

National Park Service  
U.S. Department of the Interior

Northeast Region  
Boston, Massachusetts



## **The Role Of Disturbance In The Long-Term Viability Of A Coastal Maritime Forest Fragment**

Technical Report NPS/NER/NRTR--2008/104



**ON THE COVER**

The herbivore-impacted holly forest understory of the Sunken Forest, a maritime forest fragment on Fire Island National Seashore, New York.

Photograph courtesy of the authors.

---

# **The Role Of Disturbance In The Long-Term Viability Of A Coastal Maritime Forest Fragment**

Technical Report NPS/NER/NRTR--2008/104

Jodi A. Forrester<sup>1</sup>, Donald J. Leopold<sup>1</sup> and H. Brian Underwood<sup>2</sup>

<sup>1</sup>State University of New York, College of Environmental Science & Forestry  
Department of Environmental & Forest Biology  
Syracuse, NY 13210

<sup>2</sup>USGS Patuxent Wildlife Research Center, State University of New York  
College of Environmental Science & Forestry  
Syracuse, NY 13210

January 2008

U.S. Department of the Interior  
National Park Service  
Northeast Region  
Boston, Massachusetts

The Northeast Region of the National Park Service (NPS) comprises national parks and related areas in 13 New England and Mid-Atlantic states. The diversity of parks and their resources are reflected in their designations as national parks, seashores, historic sites, recreation areas, military parks, memorials, and rivers and trails. Biological, physical, and social science research results, natural resource inventory and monitoring data, scientific literature reviews, bibliographies, and proceedings of technical workshops and conferences related to these park units are disseminated through the NPS/NER Technical Report (NRTR) and Natural Resources Report (NRR) series. The reports are a continuation of series with previous acronyms of NPS/PHSO, NPS/MAR, NPS/BSO-RNR and NPS/NERBOST. Individual parks may also disseminate information through their own report series.

Natural Resources Reports are the designated medium for information on technologies and resource management methods; "how to" resource management papers; proceedings of resource management workshops or conferences; and natural resource program descriptions and resource action plans.

Technical Reports are the designated medium for initially disseminating data and results of biological, physical, and social science research that addresses natural resource management issues; natural resource inventories and monitoring activities; scientific literature reviews; bibliographies; and peer-reviewed proceedings of technical workshops, conferences, or symposia.

Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the National Park Service.

This report was accomplished under USGS Cooperative Agreement 04ERAG0016 with assistance from the NPS. The statements, findings, conclusions, recommendations, and data in this report are solely those of the author(s), and do not necessarily reflect the views of the U.S. Department of the Interior, US Geological Survey or National Park Service.

Print copies of reports in these series, produced in limited quantity and only available as long as the supply lasts, or preferably, file copies on CD, may be obtained by sending a request to the address on the back cover. Print copies also may be requested from the NPS Technical Information Center (TIC), Denver Service Center, PO Box 25287, Denver, CO 80225-0287. A copy charge may be involved. To order from TIC, refer to document D-451.

This report may also be available as a downloadable portable document format file from the Internet at <http://www.nps.gov/nero/science/>.

Please cite this publication as:

Forrester, J. A., D. J. Leopold, and H. B. Underwood. January 2008. The Role of Disturbance in the Long-Term Viability of a Coastal Maritime Forest Fragment. Technical Report NPS/NER/NRTR--2008/104. National Park Service. Boston, MA.

## TABLE OF CONTENTS

<b>INTRODUCTION</b> .....	1
<b>Question 1: Do temporal trends in forest structure and composition indicate that both locations are on similar successional trajectories?</b> .....	2
<i>Sunken Forest</i> .....	2
<i>Sandy Hook</i> .....	4
<i>Establishment and age patterns</i> .....	4
<b>Question 2. How do canopy trees establish within this forest type?</b> .....	4
<i>Mortality patterns</i> .....	4
<i>Disturbance History</i> .....	11
<b>Question 3. What does the current vegetation in canopy gaps and seed bank suggest about the future composition of the SF?</b> .....	13
<i>Propagule Bank</i> .....	14
<b>Question 4. Is herbivory responsible for the documented change in vegetation composition and structure within the SF?</b> .....	14
<i>Long-term plots and deer exclosures</i> .....	14
<i>Rabbit herbivory</i> .....	20
<i>Short-term paired plots</i> .....	20
<b>Question 5. What are the prospects for conserving the essential character of the maritime holly forest under different disturbance regimes?</b> .....	24
<b>CONSERVATION GOALS</b> .....	31
<b>ACKNOWLEDGMENTS</b> .....	32
<b>LITERATURE CITED</b> .....	32
<b>APPENDIX I.</b> .....	34

## INTRODUCTION

The maritime holly forest is a unique assemblage of species dominated by the broadleaf evergreen, *Ilex opaca* (American holly). 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) because of extreme rarity or very few remaining acres. The only two examples known of the maritime holly forest include: the Sunken Forest (SF; 16 ha) occurring on Fire Island National Seashore, a barrier island protecting Long Island, NY; and the Sandy Hook (SH) holly forest (30 ha) occurring on a barrier spit on the NJ shore that is a unit of Gateway National Recreation Area (GNRA). This project was born from the uncertainty surrounding key conservation issues, and in 2004 was listed as the primary research priority for Fire Island National Seashore due to the uniqueness of the SF among maritime forests of the Atlantic coast, its prominence in the park's enabling legislation and Resource Stewardship Plan, and its interpretive value to the visiting public. An important objective of the research was to assist the park in developing reasonable conservation goals for sustaining the essential characteristics of the SF.

The *I. opaca* at the SF are older, and appear stunted and gnarled while those at SH are larger in diameter and height (Stalter 1979). Earlier studies of both locations indicate that the holly forest at FIIS is in an old-growth condition, while that at GNRA is an example of a mature stage of development (Art 1976, Stalter 1979). Based upon monitoring of permanent plots established just after Fire Island National Seashore was established, Art (H. W. Art, unpublished data) documented decreases in the cover and composition of the herbaceous layer and shrub species composition of the SF during a reassessment in the mid-1980s. During the same time period, the white-tailed deer (*Odocoileus virginianus*) population in the area increased from <10 deer km<sup>-2</sup> to >50 deer km<sup>-2</sup> (Underwood 2005). This research investigated whether canopy constituents of this maritime holly forest are maintaining themselves under the current levels of herbivory and other disturbances. We present this report in executive summary format through a series of questions that probe different aspects of vegetation dynamics of the SF. We do this for two reasons. First, the scope of the work is broad and includes research approaches and methods that are somewhat disparate and unrelated, making the presentation of the full work awkward. Second, the research on which the report is based already appears in the peer-reviewed scientific literature as discrete units with specific objectives and methodologies. We refer the reader directly to those published accounts for the methodological details.

We compared the vegetation trends measured in the SF to the trends occurring at the other maritime holly forest located at SH. Permanent vegetation plots were established in the SH holly forest in 1989 by H. W. Art. With Dr. Art's collaboration, we relocated most of the plots and sampled the vegetation in summer 2003 and compared this dataset to that of the permanent vegetation plots in the SF (1967 to 2002). In particular, the effects of herbivory are elucidated by the simple fact that there are few deer on SH due to its remote location and isolation from the mainland. The first three questions address the degree to which the ecology of these two forests differ.

Specifically,

- 1) Do temporal trends in forest structure and composition indicate that both locations are on similar successional trajectories?
- 2) How do canopy trees establish within this forest type, and are major disturbances (e.g., hurricanes, nor'easter storms) more important than minor disturbances (e.g., treefall gaps) in their persistence?
- 3) What does the current vegetation in canopy gaps and seed bank suggest about the future composition of the SF?
- 4) What role has herbivory played in the documented change in vegetation composition and structure of the SF?
- 5) What are the prospects for conservation of the essential character of the maritime holly forest under different disturbance regimes?

We used a combination of diameter structures, compositional trends and age distributions built from tree cores collected from permanent vegetation plots monitored in the SF and at SH to answer Questions 1 and 2 (Forrester et al. 2007). Through a series of soil seed bank studies, we focused the third question on the degree to which the forest growing up from the seed bank looks like the extant forest of today (Forrester and Leopold 2006). We evaluated the effects of deer herbivory through the use of permanent and temporary vegetation enclosures to address the fourth question (Forrester et al. 2006). Finally, we synthesized our understanding of the regeneration and maintenance dynamics of the SF to consider future states of the SF and potential conservation strategies. We expanded the scope of the original project statement (Questions 2, 3 and 5) by the fortuitous inclusion of data from the holly forests at SH (Question 1), and the implementation of a new vegetation enclosure experiment (Question 4).

### **Question 1: Do temporal trends in forest structure and composition indicate that both locations are on similar successional trajectories?**

#### *Sunken Forest*

The relative importance of the most shade-tolerant species, *I. opaca*, has increased from 32 to 39% within the canopy due to significant increases in basal area occurring from 1967 to 2002 (Table 1). The importance of *Amelanchier canadensis* in the canopy has declined, due to a significant decrease in stem density from 1986 to 2002 (961 to 750 stems ha<sup>-1</sup>). *Sassafras albidum* and *Nyssa sylvatica* maintained their relative importance within the canopy due to increasing basal areas despite decreasing densities. The density of the shrub and sapling layer fluctuated over the sampling period, significantly decreasing from greater than 8500 stems ha<sup>-1</sup> in 1967 to 2157 stems ha<sup>-1</sup> in 1986 and increasing to 4980 stems ha<sup>-1</sup> by 2002. The decline in stem density from 1967 to 2002 is due to significant decreases in *Vaccinium corymbosum*, *Gaylussacia baccata*, and *Toxicodendron radicans*. Basal area of the shrubs declined significantly from 1967 to 1986 (from 4.0 to 2.4 m<sup>2</sup> ha<sup>-1</sup>, respectively) and continued to decline to 1.5 m<sup>2</sup> ha<sup>-1</sup> by 2002. 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: *V. corymbosum* and *Baccharis halimifolia*.

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 <sup>2</sup> ha <sup>-1</sup>			DENSITY Stems ha <sup>-1</sup>			IV %		
		1967	1986	2002	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	32	32	↑39
	<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	34	33	30
	<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	20	21	21
	<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	6	6	6
	<i>Quercus velutina</i>	0.9 $\pm$ 0.8	0.9 $\pm$ 0.8	1.5 $\pm$ 1.3	7 $\pm$ 5	14 $\pm$ 8	15 $\pm$ 8	2	2	3
	<i>Pinus rigida</i>	0.2 $\pm$ 0.2	0.2 $\pm$ 0.2	0.5 $\pm$ 0.5	7 $\pm$ 7	7 $\pm$ 7	15 $\pm$ 15	1	1	1
	Other*	0.7	0.6	0.1	121	196	25	4	6	1
	<b>Total</b>		21.3 $\pm$ 2.1	↑25.5 $\pm$ 2.5	↑33.5 $\pm$ 2.9	2107 $\pm$ 200	2186 $\pm$ 213	↓1775 $\pm$ 202		
<3 cm dbh	<i>Vaccinium corymbosum</i>	1.6 $\pm$ 0.5	1.0 $\pm$ 0.3	1.1 $\pm$ 0.4	2357 $\pm$ 629	↓943 $\pm$ 247	2260 $\pm$ 881	34	43	58
	<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	3	18	29
	<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	17	11	4
	<i>Gaylussacia baccata</i>	0.1 $\pm$ 0	0.1 $\pm$ 0	0	743 $\pm$ 342	↓171 $\pm$ 110	240 $\pm$ 175	6	5	3
	<i>Rhododendron viscosum</i>	0.2 $\pm$ 0.2	0	0	429 $\pm$ 429	0	20 $\pm$ 20	5	0	1
	<i>Aronia arbutifolia</i>	0.5 $\pm$ 0.2	0.2 $\pm$ 0.1	0	1086 $\pm$ 530	200 $\pm$ 136	20 $\pm$ 20	12	8	0
	<i>Toxicodendron radicans</i>	0.1 $\pm$ 0	↓0	0	1214 $\pm$ 439	↓71 $\pm$ 71	0	9	↓2	0
	<i>Ilex glabra</i>	0.1 $\pm$ 0.1	0	0	386 $\pm$ 209	57 $\pm$ 45	0	4	2	0
	<i>Rosa carolina</i>	0.1 $\pm$ 0	0	0	671 $\pm$ 497	0	0	5	0	0
	<i>Rhus copallinum</i>	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0	229 $\pm$ 229	29 $\pm$ 29	0	3	2	0
	<i>Sassafras albidum</i>	0.1 $\pm$ 0	0.1 $\pm$ 0.1	0	100 $\pm$ 49	57 $\pm$ 45	20 $\pm$ 20	1	2	1
	<i>Myrica pensylvanica</i>	0	0	0	0	129 $\pm$ 90	100 $\pm$ 81	0	4	1
	Other**	0.1	0.2	0	643	257	260	7	10	4
	<b>Total</b>		4.0 $\pm$ 1.2	↓2.4 $\pm$ 0.7	1.5 $\pm$ 0.5	8586 ±2088	↓2157 ±554	4980 ±2119		

\*Other includes: *Aronia arbutifolia*, *Prunus serotina*, *Acer rubrum*, *Rhus copallinum*, *Quercus stellata*, and *Q. coccinea* (all <2% relative importance) in 1967; only the first 4 species listed previously in 1986; and only first 2 species in 2002.

\*\*Other includes: *Nyssa sylvatica*, *Ilex opaca*, *Prunus serotina*, *Rubus allegheniensis*, *Sambucus canadensis* in 1967; *N. sylvatica*, *I. opaca*, and *Vitis* sp. in 1986; and *N. sylvatica*, *P. serotina*, and *Parthenocissus quinquefolia* in 2002.

The diameter structures of the dominant tree populations support the view that this is a self-perpetuating forest type (Fig. 1). The positively skewed diameter distributions for *I. opaca*, *S. albidum* and *A. canadensis* in 1967 suggest a pattern of continuous regeneration for these species. By 2002, the diameter structures of *Ilex* and *Sassafras* have shifted and no longer display the most numerous stems in the smaller size classes. The *A. canadensis* population is the only to retain the positively skewed distribution. Age-diameter relationships were not consistently strong for any species however, so only weak inferences should be made about stand development and dynamics based on the size structures alone (Fig. 2).

### *Sandy Hook*

The dominance of *I. opaca* increased within the SH holly forest, as its relative importance increased from 72 to 82% (Table 2) due to a significant increase in basal area. *Prunus serotina*, *Celtis occidentalis*, and *A. canadensis* decreased in importance from 1989 to 2003, due to decreases in both density and basal area.

The density of woody stems in the understory increased 34% from 1989 to 2003, from 561 to 850 stems m<sup>-2</sup> (Table 2). *Prunus serotina* saplings and *T. radicans* dominated the woody understory in 1989, accounting for 70% of the stems. By 2003, *I. opaca* saplings significantly increased in diameter and number, becoming the most important understory species (47% IV). The density of *P. serotina* stems fell significantly from 261 stems ha<sup>-1</sup> to 156 stems ha<sup>-1</sup>. Many of the large *T. radicans* stems died, but numerous new stems and vines established increasing the density of the species from 139 to 256 stems m<sup>-2</sup> from 1989 to 2003. *Rhus typhina* and *Rhus copallinum* decreased throughout the forest, while *Rubus allegheniensis* increased.

### *Establishment and age patterns*

Both SF and SH are all-aged forests (Fig. 3). The *I. opaca* within the SH holly forest ranged in age from 15 to 162 years old. Recruitment was nearly continuous in this forest as within the SF, 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 SH.

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 (Fig. 4). Almost no overstory recruitment has occurred in the SF since 1970. At the SF, we were unable 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 SH has increased, with numerous new individuals established since the initial sampling period.

## **Question 2. How do canopy trees establish within this forest type?**

### *Mortality patterns*

The overall mortality rate of all canopy trees (stems >10 cm dbh) was higher at the SF during the period of 1967-1985 than from 1986-2002, 1.9% year<sup>-1</sup> vs. 1.2% year<sup>-1</sup> (Table 3). Overall mortality at SH was 0.9% year<sup>-1</sup>. *Ilex opaca* had the lowest mortality rates relative to the

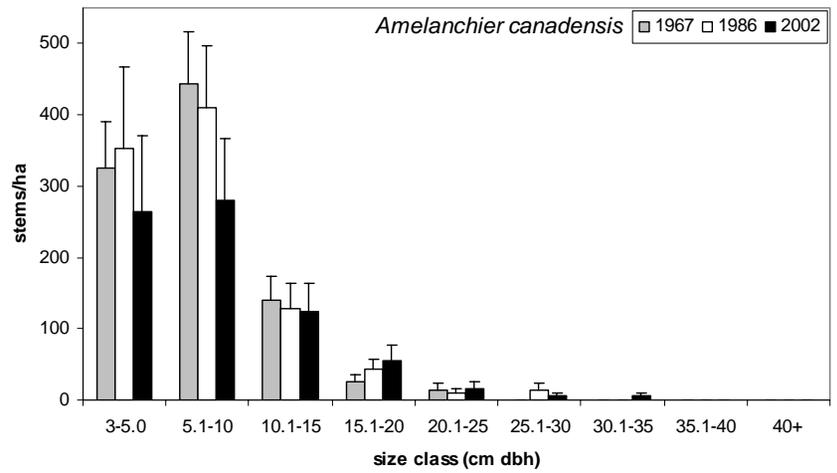
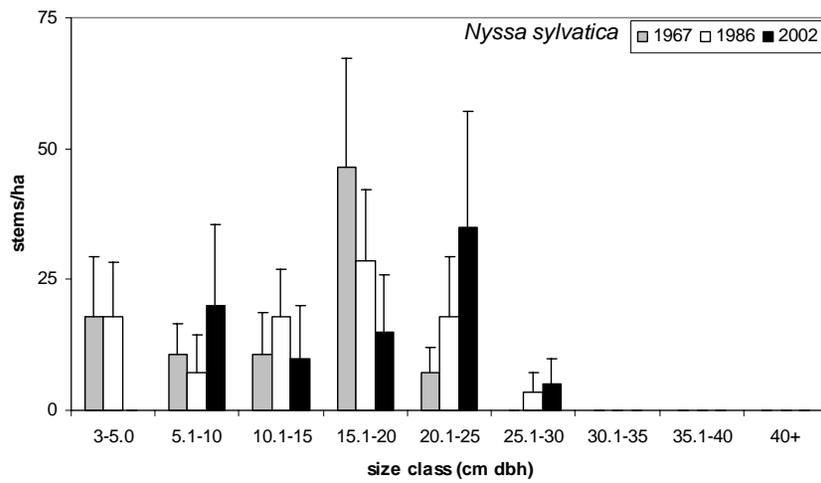
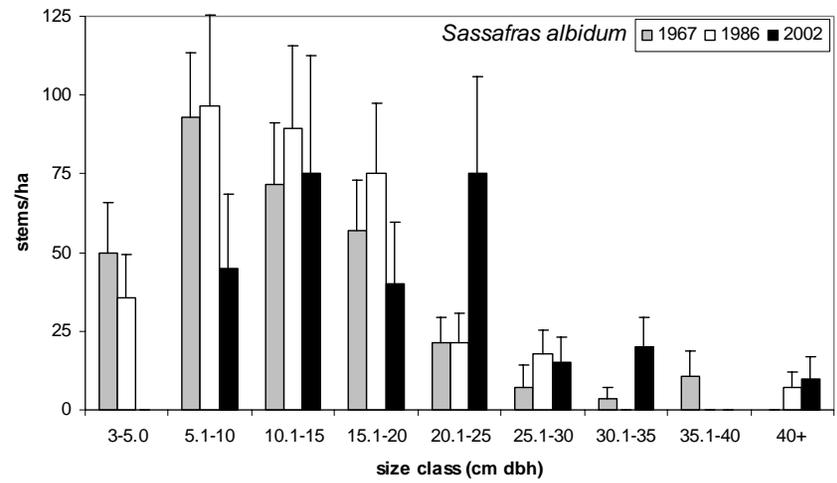
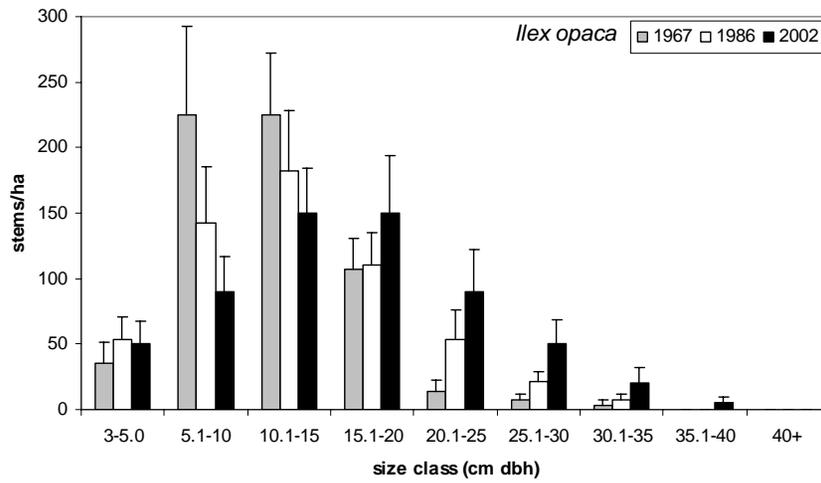


Figure 1. Diameter distributions for four dominant canopy species in the Sunken Forest 1967-2002.

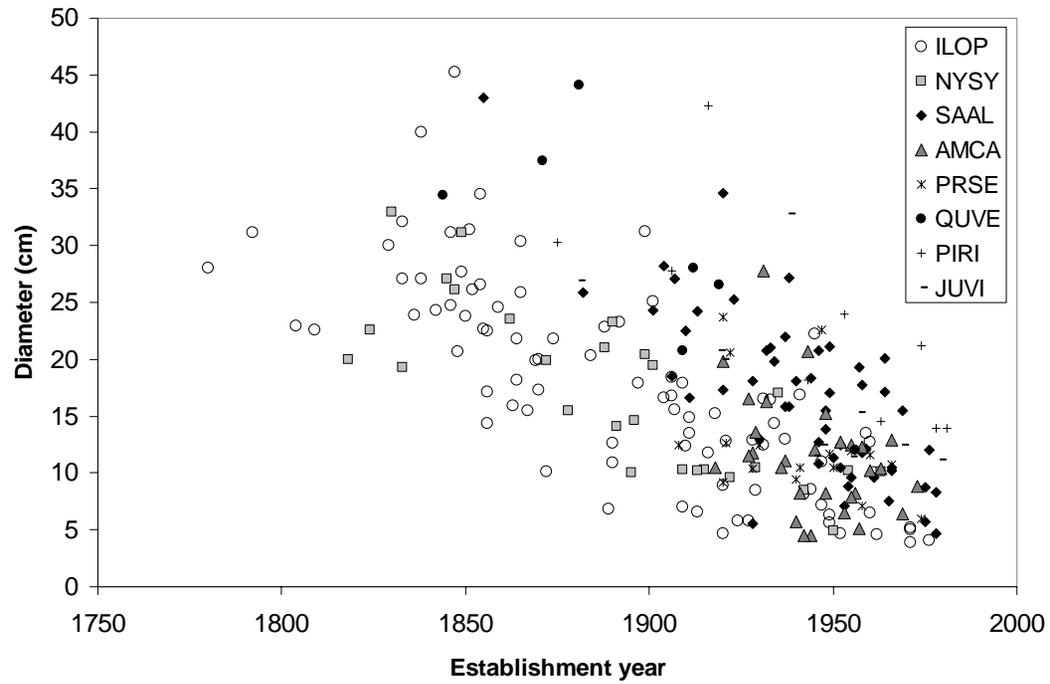


Figure 2. Age-diameter relationships for all trees cored at Sunken Forest, Fire Island National Seashore. Individuals are coded by the first two letters of the genus and species.

Table 2. 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 (m <sup>2</sup> ha <sup>-1</sup> )		DENSITY (stems ha <sup>-1</sup> )		IV (%)	
		1989	2003	1989	2003	1989	2003
≥ 3 cm dbh	<i>Ilex opaca</i>	21.5±2.0	↑26.3±2.5	850±120	822±96	72	↑82
	<i>Prunus serotina</i>	4.1±0.9	3.7±1.0	289±74	↓128±33	19	↓12
	<i>Celtis occidentalis</i>	0.9±0.5	0.7±0.4	67±37	33±18	4	3
	<i>Amelanchier canadensis</i>	0.6±0.5	0.3±0.3	44±30	28±19	3	2
	<i>Juniperus virginiana</i>	0.3±0.3	0.3±0.3	6±6	6±6	1	1
	<i>Rhus copallinum</i>	0	0	39±39	6±6	2	0
	All species	27.3±2.1	↑31.3±2.8	1294±135	↓1022±98		
< 3 cm dbh*	<i>Ilex opaca</i>	0.06±0.04	↑0.16±0.03	78±44	↑222±57	15	↑47
	<i>Prunus serotina</i>	0.14±0.04	0.07±0.04	261±100	↓156±83	41	↓19
	<i>Toxicodendron radicans</i>	0.11±0.06	0.03±0.02	139±84	256±166	30	18
	<i>Rubus allegheniensis</i>	0	0	0	183±183	0	11
	<i>Baccharis halimifolia</i>	0.03±0.03	0.02±0.02	39±39	11±11	5	7
	<i>Rhus copallinum</i>	0.01±0.01	0	28±23	11±8	4	1
	Other**	0	0	17	11	1	1
	All species	0.35±0.1	0.28±0.1	561±155	850±272		

\*Basal diameter was recorded instead of dbh for stems in this category.

\*\*Other includes: *Rosa multiflora*, *Rhus typhina*, *Amelanchier canadensis*, *Myrica pensylvanica*, *Prunus maritima*, and *Vaccinium corymbosum* (all <1% relative importance).

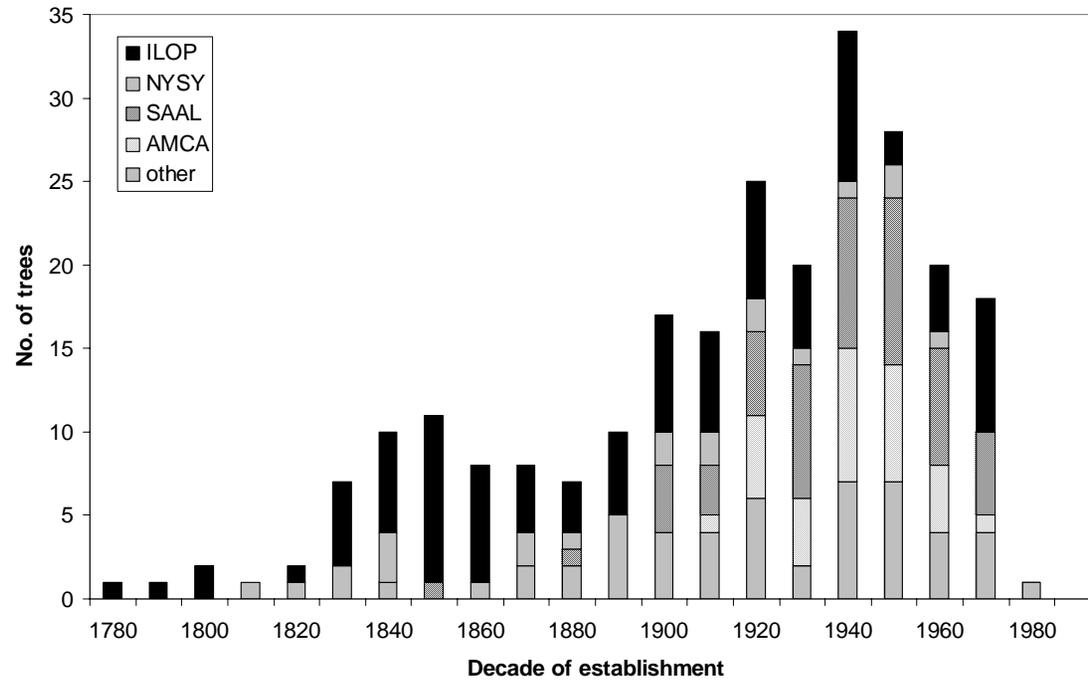


Figure 3. Establishment patterns of stems cored in the Sunken Forest, Fire Island National Seashore, NY. Individuals are coded by the first two letters of the genus and species.

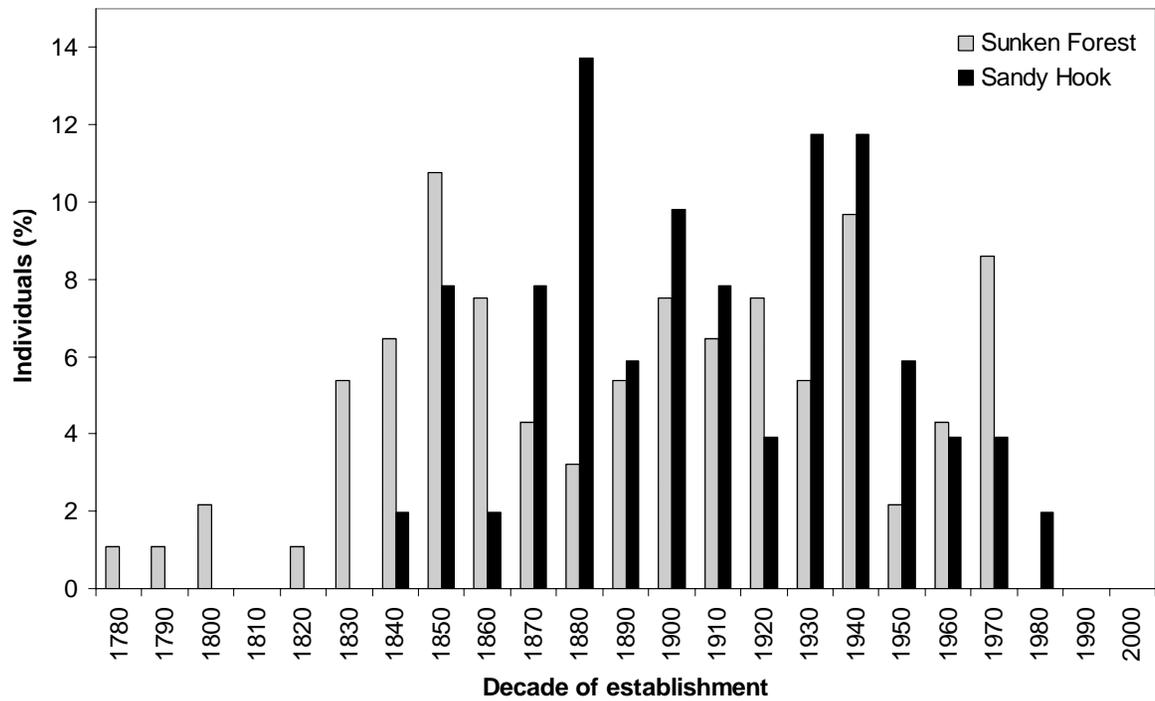


Figure 4. Establishment patterns for *Ilex opaca* at the Sunken Forest, FIIS, NY (n=93) and Sandy Hook, GNRA, NJ (n=51).

Table 3. Mortality and recruitment of canopy trees (>10 cm dbh) at two maritime holly forests.

	$N_0^*$	Mortality (% yr <sup>-1</sup> )	Recruits (#/ha-yr <sup>-1</sup> )	$N_0^*$	Mortality (% yr <sup>-1</sup> )	Recruits (#/ha-yr <sup>-1</sup> )
<b>Sunken Forest</b>		<b>1967-1986</b>			<b>1986-2002</b>	
<i>Ilex opaca</i>	100	0.9	4.3	103	0.3	3.5
<i>Sassafras albidum</i>	49	2.9	5.6	55	2.0	3.3
<i>Amelanchier canadensis</i>	52	3.2	5.1	51	2.5	4.1
<i>Nyssa sylvatica</i>	18	2.1	0.4	17	0.4	0.0
<b>Sandy Hook</b>		<b>1989-2003</b>				
<i>Ilex opaca</i>	95	0.1	3.6			
<i>Prunus serotina</i>	26	3.9	4.0			
<i>Celtis occidentalis</i>	7	2.4	0.0			
<i>Amelanchier canadensis</i>	4	4.8	0.4			

\* $N_0$  is the number of living stems at time of initial measurement.

other species present at both sites. *Ilex opaca* mortality at the SF was 0.8% yr<sup>-1</sup> from 1967-1986 and 0.3% yr<sup>-1</sup> 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; from 2.9 to 2.0% yr<sup>-1</sup> for *S. albidum* and from 3.2 to 2.5% yr<sup>-1</sup> for *A. canadensis*. *Nyssa sylvatica*, another shade-tolerant species exhibited high annual mortality (2% yr<sup>-1</sup>) from 1967-1986, but then mortality slowed from 1986 to 2002 (0.4% yr<sup>-1</sup>).

At SH, *I. opaca* mortality is infrequent, occurring less than 0.1% yr<sup>-1</sup>. However, *P. serotina*, *C. occidentalis* and *A. canadensis* mortality is much higher (3.9, 2.4 and 4.8% yr<sup>-1</sup>, respectively) than *I. opaca*. Note the small sample size available to determine the mortality rates of *A. canadensis* and *C. occidentalis*.

### *Disturbance History*

Results from tree-ring analyses indicate that moderate disturbances have occurred throughout the lifetime of the oldest hollies (Fig. 5). Perhaps these disturbances can be attributed to numerous hurricanes, tropical and nor'easter storms 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 yrs for F0 damage on the Fujita scale (loss of leaves and branches); 15 yrs for F1 damage (e.g., scattered blowdowns, small gaps); and 150 yrs for F2 damage (e.g., extensive blowdowns, large gaps). From 1788-1991, it appeared that the SF and SH 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 SF than at SH. The unique east-west geographic orientation and island topography of FIIS may account for these differences. The height of the primary dune (~7 m) and presence of a secondary dune (~9 m) at SF 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 SF 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 SF portion of Fire Island, but deposits appeared to occur on either side of the forest. This observation is supported by the tree-ring cores. Several *I. opaca* individuals are older than any other species aged in the forest and are well-distributed spatially throughout the forest indicating a lack of stand-wide, catastrophic disturbance in the past two centuries.

SH 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 SH is in a more protected location from hurricane winds, it has little protection from nor'easters that commonly occur up to three times per winter in this region. The 90° bend between the NJ and Long Island

Percent trees released

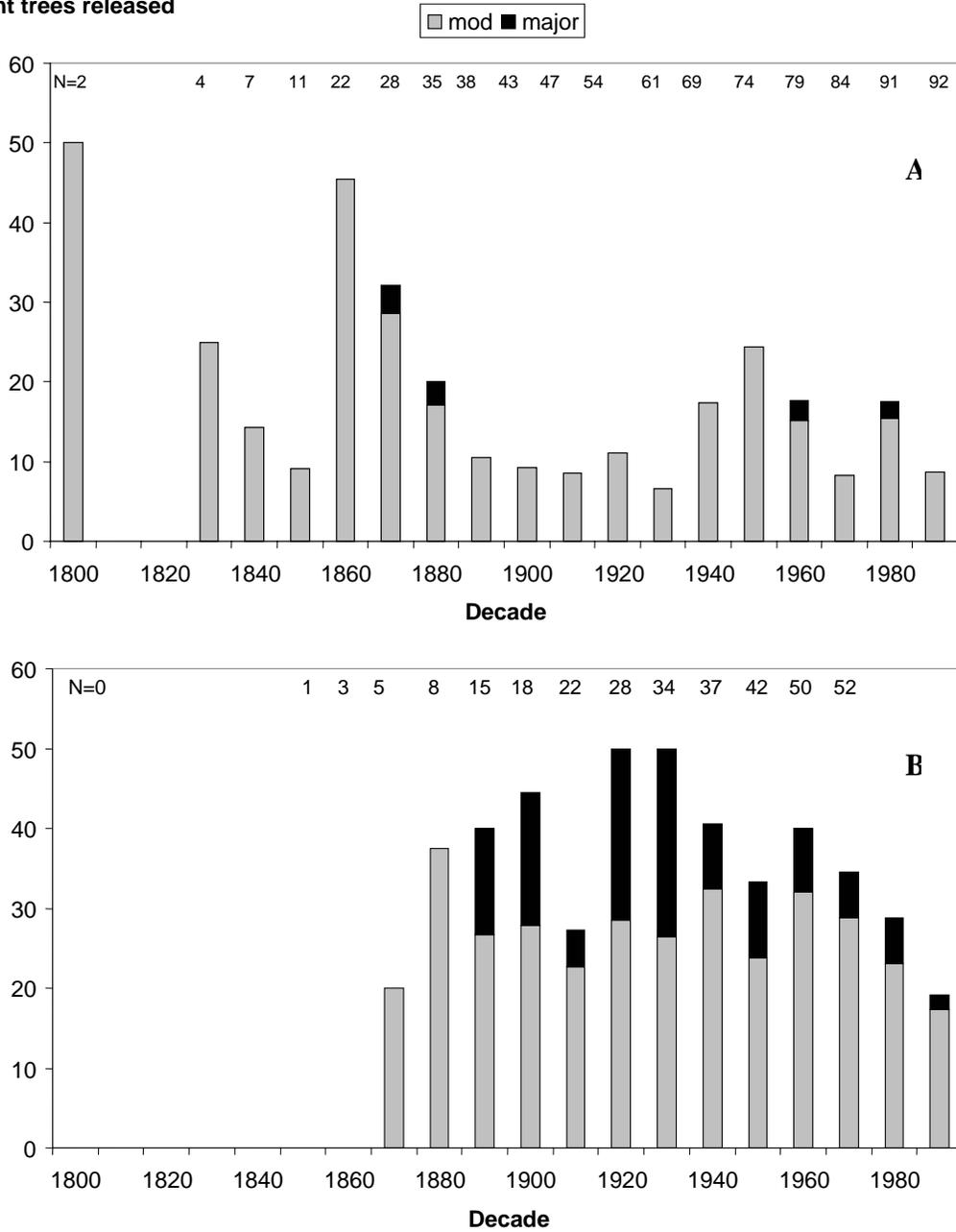


Figure 5. *Ilex opaca* releases in Sunken Forest (A) and Sandy Hook (B), two maritime holly forests. Major releases occurred between 50-100% of the value of the boundary line and moderate releases were between 20-49.9%.

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 NJ coast with 43 cm of precipitation in early February; the 1933 nor'easter (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 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 SH tide gauge was the Ash Wednesday Storm of 1962. The combination of large waves and higher seasonal tides occurring over 5 continuous high tides caused substantial beach erosion (Zhang et al. 2002).

The early peaks in the release frequency for SF *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 was a delayed response to damage from the great hurricane.

Thirty-fourty percent of the *S. albidum* exhibited major releases in the 1940-50s as well. Minimal tree mortality occurred after Hurricane 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, unpublished data). In the two growing seasons following Hurricane Gloria, a nearly five-fold increase in *I. opaca* seedling density occurred (H.W. Art, unpublished 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).

### **Question 3. What does the current vegetation in canopy gaps and seed bank suggest about the future composition of the SF?**

The extant and potential (i.e., seed bank) vegetation of the SF was described to assess whether treefall gaps act as a mechanism for the persistence of the species composition of the maritime holly forest community over time. Using the line intercept method for sampling canopy gaps, 17 gaps were identified on the four southernmost transects that spanned the widest portion of the forest. When a canopy opening was encountered along a transect, a gap plot was established and was later compared with a plot that had been located systematically on the transect and was beneath closed canopy conditions. The composition and density of the seed bank were described using the emergence method. Germination from soil samples placed in the greenhouse was monitored over two years.

Sapling and shrub density was highly variable between plots and numerous plots contained no individuals meeting the defined size criteria. Densities beneath the closed canopy, ( $518 \pm 265$  stems  $ha^{-1}$ ) and within gaps ( $2071 \pm 991$  stems  $ha^{-1}$ ) were not significantly different (p-values for all spp. and for individual sp.  $> 1.6$ ). *Amelanchier canadensis* (55%), *V. corymbosum* (24%) and *Rhododendron viscosum* (18%) were most important beneath closed canopy, while *P. serotina* (36%), *G. baccata* (26%) and again *V. corymbosum* (31%) were most important in

canopy gaps (Table 4). The mean cover and density of herbaceous and woody vegetation < 1 m tall were higher beneath treefall gaps than closed canopy ( $p=0.001$  and  $0.048$ , respectively; Table 5). The mean plant cover was  $45\pm 10\%$  in the gaps and  $4\pm 0.6\%$  beneath the closed canopy. Plant density was  $49\pm 7$  stems  $m^{-2}$  within gaps and  $32\pm 6$  stems  $m^{-2}$  outside the gaps. Species richness of the ground-layer vegetation did not differ between gaps and the closed canopy, with richness in both locations ranging from 2-10 species and a mean of 5 species per plot. Several species were higher in cover within gap openings than beneath the closed canopy, including: *P. serotina*, *A. canadensis*, *Parthenocissus quinquefolia*, and *Smilax rotundifolia* ( $p$ -values  $< 0.01$ ). No individual species' density differed significantly between gaps and closed canopy plots (all  $p > 0.05$ ). Plant cover was positively related to the size of the gap ( $r^2=0.31$ ,  $p=0.025$ ).

#### *Propagule Bank*

*Rhus copallinum*, *S. rotundifolia*, and *Digitaria sanguinalis* were the most abundant germinants from the propagule bank ( $57.2\pm 15.6$ ,  $37.5\pm 13.3$ , and  $31.9\pm 10.4$  stems  $m^{-2}$ ; Table 6). *Ilex opaca* germination occurred only after the second cold stratification period (from Feb-July 2003) eventually reaching  $17.8\pm 6.7$  stems  $m^{-2}$ . Several species common in the forest had very low germination including *S. albidum* and *A. canadensis*. *Nyssa sylvatica*, *V. corymbosum* and several herbaceous species were absent from the seed bank.

Comparisons of the vegetation in the seed bank, understory and overstory of the SF indicate that the future canopy will likely differ from its current composition. Most of the dominant canopy species are present in the seed bank and ground layer but are not present in the sapling and shrub layer, with the exception of *A. canadensis*. *Prunus serotina* is not an important component of the current forest canopy, yet by far, is the dominant species in the understory.

#### **Question 4. Is herbivory responsible for the documented change in vegetation composition and structure within the SF?**

Browse lines were noted within this forest in the 1980s (O'Connell *et al.*, 1989) and early indicator species present in the 1960s have already been reduced or extirpated (e.g., *Aralia nudicaulis*; H.W. Art, unpub. data). The white-tailed deer population has experienced rapid growth on the western portion of Fire Island, increasing from approximately 7 deer  $km^{-2}$  in 1983 to 80 deer  $km^{-2}$  in 2002 and 2003 (Underwood 2005). Other herbivores common within the SF include the eastern cottontail rabbit (*Sylvilagus floridanus*) and meadow vole (*Microtus pennsylvanicus*). Three decades of change in the plant community was described using permanent plots and nearly two decades of recovery using deer exclosures. In addition, we used short-term exclosures to isolate the effects of rabbit, vole and deer herbivory and the influence of canopy type on understory vegetation (Table 7).

#### *Long-term plots and deer exclosures*

Plant cover decreased within permanent plots from 1967 to 1986, with the cover of woody species declining from 19% to 6%, vine species from 7% to  $< 1\%$ , and herbaceous species from 7% to 2% (Table 8). Several woody and vine species including *V. corymbosum*, *A. canadensis*, and *T. radicans* significantly decreased to less than one percent cover. Though mean cover of several additional herbaceous species decreased over the time period, the sample size

Table 4. Importance values<sup>1</sup> of dominant woody species in canopy, shrub and sapling layers and in the seed bank relative to canopy gaps of the Sunken Forest, Fire Island National Seashore, New York.

Species	Canopy	Shrub & Sapling		Seedling & Herbaceous		Seed bank
		Gap	Closed	Gap	Closed	
<i>Ilex opaca</i>	28	4	–	3	3	7
<i>Nyssa sylvatica</i>	11	–	–	1	2	–
<i>Amelanchier canadensis</i>	22	–	55	18	14	1
<i>Sassafras albidum</i>	21	–	–	6	12	1
<i>Prunus serotina</i>	3	36	–	27	18	2
<i>Vaccinium corymbosum</i>	1	31	24	–	<1	–
<i>Gaylussacia baccata</i>	–	26	–	3	–	–
<i>Rhododendron viscosum</i>	1	–	18	–	1	–
<i>Rhus copallinum</i>	–	–	–	–	<1	26
<i>Rhus glabra</i>	–	–	–	–	–	2

<sup>1</sup>Importance values synthesize (Relative density + Relative basal area)/2 for canopy and sapling layers, (Relative density + Relative percent cover)/2 for herbaceous and seedling layer and relative density for seed bank.

Table 5. Mean cover and density ( $\pm$ standard error) of ground-layer vegetation in gap and closed canopy plots in the maritime *Ilex* forest. Paired t-tests were performed on differences of cover and density between plots (n=17).

Species	Cover (%)		p-value	Density (stems m <sup>-2</sup> )		p-value
	Gap	Closed		Gap	Closed	
<i>Prunus serotina</i>	21 $\pm$ 6.6	1.2 $\pm$ 0.3	<b>0.008</b>	7.8 $\pm$ 1.8	4.7 $\pm$ 1.0	0.378
<i>Gaylussacia baccata</i>	5.1 $\pm$ 5.1	0 $\pm$ 0	0.332	1.5 $\pm$ 1.5	0 $\pm$ 0	0.332
<i>Smilax rotundifolia</i>	3.7 $\pm$ 0.7	0.6 $\pm$ 0.1	<b>&lt;0.001</b>	9.8 $\pm$ 1.7	8.3 $\pm$ 1.1	0.584
<i>Parthenocissus quinquefolia</i>	3.6 $\pm$ 1.1	0.4 $\pm$ 0.1	<b>0.011</b>	4.7 $\pm$ 1.4	2.1 $\pm$ 0.6	0.099
<i>Sassafras albidum</i>	3.3 $\pm$ 1.4	0.7 $\pm$ 0.2	0.085	2.5 $\pm$ 0.8	1.4 $\pm$ 0.4	0.401
<i>Amelanchier canadensis</i>	2.5 $\pm$ 0.7	0.4 $\pm$ 0.1	<b>0.011</b>	14.4 $\pm$ 5.7	9.7 $\pm$ 5.0	0.232
<i>Trientalis borealis</i>	1.9 $\pm$ 0.9	0.2 $\pm$ 0.2	0.094	4.9 $\pm$ 3.1	2.5 $\pm$ 1.4	0.578
<i>Toxicodendron radicans</i>	1 $\pm$ 0.6	0.1 $\pm$ 0.1	0.173	0.4 $\pm$ 0.3	0.7 $\pm$ 0.4	0.585
<i>Rubus</i> sp.	0.9 $\pm$ 0.9	0 $\pm$ 0	0.332	0.2 $\pm$ 0.2	0 $\pm$ 0	0.332
<i>Ilex opaca</i>	0.7 $\pm$ 0.4	0.2 $\pm$ 0.1	0.259	1.4 $\pm$ 0.6	0.8 $\pm$ 0.4	0.729
ALL species*	44.7 $\pm$ 10.1	4.4 $\pm$ 0.6	<b>0.001</b>	49 $\pm$ 7.2	31.8 $\pm$ 6.1	<b>0.048</b>

\*Includes other species present at <0.5% cover and <1 stem m<sup>-2</sup>: *Aronia arbutifolia*, *Baccharis halimifolia*, *Carex* species, *Triadenum virginica*, *Maianthemum canadensis*, *Nyssa sylvatica*, *Pinus rigida*, *Teucrium canadense*, *Vaccinium corymbosum*, and *Vitis* species.

Table 6. Mean soil seed bank density and life history characteristics<sup>1</sup> for species common to the Sunken Forest, Fire Island National Seashore, New York.

<i>Species</i>	<i>Shade tolerance</i>	<i>Max age</i>	<i>Fruit type</i>	<i>Fruit maturation</i>	<i>Dispersed</i>	<i>Dispersal by</i> <sup>3</sup>	<i>Salinity tolerance</i>	<i>Seed bank density (m<sup>-2</sup>)</i>
<i>Ilex opaca</i>	Very tolerant	202 <sup>2</sup>	Drupe	Sept-Oct	March	B, A	Low	17.8+6.7
<i>Nyssa sylvatica</i>	Tolerant	600	Drupe	Sept-Oct	Sept-Nov	G, A, B	Low	-
<i>Quercus velutina</i>	Intermediate	200	Acorn	Aug-Oct	Sept-Dec	G, A	None	-
<i>Amelanchier canadensis</i>	Intermediate	78 <sup>2</sup>	Drupe	June	Summer	B, A	None	2.8+1.6
<i>Juniperus virginiana</i>	Intolerant	581	Berry-like cone	Sept-Nov	Feb-March	B, A	Low	-
<i>Quercus stellata</i>	Intolerant	371	Acorn	Sept-Nov	Sept-Dec	G, A	None	-
<i>Prunus serotina</i>	Intolerant	200	Drupe	July-Sept	Sept	G, B, A	None	3.7+2.6
<i>Pinus rigida</i>	Intolerant	200-350	Cone	Sept	Nov-Apr	W	None	-
<i>Sassafras albidum</i>	Intolerant	118 <sup>2</sup>	Drupe	Aug-Sept	Sept-Oct	B	None	1.9+1.3
<i>Rhus copallinum</i>	Intolerant	-	Drupe	Sept-Oct	Fall-spring	B, A	None	57.2+15.6

<sup>1</sup>Referenced from Davis (1996); Baskin and Baskin (1998); Dirr (1998); Hardin et al. (2001).

<sup>2</sup>Ages approximated based on cores from Sunken Forest.

<sup>3</sup>B=birds, A=other animals, G=gravity, W=wind.

Table 7. Description of establishment date, dimensions, and animals excluded by a series of exclosures used in the Sunken Forest, FIIS.

Target animal	Size (m <sup>2</sup> )	Mesh size (cm)	Establishment date	Sample size
Deer	169	7.6 x 15.2	1986	3
Rabbit*	1	1.3	2002	9
Deer and rabbit	1	2.5	2002	26
Vole*	0.25	1.3	2002	26

\*indicates this exclosure is nested within the larger exclosure listed directly above

Table 8. Mean percent cover ( $\pm$ se) of the ground-layer vegetation in 1967 and 1986 in Sunken Forest. Differences in cover between time periods were compared using a paired t-test (n=6).

Species or group	Cover (%)		Significance
	1967	1986	
Woody	18.9 $\pm$ 5.7	5.6 $\pm$ 2.4	**
<i>Vaccinium corymbosum</i>	8.5 $\pm$ 5.1	0	*
<i>Ilex glabra</i>	4.0 $\pm$ 4.0	0.1 $\pm$ 0.1	
<i>Amelanchier canadensis</i>	2.3 $\pm$ 0.7	0.7 $\pm$ 0.1	**
<i>Gaylussacia baccata</i>	0.5 $\pm$ 0.3	3.2 $\pm$ 2.2	
<i>Prunus serotina</i>	0.2 $\pm$ 0.2	0.5 $\pm$ 0.3	
<i>Ilex opaca</i>	0	0.1 $\pm$ 0.05	
Vine	7.2 $\pm$ 2.9	0.4 $\pm$ 0.1	**
<i>Toxicodendron radicans</i>	6.5 $\pm$ 3.0	0.1 $\pm$ 0.03	**
<i>Parthenocissus quinquefolia</i>	0.7 $\pm$ 0.4	0.1 $\pm$ 0.1	
Herb	6.5 $\pm$ 1.7	2.4 $\pm$ 2.0	*
<i>Aralia nudicaulis</i>	3.2 $\pm$ 1.7	0	*
<i>Pteridium aquilinum</i>	1.8 $\pm$ 1.0	0.02 $\pm$ 0.02	
<i>Trientalis borealis</i>	0.8 $\pm$ 0.5	0.4 $\pm$ 0.3	
<i>Smilacina stellata</i>	0.4 $\pm$ 0.1	0.02 $\pm$ 0.02	*
<i>Polygonum hydropiperoides</i>	0	1.8 $\pm$ 1.8	

\* significant at P<0.1, \*\* significant at P<0.05; results of paired t-test on log transformed cover values (raw means shown).

likely limited the ability to detect significant differences. *Aralia nudicaulis* represented almost half of the herbaceous cover in 1967 and was no longer present in any plots by 1986.

Changes during the same time period were also examined for each group of pairs in order to present the pre-condition changes that had occurred on the plots before the initiation of the deer herbivory experiment. The patterns of change presented in Table 9 indicate that most species were declining, with only a few exceptions, before 1986. The decrease in *T. radicans* in the unfenced plots appears to be the only change that is both biologically and statistically significant. Few differences in plant cover within fenced and unfenced plots were statistically significant from 1986 to 2002 although visual differences were striking in two of the three fenced plots. *Amelanchier canadensis* and *G. baccata* increased moderately (~0.5%) in plots that were exposed to deer, while declining in fenced areas (~0.3%, both P-values < 0.1). The differences in cover were slight again with *T. radicans* but the directions of change were reversed and cover declined in unfenced plots (P=0.05). Temporal changes in the understory are evident in the comparison of mean cover and density of plants in 1967 and 1986.

Significant decreases in both woody and vine species occurred in the two decades following the initial establishment of the permanent plots. The mean cover of nearly every herbaceous species declined during this time period as well, though the sampling effort was not great enough to accurately capture their patchy distribution within the understory.

#### *Rabbit herbivory*

Plots excluding rabbits had higher woody plant cover (28% vs. 13%, P=0.04) but not density (28 stems m<sup>-2</sup> for both, P=0.8) than those plots accessible to rabbits (Table 10). The density of all species was significantly higher in fenced than unfenced plots (121 vs. 90 stems m<sup>-2</sup>, P=0.01). The cover of *Trientalis borealis* tended to be higher in plots excluding rabbits, though differences were not statistically significant.

Conversely, the densities of *P. serotina* and *A. canadensis* were more abundant in the plots accessible to rabbits. *Smilax*, *T. borealis*, *S. albidum*, *Aronia arbutifolia* and *P. quinquefolia* had higher density in fenced plots, though again differences were not significantly different. The proportion of stems ≥ 0.5 m tall was not significantly different between open and fenced plots (P=0.52).

#### *Short-term paired plots*

By 2003, significantly more woody seedlings and vine species occurred in areas excluding voles (P-values=0.05 and <0.01, respectively; Table 11). The density of *Smilax* germinants was significantly greater in plots that excluded voles as well as deer and rabbits in both years plots were monitored (23 stems m<sup>-2</sup> versus 15 stems m<sup>-2</sup>, P<0.01 in 2003). The difference in the density of *P. serotina* stems likely accounts for the differences in woody stems observed (P=0.05). No significant differences in the percent cover of vegetation in plots fenced to deer and rabbit versus plots that additionally excluded voles were observed.

The cover of all species depended on the interaction of fencing and canopy type with significantly higher plant cover in fenced plots beneath mixed (26% in fenced vs. 10% in open plots) or exclusively deciduous canopy (34% in fenced vs. 22% in open plots) and the lowest

Table 9. Mean percent cover of the herbaceous layer measured in the plots used for the deer herbivory study in the Sunken Forest. The first two time periods (1967 and 1986) are included to represent pre-experiment conditions; plots were not fenced until after the vegetation survey in 1986. \* indicates a statistically significant ( $\alpha=0.1$ ) change based on paired t-test between cover in 1967-1986. No differences in cover were significant between 1986 and 2002.

	Fenced (n=3)			Unfenced (n=3)		
	1967	1986	2002	1967	1986	2002
All species	38.9	10.1	15.1	34.5	8.4*	8.6
Woody species	20.7	2.3	2.6	22.9	7.9	8.1
<i>Vaccinium corymbosum</i>	10.1	-	0.2	6.8	-	-
<i>Ilex glabra</i>	6	-	-	7.9	-	-
<i>Nyssa sylvatica</i>	1.7	0.1	0.1	-	-	<0.1
<i>Sassafras albidum</i>	0.9	0.1	0.2	2.6	1.0	0.6
<i>Aronia arbutifolia</i>	1	0.1	<0.1	0.9	0.7	-
<i>Ilex opaca</i>	-	<0.1	<0.1	-	0.1	<0.1
<i>Amelanchier canadensis</i>	0.8	1.1	0.9	3.4	0.3*	0.9
<i>Gaylussacia baccata</i>	-	0.8	0.4	0.9	5	5.4
<i>Prunus serotina</i>	<0.1	<0.1	0.8	<0.1	0.7	1.2
Vine species	10.8	3.5	3.6	7.9	5.9	5.7
<i>Toxicodendron radicans</i>	9.3	0.1	0.4	3.6	0.2*	<0.1
<i>Parthenocissus quinquefolia</i>	0.6	0.1	0.1	2.4	<0.1*	0.2
<i>Smilax rotundifolia</i>	0.4	2.5	3.1	1.6	2.1	5.5
<i>Smilax glauca</i>	0.4	0.8	-	0.3	3.6	-
Herbaceous species	8.3	7.7	12	5.6	0.2	0.3
<i>Aralia nudicaulis</i>	2.8	-	-	3.6	-	-
<i>Pteridium aquilinum</i>	2.8	-	-	1.6	0.1	-
<i>Smilacina stellata</i>	0.5	-	-	0.3	0.1	-
<i>Trientalis borealis</i>	1.5	0.8	4.9	0.2	<0.1	0.1
<i>Polygonum hydropiperoides</i>	-	6.3	6.3	-	-	-

Table 10. Mean cover (%) and density (stems m<sup>-2</sup>) in open and fenced to rabbit plots within permanent deer exclosures, FIIS 2003. An asterisk indicates a significant difference from a paired t-test (P-value=0.041).

	<b>Cover (n=3)</b>		<b>Density (n=3)</b>	
	<b>%</b>		<b>Stems m<sup>-2</sup></b>	
	<b>Open</b>	<b>Fenced</b>	<b>Open</b>	<b>Fenced</b>
Woody species	13.2 ± 5.1	27.7 ± 7.1*	28.2 ± 5.9	27.6 ± 6.8
Vine species	2.4 ± 0.6	4.8 ± 1.0	13.8 ± 4.3	23.9 ± 10.0
Herbaceous species	10.2 ± 3.7	17.9 ± 6.1	47.9 ± 15.9	69.6 ± 20.1

Table 11. Mean density of germinants in 2003 where all small to large herbivores were excluded versus where only medium and large herbivores were excluded. P-values are reported from paired t-test conducted on differences between fenced plots (n=26). The only two specific differences are reported.

	Voles permitted	Voles, rabbits & deer excluded	P
All species	69.3 ± 16.1	86.9 ± 24.0	0.08
Woody species	41.4 ± 8.5	47.2 ± 9.3	0.05
Vine species	22.0 ± 4.0	29.7 ± 5.0	<0.01
Herbaceous species	16.3 ± 14.0	23.2 ± 22.3	0.41
<i>Smilax rotundifolia</i>	14.7 ± 2.1	22.8 ± 3.9	<0.01
<i>Prunus serotina</i>	4.9 ± 0.8	6.9 ± 1.5	0.05

cover observed beneath the canopy with the highest proportion of holly (7% in fenced plots vs. 11% in open plots; Fig. 6). The main effect of canopy type showed no influence on plant cover, though it did affect the density of woody stems. Woody species were more numerous beneath a mixed canopy (54 stems m<sup>-2</sup>), than an exclusively deciduous (26 stems m<sup>-2</sup>) or exclusively evergreen canopy (17 stems m<sup>-2</sup>). The density of *A. canadensis* was the only significant specific response to canopy type (P=0.05).

Fencing had a stronger effect than canopy type on plant cover and density. Woody plant density was significantly higher in plots excluding deer and rabbits (40 vs. 25 stems m<sup>-2</sup>, P=0.04) and in plots excluding voles (47 vs. 33 stems m<sup>-2</sup>, P=0.06). *Amelanchier canadensis* density was significantly higher in fenced than unfenced plots (18 vs. 8 stems m<sup>-2</sup>, P=0.07). Several other statistically significant differences in species densities were found (due to fencing or the interaction of fencing and canopy), though few appeared to be biologically significant (differences of <1 stem m<sup>-2</sup>). The cover of woody species was significantly higher in fenced plots than unfenced plots (14% vs. 5%, P<0.01), attributable to higher percent covers of *S. albidum*, *N. sylvatica*, *G. baccata*, and *P. serotina* in fenced plots. The cover of vine species was slightly higher in fenced plots than unfenced plots in 2003 (6 vs. 2%, P<0.01) due primarily to differences in *Smilax* and *P. quinquefolia*.

Evidence of browsing was apparent on approximately a quarter of the total vegetation surveyed. Greater than 25% of *Smilax*, *P. serotina*, *S. albidum*, *N. sylvatica*, *G. baccata* and *R. viscosum* stems were browsed. The proportion of stems growing to over 0.5 m tall when fenced was significantly greater than stems in open areas (P<0.01).

Both the enclosure study and browsing survey illustrate the severe biotic impacts of browsing by deer on woody seedlings and saplings. Woody plant cover was highest where both deer and rabbits were excluded (Table 12). Though strong differences in vegetation were present in plots excluding both herbivores, only minor differences were evident in the areas fenced to rabbits or excluding voles, suggesting that white-tailed deer are the dominant herbivore within the SF.

Several species exhibited a trend of higher cover and density in plots excluding deer and rabbits versus plots only excluding deer, though differences were variable enough that these patterns were not statistically significant. The combination of herbivores appear to have additive and similar impacts on the most common woody and vine species that characterize the forest.

#### **Question 5. What are the prospects for conserving the essential character of the maritime holly forest under different disturbance regimes?**

*I. opaca* occurs in 44 SAF forest cover types of the eastern United States. Nowhere does it occur in a dominant or co-dominant position in the forest canopy except at SF and SH. In addition, its association with the canopy co-dominants in these two locations is unique to the northern range limits of the species, and together, define the maritime holly forest type. Disregarding the total vegetation community, which includes an undifferentiated flora of herbs, shrubs and vines, the primary task contained in the question is to determine the persistence of the type under different disturbance regimes.

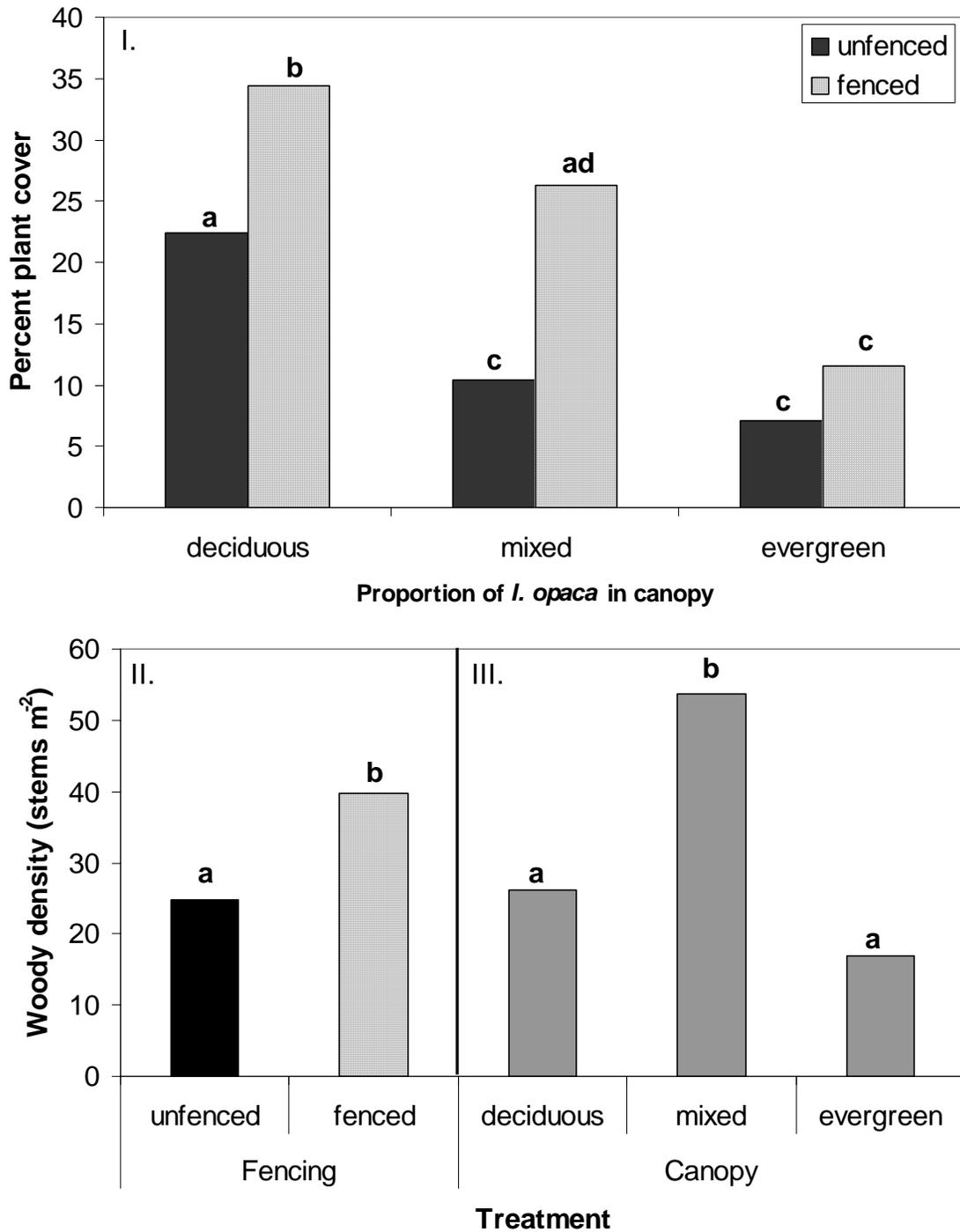


Figure 6. Simple effects and main effects for short-term enclosure experiment excluding rabbits and deer. I. Simple effects on the mean percent cover of all species. II-III. Main effects on the density of woody stems. Means with different letters within treatment are significantly different at  $\alpha=0.05$ .

Table 12. Additive changes in plant cover (%) and density (stems m<sup>-2</sup>) in exclosures established for two years versus those established for 17 years.

	short-term		long-term	
	cover	density	cover	density
All herbivores present	14 ± 5	58 ± 11		
Deer excluded			23 ± 6	81 ± 15
Deer & rabbit excluded	25 ± 5	80 ± 16	39 ± 7	108 ± 19
Deer, rabbit & vole excluded	29 ± 6	100 ± 25		

Using the mortality rates in Table 3 and stem density (no. ha<sup>-1</sup>) of canopy trees >10 cm dbf measured at the end of each time period, we conclude that only *I. opaca* is replacing itself based on the observed recruitment of new stems (Table 13). This conclusion holds for both time periods indicating failure of regeneration since 1986, and is corroborated by the age class distribution of cored stems in Figure 3. The intensity of herbivory is overwhelming the capacity of the forest to perpetuate itself true to type. Further, in the event of a major canopy disturbance, the other leading co-dominants will be replaced by *Prunus* resulting in a change in forest cover type (Fig. 7). The conservation of forest type under two levels of canopy disturbance and two levels of herbivory is illustrated in Table 14.

The first quadrant of Table 14 represents the status quo if nothing is done to alleviate the intensity of herbivory and a large, catastrophic canopy disturbance does not materialize in the near future. The forest type will eventually change as *Prunus* increases its dominance in the SF and *A. canadensis*, *N. sylvatica* and *S. albidum* are lost through normal attrition. The SF has occupied this state since 1986, and probably since the mid-1970s. Due to the very low mortality rates exhibited by these species to date, the status quo could be sustained for a very long time in the absence of catastrophic, stand-wide canopy disturbance.

The second quadrant pairs intense herbivory with a large, catastrophic canopy disturbance, which is the scenario leading to the quickest conversion of forest type. The forest of the future after a catastrophic canopy disturbance would be predicated entirely on the advance regeneration in the understory, which is dissimilar to the archetype. Recovery of type after such an event would take years and a large intervention on the part of managers.

The third quadrant attempts to ascertain what the SF would look like were herbivory to be alleviated coincident with a large, catastrophic canopy disturbance. Such a scenario, while seemingly unlikely, might come about through a destructive hurricane that not only causes massive disturbance to the canopy of the SF, but also reduces herbivory by the alteration of habitat, direct mortality on herbivores or both. The uncertainty in status of forest type is due to the time it takes for the extant vegetation to recover relative to the time it takes for the herbivores to reassert pre-disturbance browsing pressure.

The fourth quadrant represents a scenario lacking intense herbivory and large, catastrophic canopy disturbance, which allows seedlings to grow into recruitable size classes and leads to the conservation of the maritime forest cover type. The full exploration of these scenarios, including relevant ecological risks, requires computer simulation. Absent such a model, we offer these concluding observations for future consideration:

- 1) By virtue of the geographical orientation of Fire Island and a well-developed dune system, the SF has been buffered from storms capable of drastically disturbing the forest canopy. That such a storm event may never materialize in the future is uncertain, however.
- 2) Nearly four decades of intense herbivory have caused substantial change in the structure and composition of the vegetation community of the SF, particularly in the shrub and ground layers. Remarkably, only two species have been extirpated or nearly so.

Table 13. Stem density, mortality rate, projected annual stem losses and observed recruitment for characteristic canopy trees > 10 cm dbh within the Sunken Forest, Fire Island National Seashore. Positive differences (**bold**) indicate replacement in the canopy.

Species	1967-1986				
	density	mortality rate	deaths	recruits	difference
	Stems ha <sup>-1</sup>	Stems yr <sup>-1</sup>	Stems ha <sup>-1</sup> yr <sup>-1</sup>	Stems ha <sup>-1</sup> yr <sup>-1</sup>	Stems ha <sup>-1</sup> yr <sup>-1</sup>
<i>A. canadensis</i>	196	0.032	6.3	5.1	-1.2
<i>I. opaca</i>	382	0.009	3.4	4.3	<b>0.9</b>
<i>N. sylvatica</i>	68	0.021	1.4	0.4	-1.0
<i>S. albidum</i>	211	0.029	6.1	5.6	-0.5
overall	889	0.019	16.9		
1986-2002					
<i>A. canadensis</i>	205	0.025	5.1	4.1	-1.0
<i>I. opaca</i>	470	0.003	1.4	3.5	<b>2.1</b>
<i>N. sylvatica</i>	65	0.004	0.3	0.0	-0.3
<i>S. albidum</i>	235	0.020	4.7	3.3	-1.4
overall	1005	0.012	12.1		

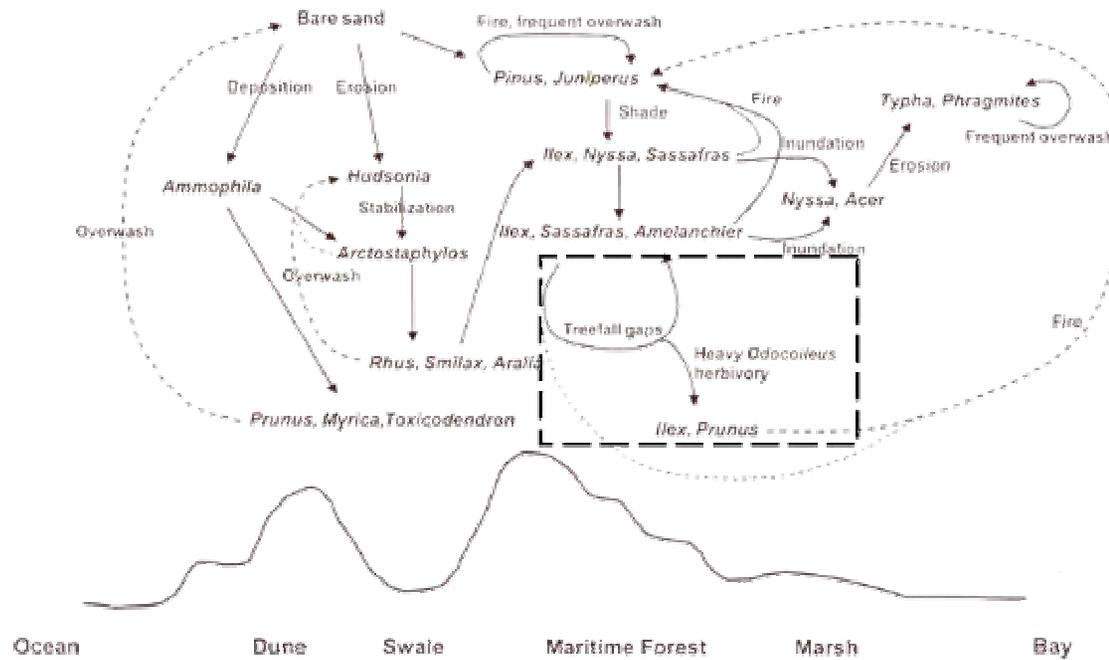


Figure 7. Successional model for the maritime holly forest on Fire Island National Seashore, NY. The model is adapted from Art (1976) and Backman and Patterson (1984) and includes the influence of treefall gaps and herbivory by deer (broken box).

Table 14. Status of forest type conservation of the maritime holly forest in the face of canopy disturbance and herbivory, Fire Island National Seashore, NY.

Herbivory	Canopy Disturbance	
	<i>frequent, small spatial extent (e.g., canopy gaps)</i>	<i>infrequent, large spatial extent (e.g., catastrophic canopy loss)</i>
<i>intensive</i>	status quo	status lost
<i>extensive</i>	status conserved	status uncertain

3) Greenbrier tangles and boardwalks provide functional refugia for many forest herbs; rescue of ground layer herbs and shrubs may be facilitated by incorporating refuges in the recovery plan.

4) In the absence of intense herbivory, recovery times for trees, shrubs and herbs can only be speculated based on known life-history characteristics of each species. Modeling and some experimentation may be necessary to make reasonable projections about recovery.

## CONSERVATION GOALS

The SF attains prominence in the enabling legislation of Fire Island National Seashore. Section 7 of the legislation (PL 88-587) states (*in part*) “*the Sunken Forest shall be preserved from bay to ocean in as nearly its present state as possible...*”. For over 20 years the park has been dealing with natural resource issues associated with documented increases in the numbers of deer island-wide. These issues have been particularly acute in western Fire Island due to the presence of the SF. In light of the implications of this research, we offer the following goal suggestions as a place to start:

Goal (1) *Reduce or eliminate intense browsing by deer and other forest herbivores to allow the rescue of recoverable species* — Because the SF is relatively small, the most expedient way in which to accomplish a reduction in herbivory is to erect a fence. There are a number of logistical constraints and issues associated with access that make building a fence somewhat problematic. First, the sandy substrate means that maintenance will be high to prevent gaps under the fence from emerging. In addition, the fence in some locations around the SF may capture and accumulate windborne sand creating a new set of maintenance problems. Moreover, the SF serves as escape cover for deer as well as a place to forage. Excluding them completely from the forest might force them into the adjacent communities. Finally, the SF cannot be completely enclosed due to the presence of boardwalks that facilitate movement of the visiting public. We recommend partial exclusion of large areas of the SF to promote recovery until a more permanent solution can be developed. Partial exclusion solves the problem of creating access for people and deer, promotes an experimental approach to recovery that will be visible and interpretable to the visiting public, provides scientists and managers with an idea of how best to accomplish recovery through experience, and allows the use of existing functional refugia to facilitate recovery of dwindling species.

Goal (2) *Develop an active propagation program for species which, by virtue of their life histories, will require assistance in their recovery* — We are reasonably certain that all native species found within the SF are still recoverable from local genetic seed stock. Establishing provenance, horticultural procedures and sources of extirpated species will be necessary for expedited recovery.

Goal (3) *Prepare a rigorous 10 year program of monitoring to document recovery of the structure and composition of the SF* — Aside from periodic monitoring of permanent enclosures, very little is known about how plants recover from intense herbivory. The size and location of the SF make it an ideal natural laboratory for learning about the recovery process of plants. Research areas to consider include: the relative competitive abilities of plants once released from

herbivory, the inhibitive role of secondary compounds, plant stem growth and spread, seed dispersal mechanisms, spatial location relative to the primary and secondary dunes, and the role of functional refugia in restoration success.

## **ACKNOWLEDGMENTS**

We gratefully acknowledge the National Park Service for their interest and financial support for this project. We especially thank Dr. Mary K. Foley, Chief Scientist in the Boston Support Office of the National Park Service for her continued and uncompromising support. Thanks to the staffs at Fire Island National Seashore and Gateway National Recreation Area for permitting and facilitating the research on the maritime holly forest fragments in their parks. Dr. Henry W. Art, Samuel Fessenden Clarke Professor of Biology at Williams College gave of his time, data, and incredible knowledge of and experience with the maritime holly forest. With his generous assistance, this work has been made substantially more comprehensive. This project was facilitated through a cooperative agreement between the United States Geological Survey, Patuxent Wildlife Research Center and the Research Foundation of the State University of New York, College of Environmental Science & Forestry.

## **LITERATURE CITED**

- Andrews, W. E. 1938. Report on plan to restore and protect Fire Island.
- Art, H. W. 1976. Ecological Studies of the Sunken Forest Fire Island National Seashore, New York. National Park Service Scientific Monograph Series Number 7, U.S. Government Printing Office, Washington, D. C.
- Backman, A. E. and W. A. Patterson III. 1986. Fire and the long-term development of the Sunken Forest at Fire Island, New York. In Horton, L.J., W. A. Patterson III, A. E. Backman and J. L. Rudnicky, State and Private Forestry A Cooperative Effort: Fire Regimes of Fire Island National Seashore. USDA-FS-NA.
- Baskin, C. C. and J. M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, NY. 666pp.
- Boose, E. R., K. E. Chamberlin, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. Ecological Monographs 71:27-48.
- Chrysler, M. A. 1930. The origin and development of the vegetation of Sandy Hook. Bulletin of the Torrey Botanical Club 57: 163-178.
- Davis, M. B. (ed.). 1996. Easter old-growth forests: prospects for rediscovery and recovery. Island Press, 383pp.
- Dirr, M. 1998. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses, 5<sup>th</sup> ed. Stipes Publisher, Champaign, IL, 1187pp.

- Everham, E. M., III, and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. *Botanical Review* 62: 113-185.
- Forrester, J. A. and D. J. Leopold. 2006. Extant and potential vegetation of an old-growth maritime *Ilex opaca* forest. *Plant Ecology* 183: 349–359.
- Forrester, J. A., D. J. Leopold and H. W. Art. 2007. Disturbance history and mortality patterns in a rare Atlantic barrier island maritime holly forest. *Natural Areas Journal* 27: 169-182.
- Forrester, J. A., D. J. Leopold and H. B. Underwood. 2006. Isolating the effects of white-tailed deer on the vegetation dynamics of a rare maritime American holly forest. *The American Midland Naturalist* 156: 135-10.
- Gleason, H. A. and A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2<sup>nd</sup> Edition. New York Botanical Garden. 910pp.
- Gornitz, V., S. Couch, and E. K. Hartig. 2002. Impacts of sea level rise in the New York City metropolitan area. *Global and Planetary Changes* 32: 61-88.
- Hardin, J. W., D. J. Leopold, and F. M. White. 2000. *Harlow and Harrar's Textbook of Dendrology*, 9<sup>th</sup> Edition. WCB/McGraw-Hill, New York, NY, 544pp.
- Leatherman, S. P. 1983. Barrier dynamics and landward migration with Holocene sea-level rise. *Nature* 301: 415-417.
- Leatherman, S. P. 1985. Geomorphic and stratigraphic analysis of Fire Island, New York. *Marine Geology* 63:173-195.
- Myers, R. K. and D. H. van Lear. 1998. Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. *Forest Ecology and Management* 103: 265-276.
- NatureServe. 2004. NatureServe Explorer: An online encyclopedia of life [web application]. Version 3.0. NatureServe, Arlington, Virginia. Available <http://www.natureserve.org/explorer>. (Accessed: April 25, 2004).
- O'Connell, A. F., Jr., M. W. Sayre, E. M. Bosler and H. W. Art. 1989. White-tailed deer ecology on Fire Island. *Park Science* 9: 4-5.
- Stalter, R. 1979. Some ecological observation on an *Ilex* Forest, Sandy Hook, New Jersey. *Castanea* 44: 202-207.
- Underwood, H. B. 2005. White-tailed Deer Ecology and Management on Fire Island National Seashore. Final Report to the National Park Service, General Management Planning Team. [http://www.ci.uri.edu/nacesu/Project\\_FIISGMP.htm](http://www.ci.uri.edu/nacesu/Project_FIISGMP.htm)
- Zhang, K., B. Douglas and S. Leatherman. 2002. Do storms cause long-term beach erosion along the U.S. east barrier coast? *The Journal of Geology* 110: 493-502.

APPENDIX I.

Updated species list for the maritime holly forests of Fire Island National Seashore, NY and Gateway National Recreation Area, NJ. Nomenclature follows Gleason and Cronquist (1991).

<b>Scientific Name</b>	<b>Common Name</b>
<i>Acer rubrum</i>	red maple
<i>Achillea millefolium</i>	yarrow; milfoil
<i>Agrostis gigantea</i>	red-top
<i>Amaranthus albus</i>	tumbleweed
<i>Amaranthus cannabinus</i>	salt-marsh water hemp
<i>Amelanchier canadensis</i>	eastern serviceberry
<i>Ammophila breviligulata</i>	beach grass
<i>Aralia nudicaulis</i>	wild sarsaparilla
<i>Arctostaphylos uva-ursi</i>	bearberry
<i>Aronia arbutifolia</i>	red chokeberry
<i>Artemisia campestris</i>	tall wormwood
<i>Artemisia stelleriana</i>	dusty miller; beach-wormwood
<i>Aster novo-belgii</i>	New York aster
<i>Atriplex patula</i> var. <i>hastata</i>	spearscale
<i>Baccharis halimifolia</i>	groundsel-tree; sea myrtle
<i>Berberis vulgaris</i>	European barberry
<i>Cakile edentula</i>	sea-rocket
<i>Carex pensylvanica</i>	sedge
<i>Carex silicea</i>	sedge
<i>Celastrus orbiculatus</i>	oriental bittersweet
<i>Celastrus scandens</i>	American bittersweet
<i>Chenopodium album</i>	lamb's quarters; pigweed
<i>Chimaphila maculata</i>	spotted wintergreen
<i>Cirsium horridulum</i>	yellow thistle
<i>Clethera alnifolia</i>	white alder; sweet pepper-bush
<i>Convolvulus sepium</i>	hedge bindweed
<i>Cuscuta compacta</i>	dodder
<i>Cyperus erythrorhizos</i>	redfoot flatsedge
<i>Cyperus rotundus</i>	nutsedge
<i>Cyperus strigosus</i>	false nutsedge
<i>Cypripedium acaule</i>	moccasin or pink lady-slipper
<i>Distichlis spicata</i>	salt-grass
<i>Drosera rotundifolia</i>	sundew

<b>Scientific Name</b>	<b>Common Name</b>
<i>Dryopteris carthusiana</i>	toothed woodfern
<i>Eleocharis acicularis</i>	spike-rush
<i>Eragrostis spectabilis</i>	purple lovegrass
<i>Euphorbia polygonifolia</i>	seaside spurge
<i>Galium</i> sp.	bedstraw
<i>Gaultheria procumbens</i>	wintergreen; checkerberry
<i>Gaylussacia baccata</i>	black huckleberry
<i>Geranium robertianum</i>	herb-Robert
<i>Hibiscus moscheutos</i>	rose-mallow
<i>Hieracium venosum</i>	veiny hawkweed
<i>Honckenya peploides</i>	seabeach sandwort
<i>Hudsonia tomentosa</i>	false heather
<i>Ilex glabra</i>	inkberry
<i>Ilex opaca</i>	American holly
<i>Iva frutescens</i> var. <i>oraira</i>	maritime marsh-elder
<i>Juniperus virginiana</i>	eastern red cedar
<i>Lactuca canadensis</i>	tall lettuce
<i>Lathyrus maritimus</i>	beach vetchling; wild-pea
<i>Lechea maritima</i>	pinweed
<i>Lonicera japonica</i>	Japanese honeysuckle
<i>Maianthemum canadense</i>	Canada mayflower
<i>Melampyrum lineare</i>	cowwheat
<i>Mitchella repens</i>	partridgeberry
<i>Monotropa uniflora</i>	indian pipe
<i>Myrica gale</i>	sweet gale
<i>Myrica pensylvanica</i>	northern bayberry
<i>Nyssa sylvatica</i>	black gum; black tupelo
<i>Oenothera parviflora</i>	small flowered evening-primrose
<i>Opuntia humifusa</i>	eastern prickly pear
<i>Osmunda cinnamomea</i>	cinnamon fern
<i>Osmunda regalis</i>	royal fern
<i>Panicum</i> spp.	panic-grass
<i>Parthenocissus quinquefolia</i>	Virginia creeper
<i>Phragmites australis</i>	common reed
<i>Phytolacca americana</i>	pokeweed
<i>Pinus banksiana</i>	jack pine
<i>Pinus rigida</i>	pitch pine
<i>Plantago lanceolata</i>	English plantain

<b>Scientific Name</b>	<b>Common Name</b>
<i>Pluchea odorata</i>	marsh-fleabane
<i>Polygonatum biflorum</i>	Solomon's seal
<i>Polygonella articulata</i>	jointweed
<i>Polygonum convolvulus</i>	black bindweed
<i>Polygonum punctatum</i>	dotted smartweed
<i>Prunus maritima</i>	beach-plum
<i>Prunus serotina</i>	black cherry
<i>Pteridium aquillinum</i>	bracken fern
<i>Quercus coccinea</i>	scarlet oak
<i>Quercus rubra</i>	northern red oak
<i>Quercus stellata</i>	post oad
<i>Quercus velutina</i>	black oak
<i>Rhododendron viscosum</i>	swamp azalea
<i>Rhus copallinum</i>	shining-sumac
<i>Ribes cynosbati</i>	dogberry
<i>Rosa carolina</i>	pasture rose
<i>Rosa rugosa</i>	Japanese rose
<i>Rubus allegheniensis</i>	common blackberry
<i>Rubus hispida</i>	swamp-dewberry
<i>Rumex acetosella</i>	red dock; sorrel
<i>Rumex crispus</i>	curly dock; sorrel
<i>Salsola tragus</i>	Russian thistle
<i>Sambucus canadensis</i>	common elder
<i>Sassafras albidum</i>	sassafras
<i>Sesuvium maritimum</i>	sea-purslane
<i>Smilacina stellata</i>	star-flowered Solomon's seal
<i>Smilax glauca</i>	sawbrier
<i>Smilax rotundifolia</i>	common greenbrier; catbrier
<i>Solidago odora</i>	licorice goldenrod
<i>Solidago sempervirens</i>	seaside goldenrod
<i>Spartina alterniflora</i>	smooth cord-grass
<i>Spartina patens</i>	salt-meadow cord-grass
<i>Suaeda maritima</i>	white sea-blite
<i>Teucrium canadense</i>	American wood-sage; germander
<i>Thelypteris palustris</i>	marsh fern
<i>Toxicodendron radicans</i>	poison-ivy
<i>Toxicodendron vernix</i>	poison-sumac
<i>Triadenum virginicum</i>	marsh St. John's-wort

<b>Scientific Name</b>	<b>Common Name</b>
<i>Trientalis borealis</i>	starflower
<i>Typha angustifolia</i>	narrow leaved cat-tail
<i>Vaccinium corymbosum</i>	highbush-blueberry
<i>Vaccinium macrocarpon</i>	cranberry
<i>Viburnum dentatum</i>	arrow-wood
<i>Vitis</i> sp.	grape
<i>Xanthium echinatum</i>	common cocklebur

As the nation's primary conservation agency, the Department of the Interior has responsibility for most of our nationally owned public land and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

**National Park Service**  
**U.S. Department of the Interior**



---

**Northeast Region**  
Natural Resource Stewardship and Science  
15 State Street  
Boston, Massachusetts 02109

<http://www.nps.gov/nero/science/>

**EXPERIENCE YOUR AMERICA™**