

Disturbance History and Mortality Patterns in a Rare Atlantic Barrier Island Maritime Holly Forest

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ABSTRACT: We describe the long-term regeneration dynamics of the maritime holly forest, a plant community restricted to two known locations on Atlantic barrier islands: the Sunken Forest, part of Fire Island National Seashore, New York, and the Sandy Hook holly forest, part of Gateway National Recreation Area, New Jersey. In order to assess the short-term changes in vegetation apparent at one location, we examined the long-term dynamics of these two forests. Analysis of permanent plots in the Sunken Forest indicated the overstory structure and composition had changed minimally, but the understory decreased in cover and diversity over a period of 35 years (1967–2002). Patterns differed at Sandy Hook, with little change in the forest understory evident in permanent plots monitored over a period of 14 years (1989–2003). The age distributions indicate that both forests are uneven aged, but the trees at the Sunken Forest are older than those at Sandy Hook. While there has been an overall lack of establishment of any species since the 1970s at the Sunken Forest, several stems were present in the smallest age and size classes within the Sandy Hook holly forest. Release patterns in the tree cores reveal responses to frequent moderate disturbances including hurricanes, tropical storms, and northeasters. No recent changes in the frequency of canopy disturbances were evident in the tree core analysis, but herbivory has likely increased with the dramatically rising *Odocoileus virginianus* population at the Sunken Forest since the 1970s. The maritime holly forest relies on new individuals establishing in openings created by moderate disturbances; the current high level of herbivory at the Sunken Forest is disrupting the long-term regeneration patterns of this critically imperiled maritime holly forest.

Index terms: barrier island vegetation, disturbance history, herbivory, *Ilex opaca*, maritime forest

INTRODUCTION

Barrier island vegetation patterns are influenced by the interactions of environmental stresses and natural disturbances occurring at multiple scales (Ehrenfeld 1990). The plant communities found on barrier islands are highly dynamic combinations of species that withstand stressors ranging from tidal cycles to hurricane events. Daily impacts of salt spray shape the composition and structure of the communities from ocean to bay (Wells and Shunk 1938; Boyce 1954). Overwash events and inlet creation influence the dynamics of plant communities from one end of an island to the other (Clark 1986). Natural disturbances within these coastal areas, such as hurricanes, northeasters, flooding, droughts, and insect infestations, alter the physical structure of plant communities, creating new habitat for colonization by new species and modifying habitat of former occupants (Stalter and Lamont 2000).

Since the early 1900s, anthropogenic influences, such as recreation and development pressures, have placed additional stress on coastal vegetation. The greater New York City metropolitan area, with about 19.6 million inhabitants, has approximately 2400 km of shoreline (Gornitz et al. 2002). Though much of the shoreline has already been developed, a few key ecological resources were protected and now provide

habitat for numerous state and federally endangered species (U.S. Fish and Wildlife Service 1997).

The maritime holly forest is a unique assemblage of species dominated by the broadleaf evergreen, *Ilex opaca*. Due to the highly restricted occurrence of this forest community to only two locations on barrier islands in New York and New Jersey, it has been classified as a critically imperiled community (global conservation status rank of G1; NatureServe 2004). The only two examples known of the maritime holly forest include: (1) the Sunken Forest (16 ha) occurring on Fire Island National Seashore (FINS), a barrier island protecting Long Island, New York; and (2) the Sandy Hook holly forest (30 ha) occurring on a barrier spit on the New Jersey shore that is a unit of Gateway National Recreation Area (GNRA). The *I. opaca* at the Sunken Forest are older, and appear stunted and gnarled (~6 m tall) while those at Sandy Hook are larger in diameter and height (Stalter 1979). Earlier studies of both locations indicate that the holly forest at FINS is in an old-growth condition, while that at GNRA is an example of a mature stage of development (Art 1976; Stalter 1979).

The Sunken Forest was donated by a private organization to the National Park Service (NPS) with the restriction that the forest was to be kept in its natural

state as an example of the forest primeval. Observations over several decades in the Sunken Forest indicate that the understory vegetation is decreasing in abundance and diversity despite moderate increases in light availability due to less dense *Smilax* vines enclosing the canopy trees (H.W. Art, pers. observation). Changes also were observed with the sapling and shrub layer, and a noticeable browse line attributed to *Odocoileus virginianus* had developed by the mid 1980s (O'Connell et al. 1989). Plant species diversity often declines in late successional communities in the temperate zone unless local disturbances occur frequently enough to maintain diversity (Loucks 1970; Peet 1978). In order to assess the short-term changes that appear to be occurring in the understory of the Sunken Forest, an understanding of the long-term regeneration processes and successional patterns of the maritime holly forest has become essential.

The conservation of this rare community requires a thorough understanding of both the spatial and temporal dynamics of the ecological community. Historical studies provide critical information for interpreting current conditions of an ecosystem (Foster 2000). Focusing solely on modern vegetation dynamics may be misleading when developing conservation and management objectives for communities dominated by long-lived tree species (Motzkin et al. 1993). The long-term variation in forest dynamics and history can be obtained through investigations at a variety of temporal scales using an integration of dendroecological techniques, age structure, and landuse history (Foster 1988; Abrams et al. 1999). We examined several questions: (1) Do temporal trends in forest structure and diversity indicate that both locations are on similar successional trajectories?; (2) How do canopy individuals establish within this forest type?; (3) Are major disturbances more common than minor disturbances within these forests?; and (4) Does the spatial pattern of tree mortality reflect the influence of a primary mortality agent?

This research is important because only two maritime holly forests are known to remain in North America. An understanding of the disturbance regime of these forests

increases the chances of their effective management and conservation.

METHODS

Study Area

Fire Island (FI) is part of an Atlantic barrier island chain, separated from Long Island, New York, by the Great South Bay. The National Park Service has managed sections (collectively, FINS) of the island interspersed between 18 private communities since 1964. The Island extends 51 km eastward from Fire Island Inlet to Moriches Inlet. Tides range from 1.3 m at FI Inlet to 1.0 m at Moriches Inlet (Leatherman 1985). Both longshore and on-off shore currents continue to modify the present FI shoreline. Longshore currents are responsible for the westward extension of FI Inlet that is estimated to occur at 66 m yr⁻¹ and net littoral drift of 366,400 m³ yr⁻¹ (U.S. Army Corps of Engineers 1960). The Great South Bay ranges in depth from 1.2–3.0 m, with a tidal range generally less than 0.3 m (Leatherman 1985). Prevailing winds are from the south and west, except during the winter months when they are from the north. The topographic profile of the island at the location of the Sunken Forest includes: a flat beach extending from the ocean to the primary dune (7 m ht), an interdune swale, a secondary dune (9 m ht) with a leeward maritime forest, and a salt marsh along the bay shore (Art 1976).

Sandy Hook is the northern peninsula of the Atlantic barrier island chain, spanning the shoreline of New Jersey. Raritan Bay borders the western edge of the barrier spit. The 10 km barrier beach peninsula has been protected by the United States Government since 1893, and prior to this date was operated by the War Department. The majority of the island is now managed by the NPS as a unit of the GNRA, though the northernmost portion remains U.S. Coast Guard property. GNRA was established in 1972 and includes recreational beaches on Sandy Hook, New Jersey, Staten Island and Breezy Point, New York, and wetlands of Jamaica Bay Wildlife Refuge. The annual net northward littoral drift at Sandy Hook is 376,300 m³ yr⁻¹ (Yasso and Hartman 1976).

The Sandy Hook spit accreted landward prior to 1900, eroded severely from 1900–1953, and has since stabilized.

The Atlantic Ocean and either the Great South Bay or Raritan Bay have a pronounced effect on the climate of the region. Annual precipitation is 117 cm and mean temperature is 10.7 °C. The first damaging frost occurs in late October to early November and the chance of frost extends through April. Winters are relatively mild, characterized by temperatures typically above freezing and mean snowfall of 74 cm over the past 50 years. Coastal low-pressure systems (northeasters) are the primary source of snow in the region, typically occurring during the months of December through March. Extended periods of bare ground (no snow) are common (NOAA 2004). Average absolute sea-level rise for eastern North America is approximately 1.3 mm yr⁻¹, though at Sandy Hook, New Jersey, it has been estimated to be 3.85 mm yr⁻¹ (Gornitz et al. 2002).

Long-term Vegetation Plots

Sunken Forest

In 1967, the locations of thirty-four permanent plots (10 m x 10 m) were randomly selected from a sampling grid overlaid on an aerial photograph of the forest (Art 1976). Woody individuals 3.0 cm diameter at breast height (dbh) were recorded by species from the entire plot, basal diameter of shrubs >1 m tall and <3.0 cm dbh were recorded within a 5 m x 5 m subplot, and the percent cover of all vascular plants <1 m tall was recorded to the nearest 1 percent within four, 1 m² subplots located at the corners of the 100 m² plot. *Smilax* density, not cover, was recorded within subplots (Art 1976). In 1985–1986, permanent plots were re-sampled following the same guidelines. During construction of a boardwalk, three plots were destroyed, two plots could not be found, and one plot was eroded. Only results from the 28 plots that were resampled in 1986 are presented here. By 2002, five additional plots were completely inundated and were not resampled. Following the sampling in 1986, three of the permanent plots were

fenced for a deer herbivory study, leaving the sample size of unaltered permanent plots to be 20 in 2002.

In 2002, 39 points were established at 40 m intervals along E-W transects (spaced 50 m apart N-S) established throughout the interior of the forest. At each point, four to five trees were cored with an increment borer as close to ground level as possible. Coring location was determined individually to avoid root flare and to maximize the number of rings obtained. Trees were selected to provide a range of species, size, and canopy classes. Trees cored ranged from 3.9-45.0 cm dbh.

Sandy Hook

In 1989, 20 permanent plots were randomly selected following procedures described for the Sunken Forest (SF) site. Eighteen plots were re-sampled in 2003. At each of the plots, two to three *I. opaca* were selected to be cored so that a range of sizes were represented (0.9 cm-50 cm dbh).

Analyses

Long-term Vegetation Plots

Paired t-tests and signed rank tests were performed on differences in basal area, density, and cover between sampling periods at each location. A relative importance value was calculated for each species by averaging relative basal area and relative density from all plots. Tree mortality rates (% yr⁻¹) were calculated as exponential decays following Runkle (1990) and Sheil et al. (1995):

$$\text{Mortality rate} = [1 - (S/N_o)^{(1/ny)}] * 100\%$$

where *S* represents the number of survivors, *N_o* is the original number of stems and *ny* indicates the number of years between samplings. The number of recruits in each sampling period included individuals that were <10 cm dbh at the first sampling interval and grew to be >10 cm dbh by the time of resampling. Analyses were performed using SAS version 9.0 (SAS Institute Inc.,

Cary, NC). Species richness and diversity indices (Shannon and Simpson's indices) were calculated using PC-ORD version 4.0 (MjM Software Design, Gleneden Beach, OR). Nomenclature follows Gleason and Cronquist (1991).

Tree Cores

Increment cores were air dried, mounted, sanded, and aged with a dissecting scope (Stokes and Smiley 1968; Phipps 1985). Tree age was estimated based on the curvature of the innermost rings for increment cores that missed the pith of the tree (Applequist 1958). Age distributions are based on 247 cores from the Sunken Forest and 52 cores from Sandy Hook. Intact cores of the dominant species at each site were selected for further analysis. Annual ring widths were measured to the nearest 0.01 mm using a Henson-Zahn Measurement System.

The disturbance chronology for each area was constructed by using the boundary-line technique recently proposed by Black and Abrams (2003). This method more precisely defines releases by scaling each release by its maximum physiological potential, based on the prior growth rate of an individual. Boundary lines were determined for *I. opaca* based on cores from both study sites (*n*=92 from SF and 52 from SH). Percent growth change per increment was calculated following Nowacki and Abrams (1997) as:

$$(M_2 - M_1)/M_1$$

where *M₁* is the mean growth over the prior 10 years and *M₂* is the mean growth over the subsequent 10 years. The percent growth change and mean prior growth of preceding 10 years were plotted for each increment of every series. The top 10% growth change values per 0.5 mm segment were averaged; a line fit to these averaged values formed the boundary line. Potential release events were identified for each tree, as events where the percent growth change was 10% for 10 years. To determine if these events were major or moderate releases, the events were plotted with the boundary line that represents the maximum

release and lines representing fractions of that maximum. Moderate releases were defined by release events that occurred above 20% of the value of the boundary line. Major releases occurred above 50% of the value of the boundary line.

Spatial Information

The locations of permanent plots and cored trees were recorded at the study sites using a handheld GPS (Garmin Venture). Locations were transferred to display in a GIS (Geographic Information System; ArcView version 3.3, ESRI). The distance (meters) between every permanent plot and cored tree from the bay was calculated using the Nearest Feature extension in ArcView. To test if mortality rates differed with distance from the ocean, plots were divided into three groups depending on their distances from the bay: *bay* plots were < 75 m of bay; *middle* plots were within 75-125 m of the bay; and *ocean* plots were > 125 m from the bay. An ANOVA and Tukey pairwise comparison test was performed to test if mean mortality rates differed by location. Cored trees were placed in the same distance-defined groupings and a separate ANOVA tested if tree age differed with distance from the ocean.

RESULTS

Temporal Trends

Sunken Forest

In the Sunken Forest, the relative importance of the most shade-tolerant species, *I. opaca*, has increased (Table 1) within the canopy due to significant increases in basal area (from 1967-1986: *t* = 3.54, *P* = 0.0015 and from 1986-2002: *t* = 3.55, *P* = 0.0021). The importance of *A. canadensis* in the canopy has declined, due to a significant decrease in stem density from 1986 to 2002 (*t* = -2.86, *P* = 0.0099). *Sassafras albidum* and *Nyssa sylvatica* maintained their relative importance within the canopy due to increasing basal areas despite decreasing densities.

Significant change occurred in the overall shrub and sapling layer in the earliest

Table 1. Tree, sapling and shrub composition at the Sunken Forest, an old-growth maritime holly forest on Fire Island National Seashore, NY. Arrows indicate statistically significant increases or decreases from the prior sampling period (based on paired t-tests and signed rank tests between consecutive years, $\alpha=0.05$). Values are means $\pm$ standard errors.

Size class	Species	BASAL AREA ($m^2 ha^{-1}$)		DENSITY (Stems ha^{-1})		IV (%)	
		1967	1986	2002	1967	1986	2002
>3 cm dbh	<i>Ilex opaca</i>	7.6 $\pm$ 1.4	9.6 $\pm$ 1.9	14.4 $\pm$ 2.9	618 $\pm$ 130	571 $\pm$ 111	605 $\pm$ 114
	<i>Amelanchier canadensis</i>	4.9 $\pm$ 0.9	5.8 $\pm$ 0.9	5.7 $\pm$ 1.2	946 $\pm$ 140	961 $\pm$ 183	750 $\pm$ 192
	<i>Sassafras albidum</i>	5.4 $\pm$ 1.1	6.5 $\pm$ 1.3	8.9 $\pm$ 1.9	314 $\pm$ 42	343 $\pm$ 67	280 $\pm$ 77
	<i>Nyssa sylvatica</i>	1.7 $\pm$ 0.8	1.8 $\pm$ 0.9	2.4 $\pm$ 1.5	93 $\pm$ 35	93 $\pm$ 36	85 $\pm$ 45
	Total*	21.3	25.5	33.5	2107	2186	1775
<3 cm dbh		± 2.1	± 2.5	± 2.9	± 200	± 213	± 202
	<i>Vaccinium corymbosum</i>	1.6 $\pm$ 0.5	1.0 $\pm$ 0.3	1.1 $\pm$ 0.4	2357 $\pm$ 629	1943 $\pm$ 247	2260 $\pm$ 881
	<i>Baccharis halimifolia</i>	0.2 $\pm$ 0.2	0.6 $\pm$ 0.6	0.3 $\pm$ 0.3	57 $\pm$ 57	229 $\pm$ 229	2020 $\pm$ 2020
	<i>Amelanchier canadensis</i>	0.9 $\pm$ 0.4	0.3 $\pm$ 0.1	0.1 $\pm$ 0.1	1000 $\pm$ 463	229 $\pm$ 86	160 $\pm$ 160
	<i>Gaylussacia baccata</i>	0.1 $\pm$ 0	0.1 $\pm$ 0	0	743 $\pm$ 342	171 $\pm$ 110	240 $\pm$ 175
	<i>Aronia arbutifolia</i>	0.5 $\pm$ 0.2	0.2 $\pm$ 0.1	0	1086 $\pm$ 530	200 $\pm$ 136	20 $\pm$ 20
	<i>Toxicodendron radicans</i>	0.1 $\pm$ 0	0	0	1214 $\pm$ 439	171 $\pm$ 71	0
	Total**	4.0	2.4	1.5	8586	12157	4980
		± 1.2	± 0.7	± 0.5	± 2088	± 554	± 2119

*Total includes: *Quercus velutina*, *Pinus rigida*, *Aronia arbutifolia*, *Prunus serotina*, *Acer rubrum*, *Rhus copallinum*, *Quercus stellata*, and *Q. coccinea* (all <5% relative importance) in 1967; only the first 6 species listed previously in 1986; and only first 4 species in 2002.

**Total includes: *Ilex glabra*, *I. opaca*, *Myrica pensylvanica*, *Nyssa sylvatica*, *Parthenocissus quinquefolia*, *Prunus serotina*, *Rhododendron viscosum*, *Rhus copallinum*, *Rosa carolina*, *Rubus allegheniensis*, *Sambucus canadensis*, *Sassafras albidum*, and *Vitis* sp.

sampling period with both density ($t = -3.45$, $P = 0.0019$) and basal area ($t = -2.06$, $P = 0.0497$) decreasing from 1967 to 1986. The decline in stem density is due to significant decreases in *Vaccinium corymbosum*, *Gaylussacia baccata*, and *Toxicodendron radicans* ($P = 0.0216$, 0.0344 , and 0.0080 , respectively). The composition of the woody understory became increasingly simplified; by 2002, two species (rather than seven in 1967) accounted for almost 90% of the stems.

The cover of the ground-layer vegetation decreased significantly from 43% to 16% from 1967 to 1986 ($t = -5.92$, $P < 0.0001$). By 2002, the mean cover was 8%, though the change from the earlier sampling period was not statistically significant ($t = -1.35$, $P = 0.1925$). Species that were common to the ground-layer flora of the forest in 1967 became more rare by 1986 and 2002, such as: *Aralia nudicaulis*, *Parthenocissus quinquefolia*, *T. radicans*, *Smilacina stellata*, and *Maianthemum canadense* ($P = 0.0101$, <0.0001 , <0.0001 , 0.0317 , 0.0915 , respectively). Few species increased in cover over the study period (Table 2). *Smilax* density significantly increased from 1967 to 1986 ($t = 3.15$, $P = 0.0040$). Species richness of the ground-layer flora gradually changed, with a significant decrease in mean plot richness from 1986 to 2002 ($t = -3.75$, $P = 0.0014$). Statistically significant decreases in species evenness ($P = 0.0011$) and diversity ($P = 0.0002$ and 0.0004 for Shannon and Simpson indices, respectively) occurred from 1986 to 2002. Moderate shifts in the composition occurred as more hydric species (e.g., *Phragmites communis*, *Baccharis halimifolia*) appeared in several of the plots and mesic species decreased (with the exception of *Smilax*).

Table 2. Summary of cover (mean $\pm$ standard error) and diversity of seedlings and herbs $> 0.5\%$ cover in the Sunken Forest, FINS, NY and Sandy Hook, GNRA, NJ. Arrows indicate statistically significant changes from the prior sampling period (based on paired t-tests and signed rank tests, $\alpha=0.05$).

		Sunken Forest			Sandy Hook	
		1967	1986	2002	1989	2003
		cover	cover	cover	cover	cover
Total*		42.6 $\pm$ 3.5	↓16.4 $\pm$ 3.5	8.1 $\pm$ 1.9	17.7 $\pm$ 3.3	↑28.5 $\pm$ 7.6
Herbs	<i>Aralia nudicaulis</i>	6.3 $\pm$ 2.3	↓0.1 $\pm$ 0.1	-	-	-
	<i>Smilacina stellata</i>	1.3 $\pm$ 0.6	↓-	-	10.6 $\pm$ 3.1	↓3.2 $\pm$ 0.8
	<i>Maianthemum canadense</i>	1.2 $\pm$ 0.7	↓0.1 $\pm$ 0.1	-	-	-
	<i>Pteridium aquilinum</i>	1.1 $\pm$ 0.4	↓-	-	-	-
	<i>Solidago sempervirens</i>	0.2 $\pm$ 0.1	0.3 $\pm$ 0.2	-	0.3 $\pm$ 0.3	1.1 $\pm$ 1.1
Seedlings/Vines	<i>Toxicodendron radicans</i>	9.8 $\pm$ 2.0	↓1.0 $\pm$ 0.3	↓0.3 $\pm$ 0.1	2.4 $\pm$ 0.9	8.5 $\pm$ 5.2
	<i>Gaylussacia baccata</i>	5.2 $\pm$ 1.8	3.7 $\pm$ 1.4	2.8 $\pm$ 1.4	-	-
	<i>Parthenocissus quinquefolia</i>	3.7 $\pm$ 0.6	↓0.5 $\pm$ 0.2	0.4 $\pm$ 0.1	1.1 $\pm$ 0.3	3.4 $\pm$ 1.9
	<i>Vaccinium corymbosum</i>	2.9 $\pm$ 1.2	↓0.1 $\pm$ 0.1	0.2 $\pm$ 0.2	-	-
	<i>Ilex glabra</i>	1.5 $\pm$ 1.0	0.1 $\pm$ 0.1	-	-	-
	<i>Rhus copallinum</i>	1.5 $\pm$ 1.0	↓0.2 $\pm$ 0.1	-	< 0.1	0.2 $\pm$ 0.1
	<i>Sassafras albidum</i>	1.4 $\pm$ 0.3	2.1 $\pm$ 0.6	↓0.4 $\pm$ 0.1	-	< 0.1
	<i>Prunus serotina</i>	0.1 $\pm$ 0.1	↑0.6 $\pm$ 0.2	1.4 $\pm$ 0.4	0.9 $\pm$ 0.5	1.9 $\pm$ 0.8
	<i>Ilex opaca</i>	-	↑0.2 $\pm$ 0.1	< 0.1	-	↑4.6 $\pm$ 1.9
	<i>Lonicera japonica</i>	-	-	-	1.6 $\pm$ 0.6	4.4 $\pm$ 1.7
Density (stems m ⁻²)	<i>Smilax rotundifolia</i>	2.8 $\pm$ 0.5	↑5.2 $\pm$ 0.0	6.8 $\pm$ 0.9	1.4 $\pm$ 1.4	↑12.4 $\pm$ 4.9
	<i>Smilax glauca</i>	0.3 $\pm$ 0.1	0.6 $\pm$ 0.1	-	< 0.1	0.3 $\pm$ 0.2
Richness	S	9.5 $\pm$ 0.4	10.3 $\pm$ 0.5	↓8.6 $\pm$ 0.7	4.9 $\pm$ 0.5	↑6.7 $\pm$ 0.4
Evenness	E	0.7 $\pm$ 0.0	↓0.6 $\pm$ 0.0	↓0.5 $\pm$ 0.0	0.5 $\pm$ 0.0	0.7 $\pm$ 0.0
Diversity	H (Shannon)	1.6 $\pm$ 0.1	1.4 $\pm$ 0.1	↓1.0 $\pm$ 0.1	0.8 $\pm$ 0.1	↑1.2 $\pm$ 0.1
	D (Simpson)	0.7 $\pm$ 0.0	0.6 $\pm$ 0.0	↓0.5 $\pm$ 0.1	0.4 $\pm$ 0.0	↑0.6 $\pm$ 0.0

*Total is the sum cover of herbs, vines and seedlings, but does not include *Smilax* spp.

Sandy Hook

The dominance of *I. opaca* increased within the Sandy Hook holly forest (Table 3; $t = 4.47$, $P = 0.0003$) due to a significant increase in basal area ($t = 6.21$, $P < 0.0001$). The importance of *Prunus serotina*, the next most abundant tree species, declined ($t = -3.47$, $P = 0.0029$) due to a significant change in density from 1989 to 2003 ($t = -3.19$, $P = 0.0054$).

Prunus serotina saplings and *T. radicans*

dominated the woody understory in 1989, accounting for 70% of the stems (Table 3). By 2003, *I. opaca* saplings significantly increased in diameter ($t = 3.44$, $P = 0.0031$) and number ($t = 3.31$, $P = 0.0042$), becoming the most important understory species (47% IV). Concurrently the density of *P. serotina* stems fell significantly ($t = -2.13$, $P = 0.0478$). Many of the large *T. radicans* stems died, but numerous new stems and vines established, resulting in no statistically significant change from 1989 to 2003 ($t = 1.26$, $P = 0.2248$).

Cover of the ground-layer vegetation increased significantly ($t = 3.16$, $P = 0.0057$), primarily due to an increase in woody species. *Smilacina stellata* was the most abundant species within the understory in 1989, but declined in cover by 2003 ($t = -2.61$, $P = 0.0184$). In 2003, woody species (*Toxicodendron radicans*, *I. opaca*, *Lonicera japonica*, and *P. quinquefolia*) were the most abundant. *Smilax rotundifolia* density increased from 1989 to 2003 ($t = 2.63$, $P = 0.0177$). Species

Table 3. Basal area, density and relative importance of trees, saplings, and shrubs at the mature Sandy Hook maritime holly forest, Gateway National Recreation Area, NJ. Arrows indicate statistically significant changes from the prior sampling period (based on paired t-tests and signed rank tests, $\alpha=0.05$).

Size class	Species	BASAL AREA ($\text{m}^2 \text{ha}^{-1}$)		DENSITY (stems ha^{-1})		IV (%)	
		1989	2003	1989	2003	1989	2003
≥ 3 cm dbh	<i>Ilex opaca</i>	21.5 $\pm$ 2.0	$\uparrow$ 26.3 $\pm$ 2.5	850 $\pm$ 120	822 $\pm$ 96	72	$\uparrow$ 82
	<i>Prunus serotina</i>	4.1 $\pm$ 0.9	3.7 $\pm$ 1.0	289 $\pm$ 74	$\downarrow$ 128 $\pm$ 33	19	$\downarrow$ 12
	All species*	27.3 $\pm$ 2.1	$\uparrow$ 31.3 $\pm$ 2.8	1294 $\pm$ 135	$\downarrow$ 1022 $\pm$ 98		
<3 cm dbh	<i>Ilex opaca</i>	0.06 $\pm$ 0.04	$\uparrow$ 0.16 $\pm$ 0.03	78 $\pm$ 44	$\uparrow$ 222 $\pm$ 57	15	$\uparrow$ 47
	<i>Prunus serotina</i>	0.14 $\pm$ 0.04	0.07 $\pm$ 0.04	261 $\pm$ 100	$\downarrow$ 156 $\pm$ 83	41	$\downarrow$ 19
	<i>Toxicodendron radicans</i>	0.11 $\pm$ 0.06	0.03 $\pm$ 0.02	139 $\pm$ 84	256 $\pm$ 166	30	18
	<i>Rubus allegheniensis</i>	0	0	0	183 $\pm$ 183	0	11
	<i>Baccharis halimifolia</i>	0.03 $\pm$ 0.03	0.02 $\pm$ 0.02	39 $\pm$ 39	11 $\pm$ 11	5	7
	All species**	0.35 $\pm$ 0.1	0.28 $\pm$ 0.1	561 $\pm$ 155	850 $\pm$ 272		

*Includes *Celtis occidentalis*, *Amelanchier canadensis*, *Juniperus virginiana*, and *Rhus copallinum* (all <5% relative importance).

**Includes: *Rosa multiflora*, *Rhus copallinum*, *R. typhina*, *Amelanchier canadensis*, *Myrica pensylvanica*, *Prunus maritima*, and *Vaccinium corymbosum* (all <5% relative importance).

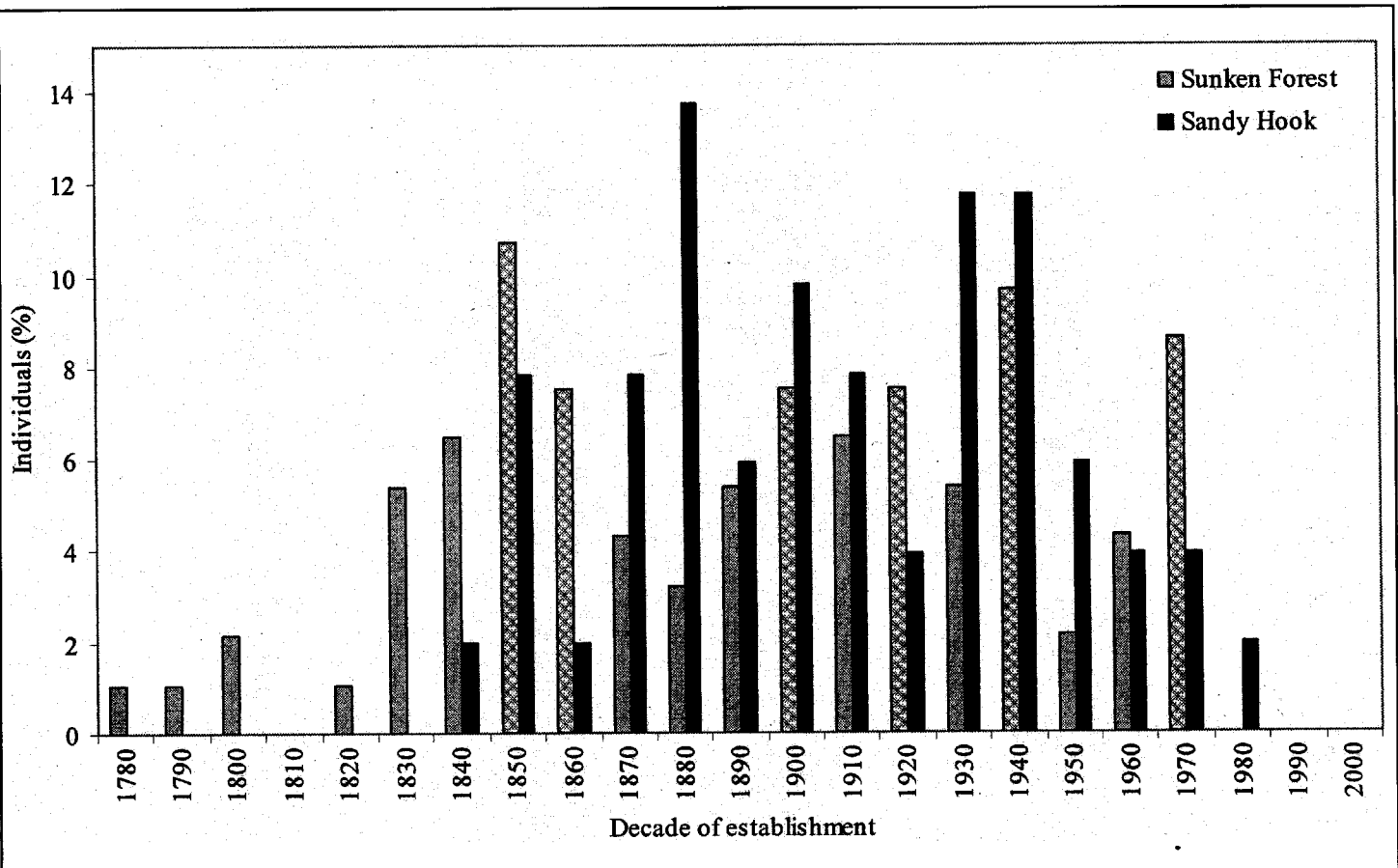


Figure 1. Age class distributions for *Ilex opaca* at the Sunken Forest, FINS, NY (n=93) and Sandy Hook, GNRA, NJ (n=51).

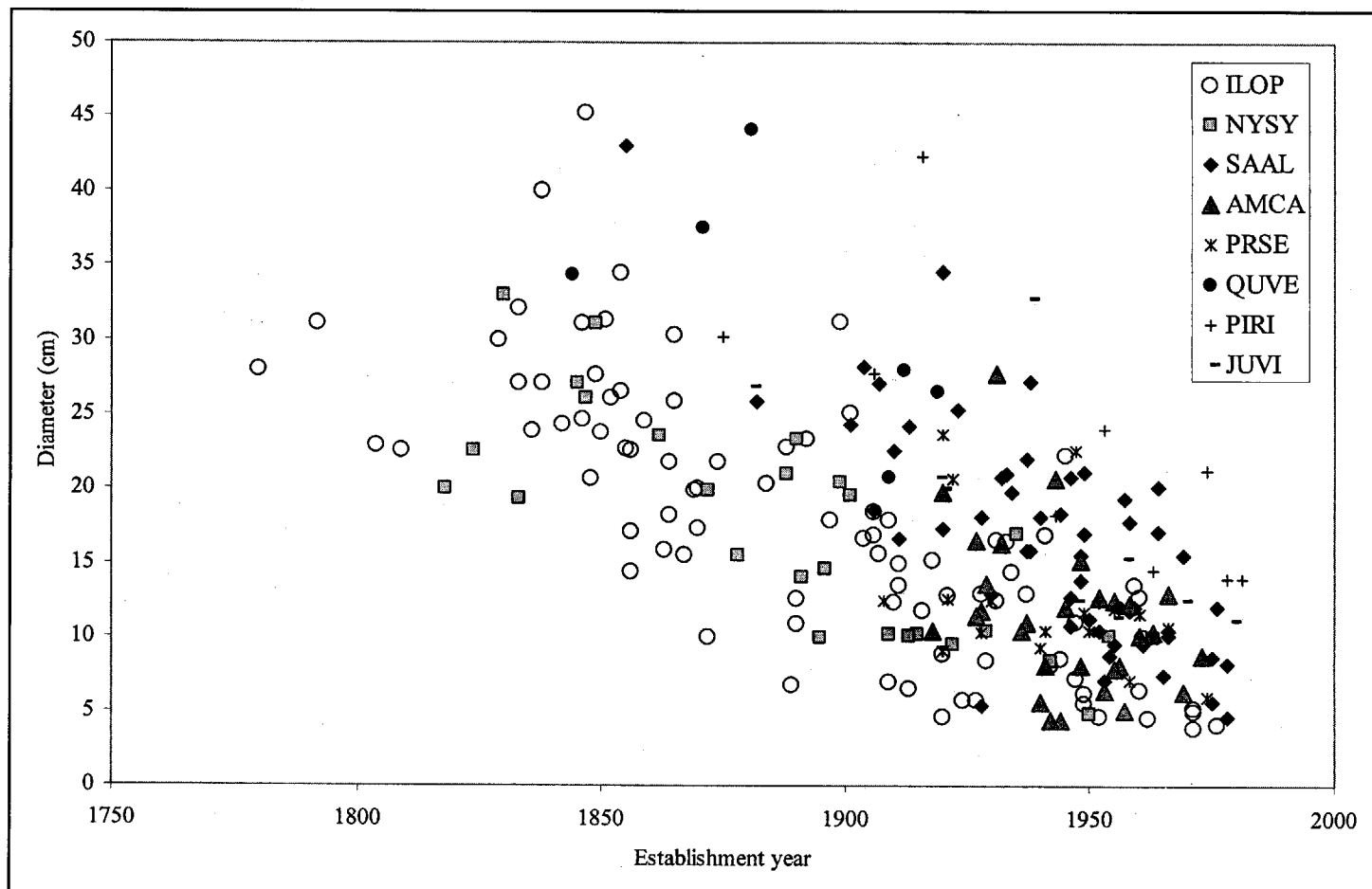


Figure 2. Age-diameter relationships for all trees cored at Sunken Forest, Fire Island National Seashore, NY. Individuals are coded by the first two letters of the genus and species.

richness and diversity of the ground-layer flora increased significantly from 1989 to 2003 ($P = 0.0004$, 0.0118 , and 0.0274 for richness, Shannon and Simpson indices, respectively).

Establishment and Age Distributions

Both Sunken Forest and Sandy Hook are uneven-aged forests (Figure 1). In the Sunken Forest, *I. opaca* ranges from 26 to 220 years old with nearly continuous recruitment since the 1800s. Low, but steady recruitment of *N. sylvatica* has occurred from the 1820s to 1960s (Figure 2). *Quercus* spp. have established sporadically, with peak recruitment of *Q. stellata* in the 1880s and *Q. velutina* in 1910s. *Sassafras albidum* and *A. canadensis* ranged in age from 24–146 and 29–83, respectively, with peak recruitment occurring for both in 1940s through 1960s.

Ilex opaca within the Sandy Hook holly forest ranged in age from 15 to 162 years old. Recruitment was nearly continuous in this forest as within the Sunken Forest, with peaks in the 1880s, 1930s, and 1940s. Though the minimum age of the cored individuals was 15 years of age, numerous new *I. opaca* recruits established within the permanent plots at Sandy Hook.

Disturbance History

A negative exponential function fit the cores examined for growth releases. The fitted boundary line for *I. opaca* was

$$y = 1166.5e^{-1.7927x}$$

with an R^2 of 0.9912.

Radial growth analysis indicated that releases occurred frequently at both locations. Approximately 10% of the cored *I.*

opaca trees exhibited moderate releases in nearly every decade of record at the Sunken Forest (Figure 3). Moderate releases were even more frequent at Sandy Hook, with a minimum of 20% of the trees released per decade. Despite shorter records, *S. albidum* and *A. canadensis* chronologies exhibit a higher percentage of released trees than the *I. opaca* within the Sunken Forest (not shown). Although relatively few major releases occurred at the Sunken Forest, major releases were present in 5–20% of the Sandy Hook *I. opaca* nearly every decade after 1890.

Patterns of Tree Age and Mortality

The overall mortality rate of all canopy trees (stems >10 cm dbh) was higher at the Sunken Forest during the period of 1967–1985 than from 1986–2002, $1.9\% \text{ year}^{-1}$ vs. $1.2\% \text{ year}^{-1}$. Overall mortality at Sandy Hook was $0.9\% \text{ year}^{-1}$. *Ilex opaca* had the

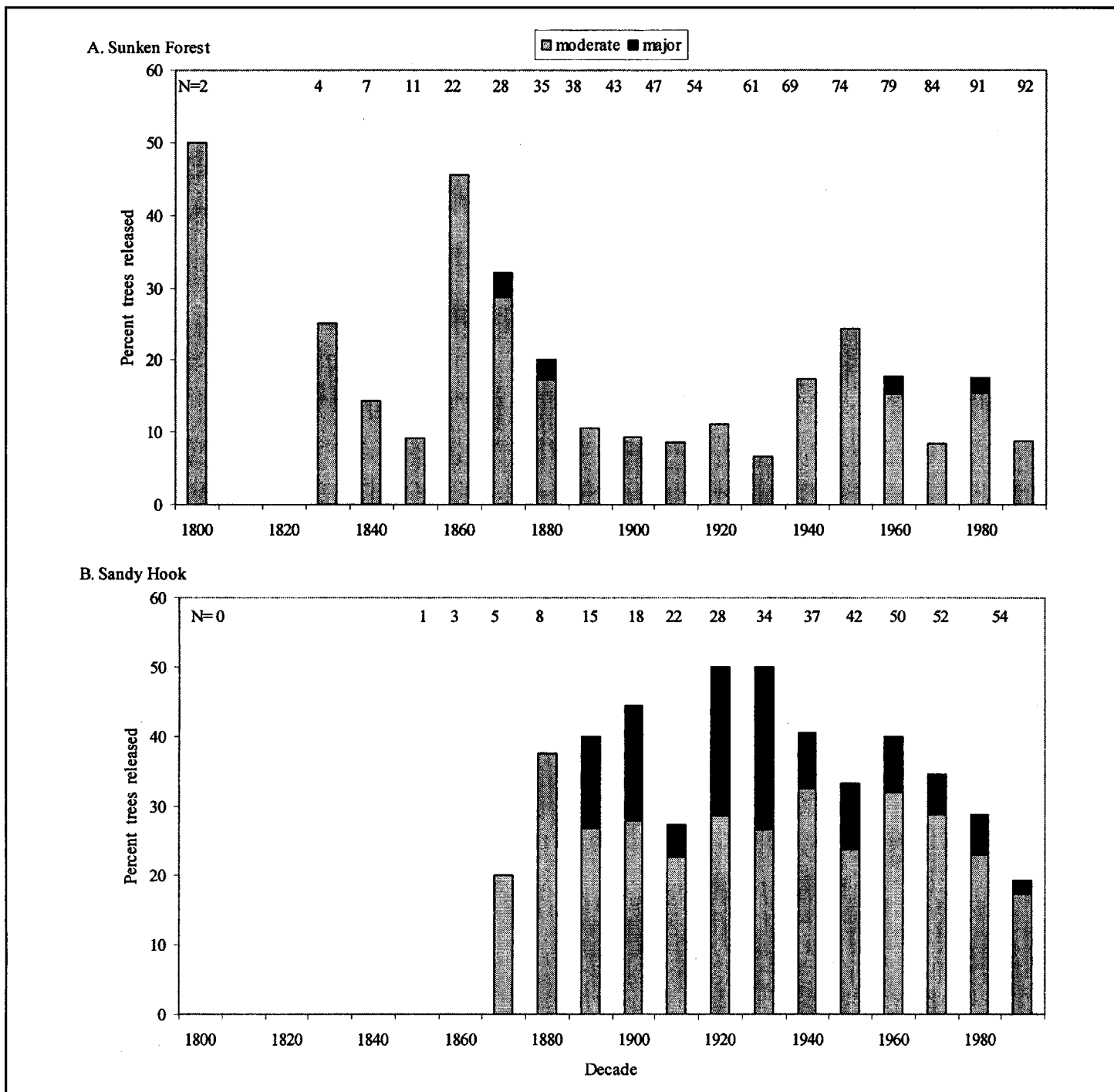


Figure 3. *Ilex opaca* releases in Sunken Forest (A) and Sandy Hook (B), two maritime holly forests. Major releases occurred between 50-100% of the value of the boundary line and moderate releases were between 20-49.9%.

lowest mortality rates relative to the other species present at both sites (Table 4). *Ilex opaca* mortality at the Sunken Forest was 0.8% yr⁻¹ from 1967-1985 and 0.3% yr⁻¹ from 1986-2002. *Sassafras albidum* and *A. canadensis* mortality rates also declined during the later sampling period, though the rates were higher in both periods for

these less shade-tolerant species.

At Sandy Hook, *I. opaca* mortality is infrequent, occurring less than 0.1% yr⁻¹. However, *P. serotina*, *C. occidentalis* and *A. canadensis* mortality is much higher (3.9, 2.4, and 4.8% yr⁻¹, respectively) than *I. opaca*.

Tree mortality within the Sunken Forest was significantly higher on the bayside plots than in plots located within the forest interior or nearest the ocean (Table 5). Several plots nearest the bay were inundated and suffered complete tree mortality; however other plots at similar

Table 4. Mortality and recruitment of canopy trees (>10 cm dbh) at two maritime holly forests.

Site	Species	N ₀ [*]	Mortality (% yr ⁻¹)	Recruits (#/ha-yr ⁻¹)	N ₀ [*]	Mortality (% yr ⁻¹)	Recruits (#/ha-yr ⁻¹)
Sunken Forest		1967-1985			1986-2002		
	<i>Ilex opaca</i>	100	0.9	4.3	103	0.3	3.5
	<i>Sassafras albidum</i>	49	2.9	5.6	55	2	3.3
	<i>Amelanchier canadensis</i>	52	3.2	5.1	51	2.5	4.1
Sandy Hook		1989-2003					
	<i>Ilex opaca</i>	95	0.1	3.6			
	<i>Prunus serotina</i>	26	3.9	4			

*N₀ is the number of living stems at time of initial measurement.

elevations, slope, and locations had very low mortality (Figure 4). The oldest tree (*I. opaca*, 220 years old) cored occurred on the secondary dune in a fairly exposed location. Otherwise, the older trees appeared to occur in a band towards the center of the island where the mean age was significantly higher than the mean age of trees nearest the ocean.

DISCUSSION

Vegetation Changes

Rank abundance plots graphically illustrate the differences in species richness and evenness between years and sites. The relative species abundances differ in the two holly forests though the trends in richness and evenness are converging (Figure 5). Clearly, richness has decreased over time at the Sunken Forest, while increasing at

Sandy Hook. The sharpening slopes of the curves for both sites indicate that the importance of the dominant species is increasing. The species richness of shrubs, saplings, seedlings, and the herbaceous layer was lower at Sandy Hook than the Sunken Forest at the time of original survey (1967). In naturalist notes dating back to 1930s, the Sunken Forest herbaceous layer was more diverse with notes of "soft carpets of ferns, wild sarsaparilla, and Canada mayflower" (Murphy 1933). However, the understory at Sandy Hook has become more diverse with several species in common with the Sunken Forest, and a few unique to the site, including *Opuntia humifusa* and *Mitchella repens*. Differences in cover between years are underestimated since *Smilax* was not included; a 90% increase in *Smilax* density at Sandy Hook had occurred between 1989 and 2003, completely entangling two of the permanent plots.

Forest Establishment

The age distributions of the two holly forests suggest that *I. opaca* has established and maintained itself within these forests through frequent small-scale disturbances. The largest difference in the two *I. opaca* populations occurs within the replacement patterns during the most recent decades and is apparent in the smallest size classes of the diameter distributions at the two sites (Figure 6). Almost no overstory recruitment has occurred in the Sunken Forest since 1970. The only mechanism that appears responsible for this unnatural disruption in the age structure of the forest and the changing understory vegetation pattern is intense herbivory (Forrester et al. 2006). A lack of tree recruitment caused by intense *Odocoileus virginianus* browsing has been reported for an old-growth white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*) forest in the eastern United States (Abrams and Orwig 1996), an old-growth *Abies-Acer-Quercus* forest in northern Japan (Abrams et al. 1999), and northern white-cedar (*Thuja occidentalis*) forests in Great Lakes forests (Anderson and Katz 1993; Cornett et al. 2000). At the Sunken Forest, we were not able to core any individuals below 3 cm dbh because few stems in this size class were even present. Minimal ingrowth of any species was recorded between the last sampling interval (1986-2002). In contrast, the *I. opaca* population of Sandy Hook has increased,

Table 5. Comparisons of tree age and plot mortality rate (1967-2002) within the Sunken Forest depending on proximity to the Atlantic Ocean. Means with the same letter are not significantly different (Tukey pairwise comparison, $\alpha = 0.05$).

Location	Tree age (mean)		Mortality rate (% stems yr ⁻¹)	
Ocean	76 ± 4	a	1.4 ± 0.3	a
Middle	95 ± 6	b	1.1 ± 0.4	a
Bay	85 ± 5	ab	38.3 ± 18.0	b

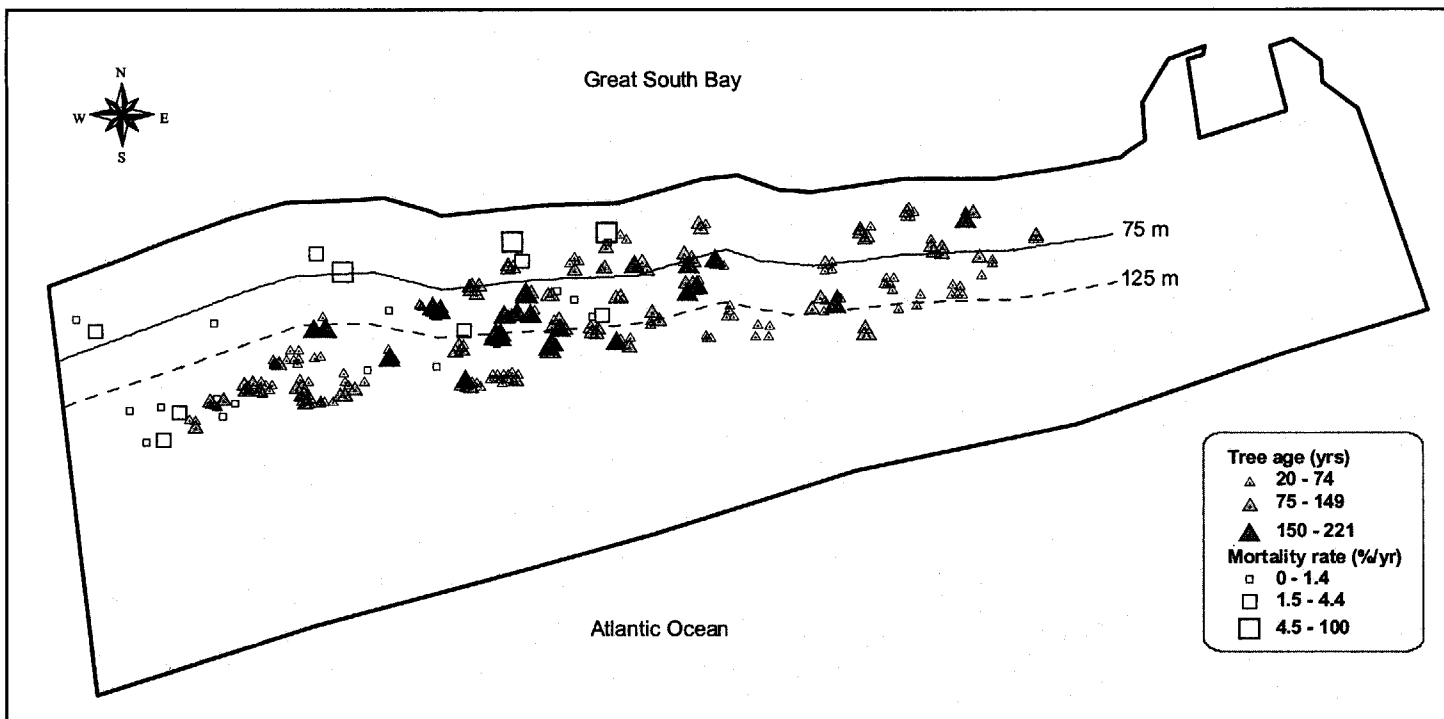


Figure 4. Aged trees and plot mortality rates (% stems dying yr^{-1}) within the Sunken Forest, Fire Island National Seashore, NY. Lines indicate the groupings based on distance from the bay. Triangles symbolize trees (smallest: <75 years old; intermediate size: 75-150 years; largest size: 150+ years). Squares indicate permanent plots and the size of the square reflects the mortality rate of the plot (smallest: <1.5%; intermediate: 1.5-4.4; and largest: 4.5-100%).

with numerous new individuals established since the initial sampling period. The *Odocoileus virginianus* population irrupted on FINS since 1960s and currently likely exceeds presettlement levels, while very few individuals are observed at Sandy Hook. More details on changing herbivore populations will follow.

Disturbance History

Results from our tree-ring analyses indicate that moderate chronic disturbances have occurred throughout the lifetime of the oldest hollies. Perhaps these disturbances can be attributed to numerous tropical storms, hurricanes, and northeasters that have occurred throughout the past two centuries. A recent regional analysis of hurricane impacts in New England showed the most severe impacts of hurricane winds occur along the southern coastline from New York City to Boston (Boose et al. 2001). Through reconstructions of the path and wind velocities associated with historical hurricanes, Boose et al. (2001) found mean return intervals of 5 y for F0 damage on the Fujita scale (loss of leaves and branches), 15 y for F1 damage (scat-

tered blowdowns, small gaps), and 150 y for F2 damage (extensive blowdowns, large gaps). From 1788-1991, it appeared that the Sunken Forest and Sandy Hook were in the path of two F2s (occurring in 1788 and 1821) and nine F1s (occurring in 1804, 1815, 1938, 1944, 1954a, 1954b, 1960, 1985, and 1991).

Growth releases attributable to major disturbances are less frequent in the *I. opaca* trees at the Sunken Forest than at Sandy Hook. The unique east-west geographic orientation and island topography of FINS may account for these differences. The height of the primary dune (~7 m) and presence of a secondary dune (~9 m) at Sunken Forest create a more sheltered location for the forest as winds are blocked and lifted upwards as they meet these dunes. In addition, the short stature of the canopy, which is thought to be maintained by salt-spray, may also be a physical adaptation of roots and shoots to nearly chronic catastrophic hurricane winds (Everham and Brokaw 1996). The Sunken Forest is built on a sequence of relict inlet ridges situated behind a secondary dune (Leatherman 1985); this topographic setting protects it from wind

and overwash events. Despite numerous storms occurring between 1938 and 1979, Leatherman (1983) found evidence of only one overwash event near the Sunken Forest portion of FI, but deposits appeared to occur on either side of the forest.

Sandy Hook extends northward with little to no topographic protection except that from the sea wall along the eastern side of the south end of the Hook (Chrysler 1930). Though this island is in a more protected location from hurricane winds, it has little protection from northeasters that commonly occur up to three times per winter in this region. The 90° bend between the New Jersey and Long Island coasts funnel surge waters northward to the New York City harbor (Gornitz et al. 2002). Approximately 20% of the holly exhibited major releases in the 1920-30s. A few major storm events in this region may account for this: The Great Snow and Sleet Storm of 1920 presented the New Jersey coast with 43 cm of precipitation in early February; the 1933 northeaster (January 25-30, 1933) brought a maximum storm surge of 0.92 m and a storm duration of 87 hours (Zhang et al. 2002); and the Hurricane of (21

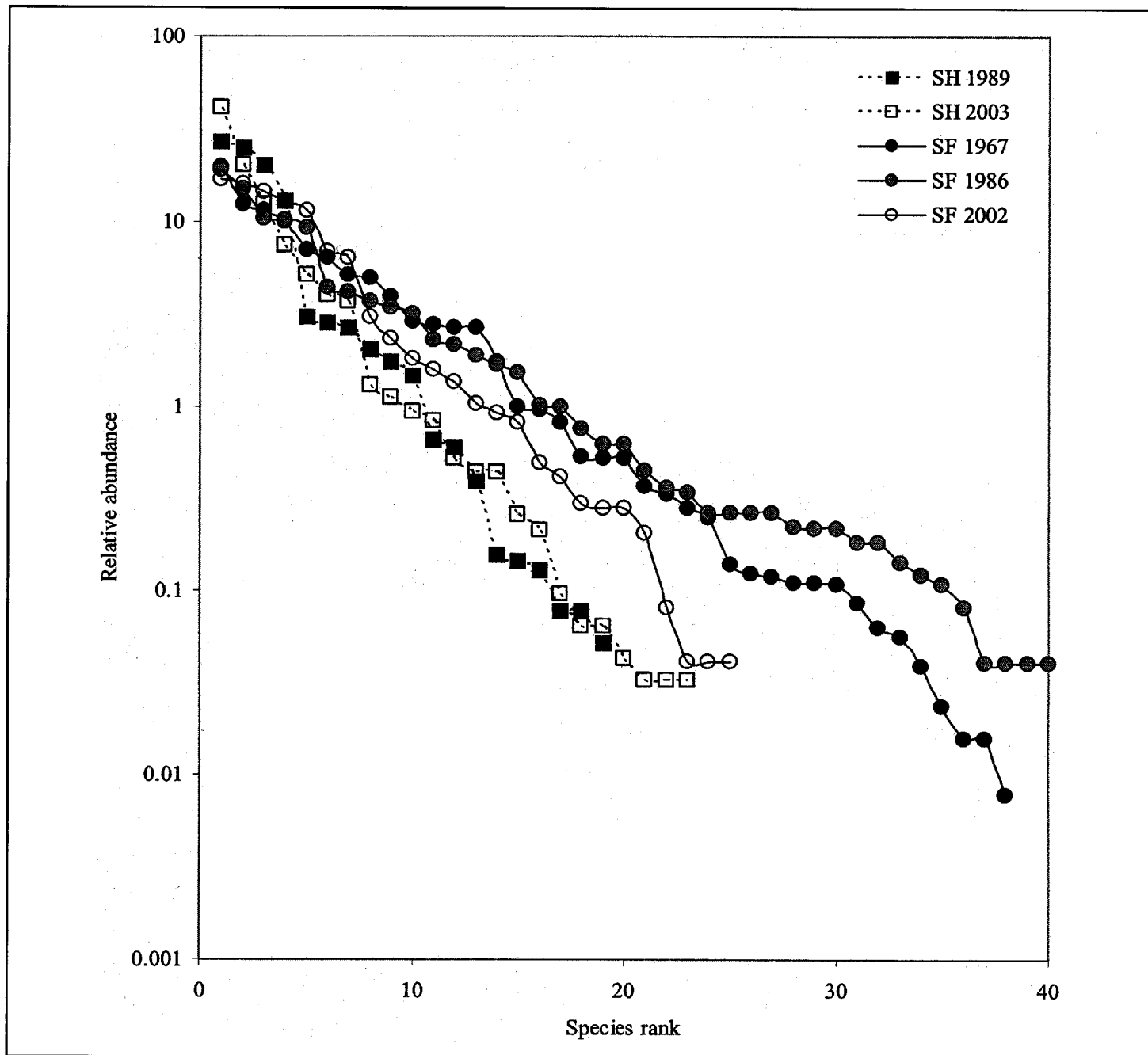


Figure 5. Rank/abundance plot of a mature and old-growth maritime holly forest community. Species richness increased over time within the mature forest at Sandy Hook, Gateway National Recreation Area and has decreased over time at the old-growth forest at Fire Island National Seashore, NY. The y-axis is plotted using a $\log_{10}$ scale.

September) 1938 brought wind velocities up to 129 km per (recorded at nearby New York City) and wave heights reaching 3-3.7 m. Another notable storm that brought the highest recorded storm surge (1.3 m maximum surge) at the Sandy Hook tide gauge was the Ash Wednesday Storm of 1962. The combination of large waves and higher seasonal tides occurring over five continuous high tides caused substantial

beach erosion (Zhang et al. 2002).

The early peaks in the release frequency for Sunken Forest *I. opaca* correspond to notable Long Island hurricanes occurring in September and October of 1804 and September 1869. It is remarkable that few releases are present in the SF *I. opaca* that correspond to the 1938 hurricane. A report from October 1938 accounts that during

the storm, the dunes from Fire Island Inlet to Southampton were leveled or damaged (Andrews 1938). It is possible that trees were highly damaged, but not uprooted, so that the increased recruitment noticeable in the 1940-50s is a delayed response to damage from the great hurricane. Thirty-four percent of the *S. albidum* exhibited major releases in the 1940-50s as well. Minimal tree mortality occurred after Hurricane

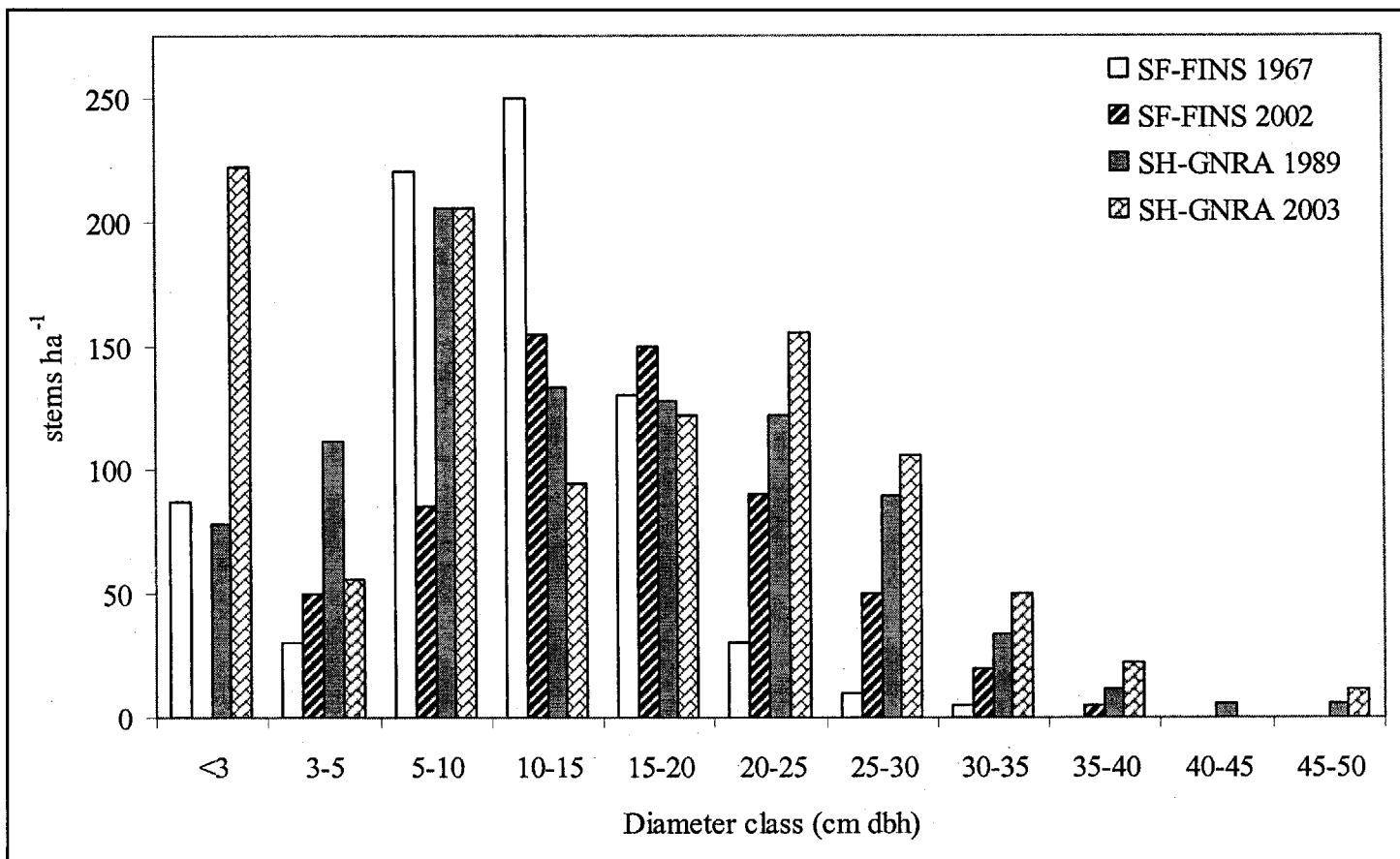


Figure 6. Changes in diameter distribution of *Ilex opaca* at two maritime holly forests: from 1967-2002 at the Sunken Forest (SF), FINS, NY and from 1989 to 2003 at Sandy Hook (SH), GNRA, NJ.

Gloria (27 September 1985), though the tipping over of several trees and removal of branches caused a 25-30% reduction in canopy cover (H.W. Art, unpubl. data). In the two growing seasons following Hurricane Gloria, a nearly five-fold increase in *I. opaca* seedling density occurred (H.W. Art, unpubl. data). Similar to southern coastal forests, the maritime holly forest has strategies for resilience that allow it to persist under a regime of recurring disturbances from hurricanes of varying magnitudes (Myers and VanLear 1998).

Landuse History

Both landuse and fire history are thought to have shaped the vegetation patterns of sand plain ecosystems found on glacial outwash in coastal areas of northeastern United States (Eberhardt et al. 2003). Fire has likely played a stronger role in the Wilderness Area, a more eastern section of FINS where *Pinus rigida* dominates.

We noticed no evidence of charcoal in either forest; *I. opaca* is extremely fire intolerant, indicating that the lack of fire is important to the formation of this plant community. Sparks from railroads are known to ignite forest fires, but timbers were removed from near the railroad in Sandy Hook (Moss 1990).

Despite accounts of proposed large-scale cutting at both locations, all proposals were declined by the War Department on Sandy Hook and by activists on Long and Fire Island (Johnson 1983; Moss 1990). *Juniperus virginiana* boles were likely extracted for fuelwood on Sandy Hook (Moss 1990). Some stems may have been removed from the SF for fuel for ships and smelt factories that historically occurred nearby on the Island. It is unknown to what degree the harvesting of *I. opaca* branches and foliage for commercial purposes affected this species. We found one mention of December harvests specifically occurring within the SF (Smith 1950) and another

referring to the restriction of harvests to open stretches of beach because of the inaccessibility of the SF (LeCluse 1940). Stalter (1979) also mentions the cutting of branches in winter at Sandy Hook during the late 19th century.

Histories of grazing and agriculture are limited on the island, though common to inland locations in Monmouth County, New Jersey, and Long Island, New York. Since the 1960s, when the NPS began managing FINS, *O. virginianus* populations and the island became more developed; *O. virginianus* increased from <10 deer km⁻² to >70 deer km⁻² (H.B. Underwood, unpubl. data). While *O. virginianus* are native to the region, the current population likely exceeds presettlement levels for the island. Only an occasional *O. virginianus* is observed at Sandy Hook, with too few individuals to require a survey of the population (NPS staff, pers. communication).

Patterns of Mortality

We expected mortality to be highest nearest the ocean, where trees were most exposed to salt spray, storm surge, and hurricane winds. Campbell (1998) noticed that *Pinus pinaster* forests in New Zealand displayed wave regeneration patterns similar to those patterns described for subalpine regions, but causes in the coastal area include the combination of strong onshore winds, salt spray, and overcrowding. Martin (1959) found *I. opaca* and *J. virginiana* to be very tolerant of salt spray. Though the mean tree age was youngest nearest the ocean, mortality was highest on the bayside of Fire Island. Several plots were completely inundated since the first sampling in 1967. Maps of the Sunken Forest shoreline between 1830 and 1979 indicate erosion was occurring on both the bay and ocean-side, causing a narrowing of the island through time rather than a landward migration often attributed to barrier islands (Leatherman 1983). The opposing actions from the coastal and backbarrier bay sides appear to make the middle ground the safest locations for trees (Figure 6).

CONCLUSION

The natural regeneration dynamics that have contributed to the persistence of the rare maritime American holly forest are similar at the Sunken Forest and Sandy Hook. The uneven-aged forests rely on the occurrence of frequent hurricanes and northeasters to provide canopy openings for new recruits. The orientation and morphology of the island moderate the effects of the storm on the canopy. Changes in storm frequencies or canopy releases in recent decades do not account for the lack of recruitment and decline of the ground-layer vegetation at the Sunken Forest. Landuse change and the ensuing protection of wildlife may offer a better explanation. Further investigation to directly quantify the impacts of *O. virginianus* herbivory is warranted at the Sunken Forest in light of the differences in replacement patterns between the two *I. opaca* forests. The conservation of the plant community at FINS likely requires active management rather than a hands-off,

preservation approach.

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