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TORREYA

Plant communities of the Napeague Dunes¹Ann F. Johnson²

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JOHNSON, ANN F. (Archbold Biol. Sta., Route 2 Box 180, Lake Placid, Florida 33852). Plant communities of the Napeague Dunes, Bull. Torrey Bot. Club 108: 76-84. 1981.—Using the Braun-Blanquet relevé method, this study documents the composition and soil profiles of three of the most mesic of the eight plant communities occurring on the Napeague Dunes, east of Amagansett, (Suffolk Co.) N.Y. Differentiation, both between and within communities, is related to the depth of the water table: in the pine forests, depth to water table is greater than 60 cm; in the tall shrub thickets, the median depth is 52 cm; in the cranberry bogs, the median depth is 16.5 cm. There is indirect evidence for autogenic succession from cranberry bog to tall shrub thicket. Succession from either of the latter to pine forest appears to require allogenic causes, such as sand burial from the the surrounding dunes. Floristically, the communities are more similar to those on the dunes at Cape Cod, Massachusetts, than to those on the barrier islands off the coast of New Jersey.

Key words: Napeague Dunes; Ronkonkoma terminal moraine; Montauk; succession.

The Napeague Dunes are a stretch of sand 6 km long by 1.5 km wide which heal a break in the Ronkonkoma moraine between the towns of Amagansett and Montauk, N.Y. They have recently been acquired by the state as an addition to Hither Hills State Park.

The source of sand for this deposit is wave erosion of the sea cliffs of glacial till forming Montauk Point. Shoals, 2 miles south of the present shoreline, indicate the probable former extent of the moraine. Its erosion supplied sand for building not only the Napeague Dunes, but also most of the beaches and barrier islands bordering the south shore of Long Island (Fuller 1914). The sand was (and is) transported by the westward-flowing longshore current.

It is possible that sand to build the dunes was also deposited by the waves of Napeague Bay on the north, connecting the west end of the morainal break with what appears to be an island of moraine separating Napeague Bay from Napeague Harbor. This island is mapped by the Suffolk County Soil Survey (1975) as Carver-Plymouth Sand (CpA), in contrast to the

surrounding Dune Sand (Du). Sand deposition on both the bay and ocean sides would help to explain the low wedge-shaped area trapped in the middle, known as Napeague Meadows (Fig. 1). Thus the age of the dune deposit can be bracketed between the time of the deposition of the terminal moraine (ca. 18,000 ybp) and the present.

The climate of the area is of the relatively mild, coastal type, characterizing the coastal plain of the northeastern United States from central New Jersey to Cape Cod, Massachusetts. In this region the length of growing season is greater than 180 days along the coast, becoming shorter as one moves inland or northward (USDA Yearbook 1941). Climate records for Bridgehampton, ca. 10 miles east of the dunes, are shown in Figure 2.

Eight plant communities occur on the Napeague Dunes: beach, dune heath, low shrub thicket, brackish meadow, tall shrub thicket, cranberry bog, and pine forest. Of these, the present study will describe only the last three, which are found intermingled in a mosaic in the central part of the dune deposit, furthest removed from the influences of salt spray, sand burial, and tidal action. The location of these communities is shown by the sample sites in Figure 1. Included also is an area of dunes east of Napeague Harbor, known as the "Walking Dunes." The other five communities are either very simple in species

¹ I am grateful to the Long Island State Park Commission for permission to collect on the site.

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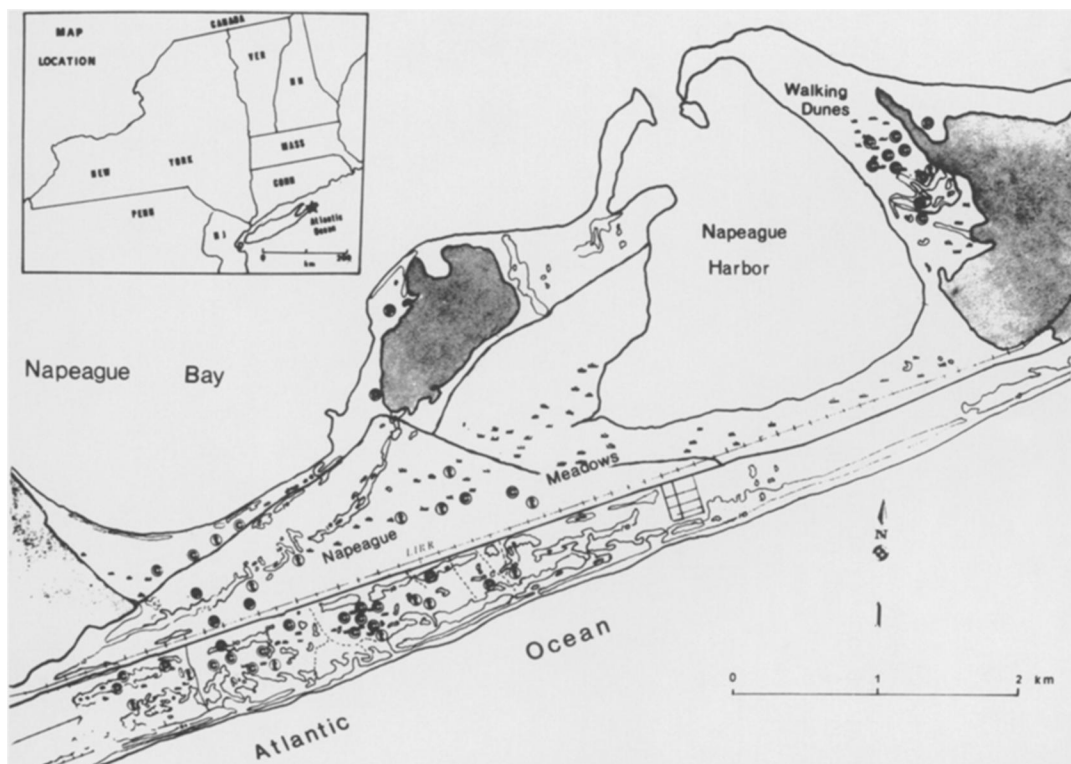


Fig. 1. Map of the Napeague Dunes. Shaded areas indicate Ronkonkoma moraine; clear areas indicate dune deposits. Circled letters are sample sites: c = cranberry bog, t = tall shrub thicket, p = pine forest.

composition, or vary in relation to factors other than substrate characteristics.

Methods. All communities were sampled using the Braun-Blanquet relevé method described by Mueller-Dombois and Ellenberg (1974). In the summers of 1975–6 a reconnaissance was made of the area, and the initial community types for sampling were selected. Relevés of 100 m² were used, except in the case of the smaller cranberry bogs and forest stands, where the area of the bog or stand itself was taken as a relevé. Per cent of ground covered by each species was estimated by eye using the Braun-Blanquet cover scale: 5 = 75–100%, 4 = 50–75%, 3 = 25–50%, 2 = 10–25%, 1 = 1–10%, + = < 1%, and r = few plants seen. Numbers and dbh of tree species were recorded. Relevés were made in the summers of 1977–1979. Twelve relevés of pine forest, 15 of tall shrub thicket, and 27 of cranberry bogs were made, the numbers reflecting the relative variability of each of the community types.

BRIDGEHAMPTON, N.Y. 10.5°C m.a.t.
40°57'N 72°18'W 1125 mm m.a.p.
66yrs of record

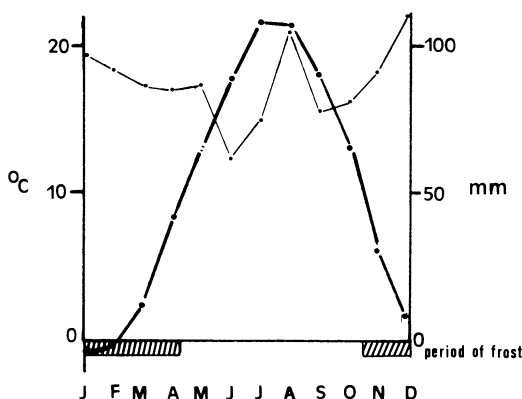


Fig. 2. Climate diagram for Bridgehampton, N.Y. Heavy line is average monthly temperature; lighter line, average monthly precipitation. Data from NOAA (National Oceanic and Atmospheric Administration), 1978.

Table 1. Napeague cranberry bogs: association table

		Relevés																											
Field No. ¹ Running No. ¹		12'	08	07	28	25	04	12	19	32	27	20	31	26	01	06	30	02	17	A	11a	18	10	15	23	24	25	26	27
Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	20	21	22	23	24	25	26	27			
	<i>Osmunda regalis</i>	3 ²	3	2	4	+	3	3	3	1	1	3	2																
	<i>Sphagnum palustris</i>	1	+	+	+	4	2	2	1	+	2		2		+	2													
	<i>Cladium mariscoides</i>	+	+	+	2			+			2		2				1												
	<i>Scirpus americanus</i>	3	4	3	+		3	3	3			3			2	4		2	2	1		3							
	<i>Juncus canadensis</i>	2	3	3	2		2	2	1		3		2		2	3	1	2	2	1		1							
	<i>Scirpus cyperinus</i>	+	+	+		2							+	2		+						+							
	<i>Lycopodium inundatum</i>	+																											
	<i>Xyris torta</i>	+										1																	
	<i>Panicum virgatum</i>																2												
	<i>Juncus dichotomus</i>				1																								
	<i>Andropogon virginicus</i> var. abbreviatus					+	+																						
	<i>Agalinis purpurea</i>	+																											
	<i>Polytrichum commune</i>																												
	<i>Vaccinium macrocarpon</i>	4	+	+	3	5	4	4	5	4	5	5	5	2	2	+	5	5	5	2	3		5	4	5				
	<i>Rhododendron viscosum</i>	+	+	+	2		+	+	+	2	1		2	3	+	+	+			+									
	<i>Pyrus arbutifolia</i>	+	+	+			+	+	+																				
	<i>Polygala cruciata</i>	+	+	+			+	+	+									2											
	<i>Vaccinium corymbosum</i>		+	+	2		+					+	2	2			1												
	<i>Clethra alnifolia</i>		+													+													
	<i>Cyperus dentatus</i>																												
	<i>Drosera filiformis</i>				1																								
	<i>Drosera intermedia</i>																												

Table 1.—(Continued)

		Relevés																											
Field No. ¹	Running No. ¹	12'	08	07	28	25	04	12	19	32	27	20	31	26	01	06	30	02	09	11b	18b	14	17	A	11a	18	10	15	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27			
Species																													
<i>Drosera rotundifolia</i>	+	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	
<i>Dryopteris thelypteris</i>	1	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Eleocharis tenuis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Eriophorum virginicum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Hypericum virginicum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Kalmia angustifolia</i>																												+	
<i>Lycopodium rubellus</i>																												+	
<i>Lyonia mariana</i>																													
<i>Myrica gale</i>	1																												
<i>Myrica pensylvanica</i>																												+	
<i>Osmunda cinnamomea</i>																												+	
<i>Pinus rigida</i>																												+	
<i>Pogonia ophioglossoides</i>																												+	
<i>Rhus radicans</i>																												1	
<i>Rhynchospora alba</i>																												1	
<i>Rhynchospora glomerata</i>																												1	
<i>Rubus hispidus</i>																												1	
<i>Solidago tenuifolia</i>	+	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>Spiraea latifolia</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Area (100 m ²)	10	600	15	0.6/1	30	1	1	0.25/0.6/1	2	1	0.5/0.4/0.3	1	0.14/0.68/1	1.2/0.35/1.6/1	1	4	1												
(pH values lost)																													
Depth to standing water (cm)	?	0	5	18	7	20	?	15	27	17	10	27	14	10	2	27	30	10	20	10	25	25	?	?	35	?	30		
Depth of peat layer (cm)	7	3	2	11	3	15	3	3	8	1	2	5	6	11	15	4	4	4	3	?	4	5	2	3	6	3	3		
No. of species/relevé	19	15	18	11	11	11	11	11	9	5	11	6	10	7	11	15	7	4	3	5	5	9	4	3	7	6	10		

¹ Field number refers to the number given the relevé in the field; running number to the number assigned it after it is ordered into a table.
² Braun-Blanquet cover classes are + = <1%, 1 = 1-10%, 2 = 10-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-100%.

Table 2. Napeague tall shrub thicket: association table.

	Relevés														
Field No.	1	6	3	15	8	14	2	13	12	10	11	4	5	7	9
Running No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Species															
Amelanchier sp.	2	3	1	5	5	2									
Rhododendron viscosum	5	3	3				4	4	3						+
Smilax rotundifolia	+		2	+	1	2	1								
Pyrus arbutifolia	2	1	1			+			+			4	3	5	5
Dryopteris thelypteris											+	1	2	2	1
Rhus radicans												1	2	2	1
Vaccinium corymbosum	2		4	2		4		2	4	5	1	3	3	2	2
Aralia nudicaulis										2	3		1		
Betula populifolia	+														
Carex pensylvanica	+			+											
Clethra alnifolia	1						2	+	+		+				
Gaylussacia baccata								+							
Ilex glabra								2			5				
Linaria canadensis									+						
Lyonia ligustrina	1					2									
Lyonia mariana	+							1	1						
Nyssa sylvatica											+				
Parthenocissus quinquefolia													+		+
Pinus rigida						2			+						
Polytrichum commune							+								
Prunus serotina			1		+										
Quercus alba	1								+						
Quercus ilicifolia	+							+			1				
Rubus sp.	+				+										
Rubus hispidus														2	
Trientalis borealis					+										
Vaccinium macrocarpon											+				
Area (100 m²)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
pH	3.7	4.4	4.4	5.5	5.9	4.2	4.2	4.3	4.3	4.5	4.2	4.6	4.1	5.3	5.2
Depth to standing water (cm)	58	38	34	73	58	48	55	61	56	60	60	48	39	33	38
Depth of peat layer (cm)	35	10	10	30	10	12	18	10	30	10	8	15	10	10	10
No. of species/relevé	12	3	5	5	5	7	5	6	9	2	7	4	6	5	7

Soil pits were dug in the center of each relevé to measure the depth of the soil horizons, and the depth to water table. In the tall thicket and pine forest communities, samples of the A₁ horizon (ca. 10 cm depth) were air dried and mixed with an equal weight of distilled water for pH determination.

Subjective selection of stands for sampling was thought to be more efficient for covering the range of variation present than uniform or random selection because 1) the communities were patchily distributed in small stands, and 2) a high proportion (25–50%) of the total number of stands present in the small area were sam-

pled. The open, one- or two-layered nature of the communities made it possible to estimate cover without further subdivision of the relevés into smaller units, e.g., 1 m² quadrats.

Results. The relevés for each community were organized into association tables (Tables 1–3) using the methods described by Mueller-Dumbois and Ellenberg (1974). Relevés having similar species composition were grouped together, and the diagnostic species (those present in some but not all of the relevés) were grouped together to produce the finished table.

CRANBERRY BOG (Table 1). Forty-three species were found in 27 relevés of this, the

most diverse and unpredictable in terms of species composition, of the three communities sampled. Cranberry bogs are usually found in rounded depressions of varying size scattered among the dune ridges or slightly higher ground occupied by pitch pine forest or dune heath (*Arctostaphylos uva-ursi*³ and *Hudsonia tomentosa*). Each bog is usually surrounded by a rim of the tall shrub thicket of varying thickness. Of the three communities studied, bogs occupy the surfaces nearest to the water table, with depth to standing water ranging from 0 to 35 cm, the median being 16.5 cm. All water table depths were measured three or more days after a rain.

Among the 27 relevés which are characterized by the cranberry, *Vaccinium macrocarpon*, two groups of diagnostic species are found which appear to separate the relevés into a drier and wetter phase on the basis of depth to water table (boxes in Table 1). Species characteristic of the wetter phase are *Scirpus americanus*, *Juncus canadensis*, *Osmunda regalis*, and *Sphagnum palustris*, where depth to water table ranges from 0 to 27 cm; those characteristic of the drier phase are *Lycopodium inundatum* and *Juncus dichotomus*, where depth to water table ranges from 25 to 35 cm. Bogs of the latter type are often found at the bottom of recent blowouts in the *Ammophila* dunes, surrounded by a thin border of young pitch pines and low shrubs. The number of species is lower in the drier bogs, with a median of only 5 species per relevé, compared to 10 per relevé for the wetter bogs. Several relevés contained few of the diagnostic species of either set and may have been intermediate in wetness, although their water table depths spanned the values of both the other groups. A typical soil profile for the cranberry bog community consists of a layer of peat from 2 to 15 cm deep, subtended by mud in some cases, or directly by gray sand in others, which extends to the water table.

TALL SHRUB THICKET (Table 2). Fifteen relevés yielded a total of 27 species in this community which consists of shrubs 2–4 m tall, forming a dense thicket with a sparse understory. It occurs on the pe-

riphery of cranberry bogs or in swales among the stabilized dunes. The characteristic species is highbush blueberry, *Vaccinium corymbosum*. This physiognomic type was the most difficult to sample using the cover estimate method, since one can neither look down on the community from above, nor walk around in it, but must look up at the shrub canopy from one point.

Again, as in the cranberry bogs, the diagnostic species of the tall shrub thicket appear to separate the relevés on the basis of depth to water table: a wetter group, characterized by *Pyrus arbutifolia*, *Dryopteris thelypteris*, and *Rhus radicans* with a range in depth to water table of 33–48 cm, and a drier group characterized by *Amelanchier* sp. and *Rhododendron viscosum* with a range in depth of 38–78 cm (boxes in Table 2). Tall shrub thicket often rims cranberry bogs, and, not surprisingly, the median depth to water table separates the two communities, that of the tall shrub thicket being 51.5 cm; of the cranberry bog, 16.5 cm. Number of species for both the wet and dry phases of the shrub thicket ranges from 2 to 12, with a median of 6, similar to that of the dry phase of the cranberry bogs. Soil profile is similar to that of the cranberry bogs, with the peat layer generally thicker, ranging from 8 to 25 cm, with a median of 10 cm, compared to a median of 4 cm for the cranberry bogs.

PINE FOREST (Table 3). Twelve relevés of pine forest yielded a total of 30 species in this community consisting of open stands of pitch pine with an understory of hairgrass, *Deschampsia flexuosa*, or bearberry, *Arctostaphylos uva-ursi*, and occasional shrubs of *Quercus ilicifolia* or *Myrica pensylvanica*. Although the total number of species in these relevés is high, they are not as evenly distributed in terms of percentage cover as in the other two communities: only eight species have a cover greater than or equal to 10% in the pine forests, compared to 11 species in the tall shrub thicket, and 27 such species in the cranberry bogs. Number of species per relevé ranges from 7 to 13 with a median of 9. Soil profile consists of an A₀ horizon 0.5–6 cm thick, subtended by grayish sand to a depth of 14–27 cm, followed by yellow sand to at least 60 cm. In all cases the water table was below 60 cm. Soil profile

³ Nomenclature follows Fernald, M. L. (1950) Gray's Manual of Botany, 8th edition. American Book Company, N.Y.

Table 3. Napeague pine forests: association table.

Field No Running No.	Relevés											
	12 1	18 2	8 3	1 4	3 5	4 6	5 7	6 8	7 9	15 10	16 11	17 12
Species												
Canopy												
Pinus rigida # >16cm dbh	8	9	12	8	11	11	18	5	20	32	38	20
“ “ # <16 cm dbh	30	11	6	13	15	5	5	23	2	0	0	4
“ “ # /100 m²	9	5	18	21	26	16	23	28	22	32	19	24
“ “ B-B cover scale	2	2	2	3	4	3	3	?	?	3	4	?
Quercus coccinea # >16 cm dbh				3								
Quercus stellata # >16 cm dbh							1					
Quercus velutina # >16 cm dbh		2								5		
Shrub layer (B-B cover scale)												
Quercus ilicifolia	+		1		1	1	3	1	1		+	
Myrica pensylvanica	1				1	2			1	1	1	
Pinus rigida (saplings)	1	1	2		1	1	1	2		1	1	1
Betula populifolia					1	1						
Prunus serotina										1		
Quercus prinoides								1				
Rhus radicans					1	+					2	1
Vaccinium angustifolium						+		1		2	1	
Vaccinium corymbosum					1	+	+			1	+	+
Herb layer (B-B cover scale)												
Deschampsia flexuosa	1	1	2	2	3	2	2	2	4	2	2	4
Arctostaphylos uva-ursi	2	2	5		2		2	1	1	1	2	2
Trientalis borealis					1	1	+		2	+	1	1
Aralia nudicaulis	+						+		1	+		
Carex pensylvanica		+						+				
Chimaphila maculata							+	+				
Cladonia sp.	1	1						1			1	1
Cypripedium acaule							1	+				
Dicranum condensatum	1			+					+			
Hudsonia ericoides	+											
Hudsonia tomentosa	1	1										
Maianthemum canadense				1								
Melampyrum lineare			+					+				
Panicum sp.	+			1								
Pinus rigida (seedling)	1			+								
Polytrichum commune	+	+										
Quercus coccinea (seedling)							1					
Quercus ilicifolia “	1		1				1				1	1
Quercus velutina “			1	1	+					1		
Smilax rotundifolia		+	1					+	1		+	
Area (100 m²)	4	4	1	1	1	1	1	1	1	1	2	1
pH	6.3	4.2	4.1	4.2	4.6	4.4	4.1	4.2	4.3	4.6	?	4.7
Depth A ₀ horizon (cm)	3.0	5.0	1.0	0.5	3.0	3.0	6.0	3.5	3.0	2.6	3.7	4.0
No. species/relevé	13	7	7	7	10	9	11	12	8	11	11	8

differences, indicating differences in drain-
age, may account for the small amount of
species overlap between the pine forests

and the other two communities, with four
species shared with the cranberry bogs,
and five with the tall shrub thickets. In

contrast, the latter two have 11 species in common. Only one set of diagnostic species was found for the pine forest community.

Discussion. SUCCESSION. One might suspect that the cranberry bogs would, over time, give way to tall shrub thicket. Peat deposition should eventually build up the surface sufficiently to permit invasion by shrubs, which would then shade out the bog species. There is indirect evidence to support this succession: 1) depth to water table is greater under tall shrub thicket than under cranberry bog, 2) the median thickness of the peat layer is 4 cm greater under the thicket than under the bog, and 3) shrubs (*Vaccinium corymbosum*, *Pyrus*, *Rhododendron*) are frequently noted in the cranberry bogs, making up varying degrees of cover.

Although young pines are seen in the cranberry bogs, and mature ones in the tall shrub thicket, there is no evidence in the form of increasing pine cover to show that autogenic processes could produce a succession from either of the latter two communities to pine forest. Once peat build-up reached the point where the rate of oxidation of the peat equalled the rate of accumulation, further build-up would cease. However, allogenic causes, such as sand blowing in from surrounding dunes, might have produced a surface high enough above the water table to support pine invasion. Soil cores of some bogs show alternating layers of peat and sand, indicating that the dunes were less well stabilized at various times in the past.

FLORISTIC RELATIONS. The plant communities of the Napeague Dunes appear to more closely resemble those of the Cape Cod dunes at Provincetown, Massachusetts (Holton 1972), than those of the New Jersey barrier islands, specifically those of Island Beach, New Jersey, described by Martin (1959). Cranberry bogs and forests dominated by *Pinus rigida* are confined to only a small portion of the north end of Island Beach. Most of the forested area is dominated by *Juniperus virginiana* with *Ilex opaca* and *Prunus serotina*. In place of cranberry bogs, the wetter areas are dominated by rushes, sedges, and cattails. Tall shrub thickets are characterized by *Vaccinium corymbosum*, as at Napeague,

but most of the other shrubs of this community at Napeague are rare or absent at Island Beach. These differences may be partly attributable to a milder climate, but, in the case of *Juniperus*, higher substrate pH may also be implicated (Au 1969).

Comparison with communities on the moraine, which would serve as seed sources for the dunes, shows the dune communities to be distinctive in several respects. Almost all of the species in the cranberry bogs and tall shrub thickets can be found in the kettleholes in the moraine at Montauk (Taylor 1923), but in very different proportions and associations, e.g., *Cephalanthus occidentalis*, a dominant in the kettles, is rare on the dunes, whereas *Vaccinium corymbosum*, rare in the kettles, is a dominant on the dunes. The dune pine forests recall the pine barrens of central Long Island, minus the dense shrub understory. It is possible that the lack of shrub understory in the dune forests is due to the poor nutrient supply of the dune soils. Woodwell *et al.* (1975), in a study of a pine-oak forest at Brookhaven, L.I., found the nutrient content of the tissues of the understory shrubs to be as much as twice the level in the tissues of the pitch pines.

In summary, this study points out the sharp vegetational and physiognomic differences characterizing three plant communities which form a complex mosaic in the center of the Napeague dune deposit. Starting from the initial deposit of bare sand, the interaction of plants and water table levels has produced three community types with three distinctive soil profiles. Comparison with communities of dune areas developed under similar conditions of substrate, climate, seed sources, and geological age (i.e. Provincetown, Fire Island), should illuminate the question of the predictability of community composition. It is hoped that this contribution will help to stimulate such comparative studies.

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