitrogen (%)	0.06	0.13	0.12	0.07	3.02
Carbon (%)	1.69	2.77	2.6	0.23	1.56
C:N Ratio	27.75 (a)	21.54 (b)	22.04 (b)	0.003	7.72
Estimated nitrogen release	54.6 (a)	86.3 (b)	89.3 (b)	0.004	7.2

suppression (decadal mean = 8.6%) occurred throughout the study period in all structural types.

SOIL PROPERTIES

Soil texture differed among structural types, with dwarf types characterized by extremely low clay content and tall types characterized by the highest clay content (Table 2). Average sand content was higher in dwarf types (mean = 85%) than tall types (mean = 67%), although this difference was not significant. Significant differences among structural types were detected for organic matter and phosphorous (ppm), with dwarf types characterized by the lowest levels and tall types by the highest levels (Table 2). Dwarf types were also characterized by the highest C:N ratios and the lowest estimated nitrogen release (Table 2). No significant differences among structural types were found for the other variables (Table 2), but dwarf types tended to have the lowest average values.

DISCUSSION

Naushon Island supports approximately 1000 ha of monodominant beech forest, representing what is thought to be the most extensive example of this forest type in eastern North America (Busby et al., 2008b). Beech accounts for >98% of stem density in all structural types, greatly exceeding levels of beech dominance reported from numerous studies across the eastern U.S. (e.g., Braun, 1950; Cogbill, 2005). In addition, both dwarf stands as well as tall-stature forests similar to those found in the study area are extremely uncommon throughout the Northeast. Although beech is an important component of the extensive northern hardwood forests that occur across inland portions of New England and New York, most inland sites have experienced heavy mortality from beech bark disease in recent decades (Twery and Patterson, 1984; Morin et al., 2006). As a result, mature stands containing large, healthy beech comparable to the tall-stature types that are common in our study area are now extremely rare elsewhere in the Northeast (Evans et al., 2005). Although comparable in age structure to nearby tall-stature forests, dwarf types are characterized by

extremely low radial growth rates, low basal area, high stem density and contorted growth forms. Our results suggest that topographically constrained edaphic factors and chronic wind disturbance contribute to the development and persistence of this unusual vegetation structure.

EDAPHIC CONDITIONS CONTRIBUTE TO STUNTED GROWTH IN DWARF BEECH STANDS

Analysis of physical and chemical soil properties confirmed that forest structural variation in the study area corresponds to an edaphic toposequence extending from hill tops to hollow bottoms. Dwarf types consistently occur on knobs and ridges that are characterized by sandy, nutrient-poor soils, with extremely low clay content, whereas tall types occur in hollows characterized by finer-textured soils with greater organic matter content and lower C:N ratios (*i.e.*, richer soils). Intermediate types are characterized by transitional soil conditions. This edaphic gradient presumably results in part from downslope movement of fine-textured soil particles, chronic removal of leaf litter from exposed knobs and ridges, and associated accumulation of organic matter on the lower slopes of hollows.

Coarse soil textures and low organic matter concentrations may limit soil water holding capacity on sites supporting dwarf types, potentially contributing to the stunted beech growth forms. On sites supporting dwarf types, oaks, which are less water-demanding than beech (Tubbs and Houston, 1990), grow larger and taller than dwarf beech trees and contribute a significant portion of the total basal area.

Leaf litter is consistently blown off dwarf types resulting in exposed mineral soils and extensive bryophyte cover (pers. obs.). Chronic removal of litter inputs from these sites presumably results in long-term nutrient depletion (Nadelhoffer *et al.*, 2004), and may contribute to the stunted growth forms and slow growth rates. This mechanism has been documented for a dwarf oak (*Quercus marilandica*) forest (Reich and Hinckley, 1980). In addition, chronic removal of litter in dwarf types may also result in root exposure, potentially increasing the likelihood of root damage and associated sprouting (Jones and Raynal, 1988).

NATURAL AND ANTHROPOGENIC DISTURBANCES VARY ALONG THE FOREST STRUCTURAL AND TOPOGRAPHIC GRADIENT

Chronic wind perturbation to dwarf types may contribute to the unusual stand structure in a variety of ways. Daily maximum wind speeds are greater in coastal than inland areas in MA (Busby, 2006). And an island-wide survey documented >40 occurrences of dwarf types located primarily on northwest to southwest aspects, the direction of predominant winter and summer winds, respectively (Busby, 2006). Wind exposure may cause desiccation, injury and reduced photosynthetic activity in trees (Telewski, 1995), potentially contributing to lower radial growth rates of trees in windward versus leeward sites (Taylor, 1923). Chronic wind perturbation has also been shown to restrict height growth (Telewski and Jaffe, 1986; Holbrook and Putz, 1989; Nzunda *et al.*, 2007), and we observed dieback of beech stems emerging above the "dwarf" canopy. Russell (1953) also noted the influence of chronic wind disturbance in the development and persistence of high elevation "beech gaps" in the southern Appalachian Mountains. In coastal areas, wind-deposited salt spray is an additional stress. Sodium leaching into soils can reduce water absorption and transpiration (Oosting and Billings, 1942; Griffiths *et al.*, 2006) and alter growth forms (Good and Good, 1970). However, we did not find a significant difference in sodium concentration among structural types, suggesting salt spray is not a major factor contributing to dwarf beech growth forms.

We did not find any evidence to suggest that variation in disturbance history contributes to the forest structural gradient. Nonetheless, beech growing in structurally distinct forest

types responded differently to two of the most severe disturbances in the study period, the 1824–1827 cutting event and the 1944 hurricane. Following the cutting event, a major pulse in beech regeneration occurred in tall and intermediate types whereas fewer beech established in dwarf types. Dwarf types may have already supported low stature vegetation at the time, which would have presumably limited cutting on these sites. Alternatively, the minor pulse of establishment at the time of the cutting operation may represent: (1) a response to the removal of only larger trees that occurred on knobs and ridges, or (2) remnants of a once larger cohort of trees that established after the cutting operation (*i.e.*, greater mortality in dwarf sites than intermediate and tall sites since the cutting operation). The extent to which structural patterns were affected by the extensive clear-cut that occurred in the 1820s remains unresolved.

The 1944 hurricane apparently had a strong impact on beech growth and regeneration in all structural types. Abundant establishment occurred following the 1944 hurricane, with nearly half of all trees in dwarf study sites establishing in the period 1940–1960, compared to roughly 1/3 in intermediate sites and 1/4 in tall sites. Lower establishment in tall types may reflect greater survival of beech. However, tip up mounds from the 1944 hurricane are common in both tall and intermediate types, suggesting that trees in tall types were not 'protected' from hurricane winds by topographic position. In fact, the crowns of trees in tall types would presumably be exposed given their average height of 20–30 m. Short trees in dwarf types may be less susceptible to uprooting, although stem die-back or other damage from the 1944 hurricane was apparently sufficient to initiate substantial establishment of new stems, apparently from root sprouts (Jones and Raynal, 1988; Busby, 2006). The lack of abundant growth releases in dwarf types associated with tree establishment may be the result of substantial storm damage (*e.g.*, structural damage to trees or salt spray).

HISTORY AND PERSISTENCE OF DWARF TYPES

The first historical reference to variation in forest structure along a topographic gradient on Naushon Island was provided by a visitor to the island in 1898, who attributed the pattern exclusively to wind:

> "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 shortened than those rooted in the depths. ***All growth was checked at the top of the hollow*** [emphasis added]. 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 have been blown on so from one direction that they all grew leeward" (Kobbe, 1898).

Kobbe's description confirms that similar structural patterns have existed in the study area for at least the past century. This is consistent with the observations of long-time island residents who have noted little change in dwarf stands since at least the 1940s (Gon and Holly Leon, pers. comm.), and with results of our age structure analyses documenting dwarf trees up to 200 y of age. Although we do not know when these structural patterns were first established, if beech trees grew at approximately similar rates in the past, then Kobbe's observation suggests that the 'checked growth' that he observed at the tops of the hollows may have been comprised of dwarf beech that had established by the late 18th to early 19th centuries. The structural patterns we document thus predate the 1944 hurricane, despite significant hurricane effects in all structural types.

Previous studies of a range of dwarf forest communities have similarly concluded that stunted growth forms may result from harsh edaphic conditions, either alone or in combination with chronic or frequent disturbance (Whittaker, 1954; Andresen, 1959; Good and Good, 1975; Westman, 1975; Reich and Hinckley, 1980; Motzkin *et al.*, 2002; Feller *et al.*, 2003). Several additional studies have investigated potential genetic controls on the occurrence of dwarf versus normal-stature trees (Andresen, 1959; Good and Good, 1975; Fang *et al.*, 2006; Foster *et al.*, 2007). For example, Foster *et al.* (2007) demonstrate the potential for local evolution of dwarf ecotypes from nearby tall-stature eucalyptus (*Eucalyptus globulus*) forests, even with only minor spatial separation among populations. No data exist on genetic variation in dwarf versus tall-stature beech forests in our study area. However, the consistent relationship of forest structure to topographic position, exposure, and edaphic conditions strongly suggests that stunted beech in the study area result from environmental rather than genetic factors. All dwarf beech forests on Naushon Island are surrounded by, and contiguous with, normal-stature (intermediate and tall) types, making restrictions on gene flow among structural types unlikely. In contrast, Russell (1953) noted that the short stature (10–15 m) and contorted beech trees characteristic of the high elevation "beech gaps" of the Great Smoky Mountains are isolated from, and may be genetically distinct from, the taller beech found commonly at lower elevations in the southern Appalachian Mountains.

REGIONAL DISTRIBUTION AND VARIATION IN DWARF BEECH FORESTS

Outside of our study area, dwarf beech forests have been reported from only a few sites in the eastern U.S. Stands with stems up to 6 m in height and 40 cm dbh have been reported at elevations >1400 m in the Balsam Mountains of Virginia (Rheinhardt and Ware, 1984), and relatively short-stature beech (10–15 m) occur at comparable elevations in the "beech gaps" of the southern Appalachian Mountains in North Carolina and Tennessee (Russell, 1953; Schafale and Weakley, 1990). Similar dwarf or short stature growth forms also occur occasionally in the mountains of central and northern New England, primarily on exposed sites with shallow soils (*e.g.*, Saddle Ball/Mt. Greylock, MA). In addition, dwarf beech forests occur in several exposed maritime locations (Good and Good, 1970; Edinger *et al.*, 2002; Engelbright *et al.*, 2000).

CONCLUSION

The extensive beech forests of Naushon Island are notable with respect to: (1) the overwhelming dominance of beech; (2) the occurrence of tall-stature stands with little mortality or stem deformation from beech bark disease; (3) dwarf types that are rare throughout the eastern U.S.; and (4) stand dynamics characterized by episodic regeneration in response to severe natural and anthropogenic disturbances, rather than small scale gap dynamics as is typical of beech in northern hardwood forests across much of New England (*e.g.*, Canham, 1990). Dwarf types apparently developed in response to stressful conditions created by dry, nutrient poor soils, chronic wind removal of litter inputs, chronic exposure to salt-laden winds and occasional storms that damage or remove emerging stems. Soil development, tree ring data and historical references suggest that these types have persisted for >100 y, although the longer-term history of these types is unknown. The extent to which growth forms and dynamics described from Naushon Island are comparable to similar sites reported elsewhere in the eastern U.S. warrants further investigation.

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