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A CLASSIFICATION OF COASTAL HEATHLANDS AND SANDPLAIN GRASSLANDS IN MASSACHUSETTS

PETER W. DUNWIDDIE

The Nature Conservancy, 217 Pine St., Suite 1100, Seattle, WA 98101

ROBERT E. ZAREMBA

The Nature Conservancy, 91 Broadway, Albany, NY 12204

KAREN A. HARPER

9826 76th Avenue, Edmonton, Alberta, T6E 1K5 Canada

ABSTRACT. A set of 372 vegetation relevés was collected from coastal sandplain communities on Nantucket, Cape Cod, and Martha's Vineyard. Sites on Nantucket had the highest average number of rare species and the lowest number of non-native species. We used TWINSPAN to identify major vegetation types from these data. The first division separated the samples into heathlands and grasslands. Heathlands subsequently were classified into two major types: 1) Tall Shrub, including Huckleberry-Scrub Oak (*Gaylussacia baccata-Quercus ilicifolia*) and Mixed Maritime Shrublands (*G. baccata, Myrica pensylvanica*, and others), and 2) Low Shrub, including Broom Crowberry (*Corema conradii*) and Bearberry (*Arctostaphylos uva-ursi*) Heathlands. The two major grassland types were designated Hairgrass (*Deschampsia flexuosa*) and Little Bluestem (*Schizachyrium scoparium*), after the dominant taxa. Hairgrass Grasslands included a Beach subtype often dominated by coastal species (*Ammophila breviligulata, Hudsonia tomentosa*), and a Heathy Grassland that includes many ericads and graminoids. Little Bluestem Grasslands were divided into several subtypes, including Weedy Grasslands with many introduced species, Pennsylvania Sedge Grasslands dominated by *Carex pensylvanica*, and High Diversity Native Sandplain Grasslands, which included many rare species, few exotics, and high species diversity. We discuss successional relationships among sandplain vegetation types.

Key Words: sandplain grassland, coastal heathland, community classification, two-way indicator species analysis, *Schizachyrium scoparium, Arctostaphylos uva-ursi, Gaylussacia baccata, Deschampsia flexuosa, Quercus ilicifolia*

The easternmost grasslands in North America occur in the coastal sandplains of the northeastern United States from Long Island (New York) to Cape Cod (Massachusetts). Similar to midwestern prairies, they usually are dominated by *Schizachyrium scoparium*, but also include a distinctive association of primarily coastal taxa. Many regionally and globally rare plants occur in

the sandplain grasslands, including such taxa as bushy rockrose (*Helianthemum dumosum*), yellow sandplain flax (*Linum intercursum*), sandplain blue-eyed grass (*Sisyrinchium fuscatum*), sandplain gerardia (*Agalinis acuta*), and eastern silvery aster (*Aster concolor*). The grasslands also provide critical habitat for various uncommon or declining fauna, including Short-eared Owls (*Asio flammeus*), Northern Harriers (*Circus cyaneus*), Upland Sandpipers (*Bartramia longicauda*), Grasshopper Sparrows (*Ammodramus savannarum*), and Regal Fritillary Butterflies (*Speyeria idalia*). This community is referred to variously as maritime grassland (Reschke 1990), New England sandplain grassland (Maine Natural Heritage Program 1991), or terrestrial *Schizachyrium scoparium* medium-tall graminoid vegetation (Sneddon and Metzler 1992). It is considered endangered throughout its range, where considerable efforts are being made to preserve and manage the remaining examples (Massachusetts Natural Heritage Program 1982; Rawinski 1984; Godfrey and Alpert 1985).

The coastal sandplain grasslands frequently include a large component of woody species, many of which are ericads. Where heath taxa are dominant, the community has been termed maritime or coastal heathlands (Reschke 1990), and can be found from New Jersey to the Canadian Maritimes. In Massachusetts, heathland and grassland plants are often intermixed, and the communities sometimes are not readily distinguished. They often share many species with other coastal communities, such as sand dunes and scrub oak/pitch pine (*Quercus ilicifolia/Pinus rigida*) barrens.

The past extent of coastal grasslands and heathlands is uncertain. A few historical accounts describe the presence of maritime grasslands along the coast, and suggest that they may predate European settlement (Harper 1912). Furthermore, it is unlikely that the many rare native species found in the coastal sandplain communities arrived in the last 300 years, the period since settlement in this area by Europeans. However, fossil pollen studies on Cape Cod and Nantucket indicate that grasslands and heathlands became extensive only following settlement (Winkler 1985; Tzedakis 1987; Dunwiddie 1989, 1990). The species found in these communities today most likely existed prior to European settlement in openings close to the coast where salt spray suppressed the growth of woody plants, and in openings created by windstorms, fires, and aboriginal agricultural activities.

Forest clearance to create fields for crops and pastures quickly

followed settlement in the 1600s (Dunwiddie 1990). Cultivation of crops often was brief, as soils were exhausted quickly (Macy 1835), but grazing, fire, salt spray, and other disturbances probably helped to maintain grasslands and heathlands in many areas for several hundred years. Introduced pasture grasses did poorly in the acidic, droughty soils, and native grassland species thrived in the pastures and abandoned fields. With the widespread abandonment of sheep grazing in the late 1800s on Cape Cod, Nantucket, and Martha's Vineyard many grasslands and heathlands have been overtaken by taller shrub and forest vegetation (Dunwiddie 1992, 1994; Dunwiddie and Adams 1994).

Today, many conservation organizations are working to preserve rare grasslands and heathlands (Godfrey and Alpert 1985). A top priority has been to develop ecological management strategies for slowing or reversing the succession of shrubs and trees (Dunwiddie and Caljouw 1990). This management has been hampered by an incomplete understanding of the compositional, environmental, successional, and historical relationships among these vegetation types. This study was undertaken to develop a classification of coastal grasslands and heathlands in Massachusetts based on their vegetational composition. Using data sets from sites on Cape Cod, Nantucket, and Martha's Vineyard, we differentiate major types of grasslands and heathlands in this region, identify those types that are most likely to contain rare species, and propose likely successional relationships among them.

METHODS

The grasslands and heathlands on Nantucket, Martha's Vineyard, and Cape Cod (Figure 1) all occur within a few kilometers of the coast on coarse-grained glacial moraine and outwash deposits. Sites were chosen for sampling based on personal knowledge and on information from the files of the Massachusetts Natural Heritage and Endangered Species Program. At each site we noted the area and extent of communities and made general descriptions of topography, land use, location, recent disturbance history (if known), and species composition.

Locations for relevés were selected to characterize the range of vegetation types that occurred at each site. The initial data set for this study consisted of 233 relevés collected on Nantucket in

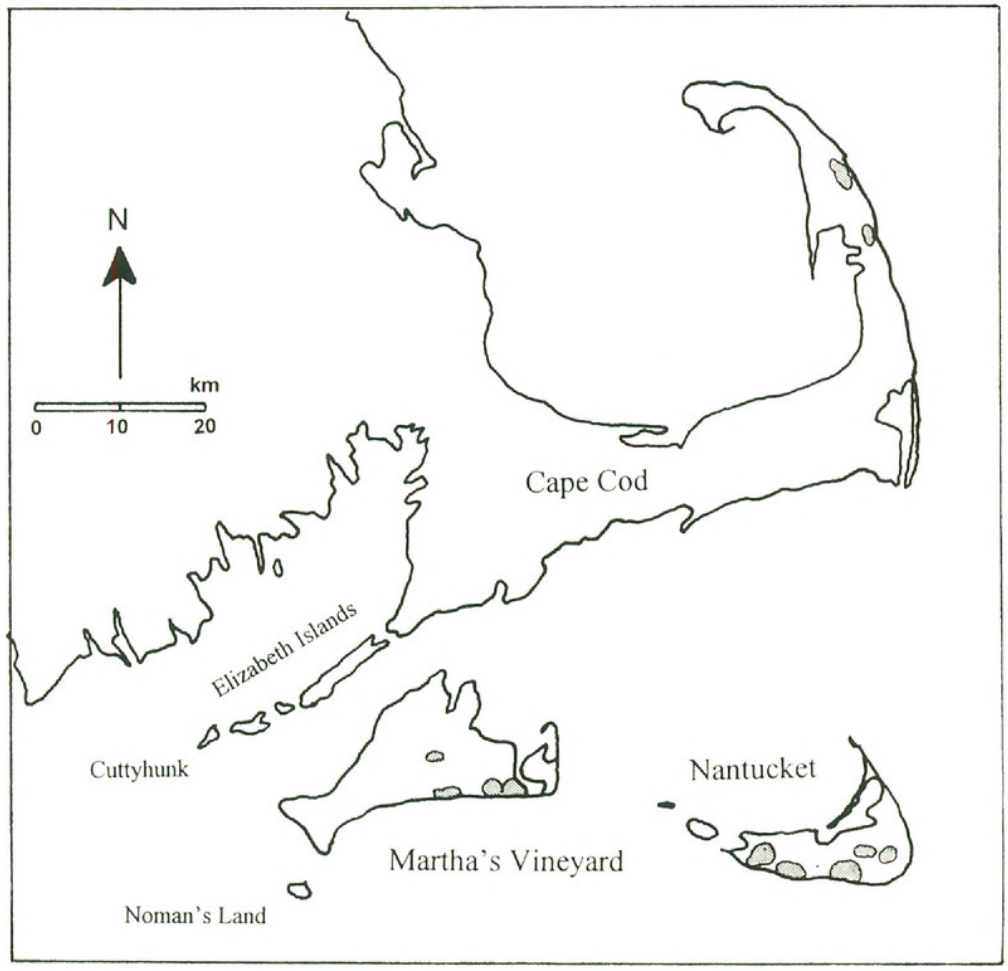

Figure 1. Locations in southeastern Massachusetts mentioned in the text. The larger grasslands and heathlands in which many relevés were located are indicated with shading. Small sites are not depicted.

1982. To maintain consistency among the data, we used the same methodologies to collect 119 additional relevés on Cape Cod and Martha's Vineyard in 1992, and an additional 20 from Nantucket. This methodology consisted of listing all species encountered within a 10 m radius plot and ranking them on a dominance scale of 1 (low) to 4 (high). Dominance values (d.v.) of 1 corresponded to rare species in each plot with <1 percent cover; values of 4 were assigned to dominant species with cover values that generally were much >50 percent. Values of 2 and 3 distinguished intermediate levels of abundance, with a cover of about 15 percent roughly separating these two classes. This methodology adequately distinguished dominant from minor species on sites and

yielded comparable results when applied by different investigators.

A total of 372 relevés, including 253 from Nantucket, 28 from 13 sites on Martha's Vineyard, and 91 from 37 sites on Cape Cod, were ordinated and classified using two-way indicator species analysis (TWINSPAN; Hill 1979) from the Cornell Ecology Program. TWINSPAN distinguishes groupings of sites with similar species associations and is particularly helpful where the high number of species and samples may obscure elements in common between sites (Jongman et al. 1987). Community classifications make more intuitive sense when based on common species rather than on species that only occur infrequently, so we explored various combinations of weightings of the dominance values. Several trials yielded similar results, and we present here results in which weights of 10 and 5 were attached to the more common species (d.v. = 4 and 3), and less common species (d.v. = 2 and 1) were left unweighted.

We included all 274 taxa recorded from the relevés in the first trial TWINSPAN classification, and made several adjustments in subsequent trials. Species for which some taxonomic confusion in the field may have resulted in differential identification by the various data gatherers were combined into several composite "supertaxa," such as species of *Agrostis,* mosses, and a few minor taxa. Lichens were omitted entirely as input to the classification since they were not identified to species. Ten relevés formed anomalous small groupings, and were discarded in the final classification. Nomenclature follows Gleason and Cronquist (1991).

For each of 20 Nantucket relevé sites, four replicate soil samples were taken from the top 15 cm of the soil profile, excluding the litter layer. Soil pH was measured in 0.01 M $CaCl_2$, and texture (percent sand, silt, and clay) was determined using Bouyoucos hydrometer methods. Exchangeable cations (magnesium, calcium, sodium, potassium) were measured by shaking samples in 1N ammonium acetate for 30 minutes, and analyzing the supernatant using a Jobin-Yvon Inductively Coupled Plasma spectrophotometer. Organic carbon:nitrogen ratios were measured using a Perkin-Elmer 2400 CHN.

RESULTS

Most of the groups of relevés produced by the dichotomies in the TWINSPAN classification include recognizable associations

Table 1. Percent frequency of species in grassland and heathland relevés. Vegetation types are derived from TWINSPAN classification (Figure 2): GL = Grassland, LB = Little Bluestem, W = Weedy, PS = Pennsylvania Sedge, HDN = High Diversity Native Sandplain Grassland, Hg = Hairgrass, HG = Heathy Grassland, B = Beach Grassland, HL = Heathland, LS = Low Shrub, BB = Bearberry, BC = Broom Crowberry, TS = Tall Shrub, HSO = Huckleberry/Scrub Oak, MMS = Mixed Maritime Shrubland. In general, species are arranged according to their decreasing frequency in several major

TWINSPAN Group	I	A	A1	A2a	A2b
Vegetation Type	GL	LB	W	PS	HDN
Schizachyrium scoparium	92	96	95	92	99
Carex pensylvanica	84	91	72	100	97
Arctostaphylos uva-ursi	76	62	15	50	91
Danthonia spicata	75	80	54	77	95
Lechea maritima	69	60	15	50	88
Myrica pensylvanica	68	72	77	50	77
Aster linariifolius	68	60	33	54	76
Quercus ilicifolia	63	53	38	73	54
Aster paternus	61	67	26	54	93
Vaccinium angustifolium	61	71	56	81	74
Gaylussacia baccata	57	70	49	62	84
Rosa virginiana	52	64	41	77	72
Deschampsia flexuosa	50	25	21	54	18
Quercus prinoides	25	27	8	35	35
Hudsonia ericoides	46	35	5	27	54
Comptonia peregrina	19	22	18	35	20
Aster dumosus	47	68	69	58	72
Rubus flagellaris	43	55	74	50	47
Pinus rigida	41	30	44	46	18
Epigaea repens	29	40	23	23	55
Helianthemum dumosum	37	43	8	54	58
Viburnum dentatum	34	46	46	35	50
Solidago puberula	23	27	26	31	26
Hieracium venosum	38	38	8	19	61
Aronia arbutifolia	14	19	21	15	19
Helianthemum propinquum	33	35	10	31	50
Amelanchier nantucketensis	13	17	8	23	20
Vaccinium pallidum	10	11	18	19	4
Gaultheria procumbens	8	12	13	15	9
Panicum spp.	40	37	31	38	41
Corema conradii	8	4	3	8	3
Corylus cornuta	3	3	0	4	4
Solidago nemoralis	51	57	41	35	73
Chrysopsis falcata	51	42	10	38	61
Juncus greenei	43	55	62	54	53
Agrostis spp.	22	32	85	46	45
Euthamia tenuifolia	31	45	41	58	43

Table 1. Extended.

sandplain vegetation types identified in the column headings, including (top to bottom): Grasslands (I), Heathlands (II), HDN Sandplain Grasslands (A2b), Weedy Grasslands (A1), and Beach Grasslands (B2). The table includes only species that occurred in >25 percent of the relevés of at least one vegetation type, as well as a few taxa listed as endangered, threatened, or of special concern by the Massachusetts Natural Heritage and Endangered Species Program (1992).

B	B1	B2	II	C	C1	C2	D	D1	D2
Hg	HG	B	HL	LS	BB	BC	TS	HSO	MMS
84	93	70	69	76	79	71	64	74	45
74	93	42	81	82	88	71	81	91	62
98	100	94	84	100	100	100	73	94	34
66	91	24	54	75	79	65	42	56	17
83	79	91	25	35	35	35	19	26	7
61	61	61	62	53	56	47	67	67	69
80	86	70	62	78	79	76	52	72	14
79	84	70	90	98	97	100	86	98	62
52	80	3	57	63	65	59	54	76	14
45	71	0	77	76	79	71	77	89	55
36	52	9	87	76	74	82	93	94	90
31	45	9	58	31	26	41	75	65	93
88	80	100	58	86	91	76	41	52	21
20	30	3	63	63	50	88	63	80	31
64	73	48	57	75	74	76	46	61	17
13	18	6	52	55	47	71	51	57	38
13	21	0	43	31	26	41	49	52	45
25	32	12	43	25	24	29	53	41	76
58	50	73	41	80	79	82	17	22	7
10	16	0	36	27	15	53	41	50	24
27	39	6	33	37	32	47	30	39	14
16	25	0	31	20	29	0	37	37	38
18	29	0	31	39	35	47	25	39	0
37	48	18	29	29	35	18	29	41	7
8	13	0	26	20	15	29	30	28	34
30	46	3	25	31	32	29	22	30	7
7	11	0	25	24	18	35	27	24	31
9	14	0	25	27	24	35	24	31	10
2	4	0	22	22	15	35	23	35	0
45	39	55	21	39	35	47	10	13	3
15	14	15	20	51	26	100	1	2	0
2	4	0	10	8	6	12	12	7	21
42	59	12	16	24	26	18	11	13	7
65	61	73	11	14	21	0	10	15	0
22	30	9	4	0	0	0	6	6	7
9	11	6	3	0	0	0	5	2	10
8	13	0	15	8	12	0	19	13	31

Table 1. Continued

TWINSPAN Group	I	A	A1	A2a	A2b
Vegetation Type	GL	LB	W	PS	HDN
Potentilla canadensis	23	32	23	15	43
Rubus hispidus	28	40	49	19	42
Sisyrinchium fuscatum	15	22	3	8	36
Aster patens	17	21	3	23	30
Aster solidagineus	11	17	8	15	23
Linum intercursum	7	12	8	12	15
Aster concolor	1	2	0	0	4
Liatris scariosa	5	6	0	4	11
Baptisia tinctoria	28	37	41	42	32
Festuca ovina	37	44	72	38	31
Solidago rugosa	14	20	64	8	1
Festuca rubra	16	19	56	12	3
Rumex acetosella	28	35	46	35	28
Toxicodendron radicans	23	27	44	15	22
Poa pratensis	11	15	44	12	1
Anthoxanthum odoratum	11	15	41	4	5
Juniperus virginiana	14	14	41	8	3
Hypochoeris radicata	11	13	41	8	0
Prunus serotina	29	26	38	23	20
Cirsium pumilum	17	24	36	15	22
Potentilla simplex	14	21	36	19	14
Holcus lanatus	7	10	33	0	1
Hieracium piloselloides	6	9	28	4	1
Panicum virgatum	6	10	28	12	0
Solidago odora	15	14	26	23	5
Hypericum perforatum	9	10	26	4	4
Plantago lanceolata	5	8	23	0	3
Asclepias syriaca	4	6	23	0	0
Asclepias tuberosa	3	5	13	8	0
Carex umbellata	21	12	10	19	9
Ammophila breviligulata	21	12	5	23	12
Prunus maritima	19	9	5	27	5
Asclepias amplexicaulis	6	4	5	8	1
Solidago sempervirens	12	9	3	4	14
Hudsonia tomentosa	15	2	3	4	1
Polygonella articulata	11	4	0	4	5
Number of vascular species	26.5	29.6	32.8	26.4	29.0
Number of rare species	0.8	1.0	0.4	1.0	1.3
Number of non-native spp.	1.6	2.2	5.3	1.1	0.9
Number of ericaceous spp.	4.1	4.2	3.0	4.0	4.9
Number of other shrubs	4.6	5.0	6.1	5.2	4.4
Number of graminoid spp.	6.4	6.9	8.9	6.8	5.9
Number of forb species	11.4	13.5	14.8	10.3	13.8

Table 1. Extended, Continued.

B	B1	B2	II	C	C1	C2	D	D1	D2
Hg	HG	B	HL	LS	BB	BC	TS	HSO	MMS
8	13	0	10	6	9	0	13	17	7
9	13	3	19	4	3	6	28	30	24
4	7	0	5	4	6	0	6	7	3
11	18	0	15	18	21	12	13	15	10
1	2	0	1	2	0	6	1	2	0
0	0	0	1	0	0	0	1	2	0
0	0	0	1	0	0	0	1	0	3
2	4	0	8	6	3	12	10	13	3
15	20	6	18	24	12	47	14	19	7
26	32	15	3	4	6	0	2	2	3
3	2	6	2	0	0	0	4	6	0
11	5	21	1	2	3	0	0	0	0
18	14	24	1	0	0	0	1	2	0
17	14	21	1	2	3	0	1	2	0
3	5	0	1	2	3	0	0	0	0
3	4	3	1	0	0	0	1	2	0
13	13	15	2	2	3	0	2	4	0
8	4	15	0	0	0	0	0	0	0
35	30	42	12	14	21	0	11	7	17
4	5	3	4	4	6	0	5	4	7
3	5	0	3	0	0	0	5	6	3
1	2	0	0	0	0	0	0	0	0
1	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
16	13	21	4	4	6	0	5	7	0
7	9	3	2	2	3	0	2	4	0
1	2	0	1	0	0	0	1	0	3
1	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
35	16	67	4	10	15	0	1	2	0
34	16	64	5	10	12	6	2	2	3
35	21	58	14	12	12	12	16	7	31
10	2	24	2	6	9	0	0	0	0
17	4	39	1	2	3	0	0	0	0
35	7	82	1	2	3	0	0	0	0
21	4	52	1	4	6	0	0	0	0
21.7	23.2	19.2	19.4	20.9	20.9	20.8	18.5	20.9	14.1
0.5	0.7	0.2	0.9	1.2	0.8	1.8	0.7	0.8	0.5
0.8	0.8	0.8	0.1	0.1	0.2	0.0	0.1	0.1	0.1
4.0	4.4	3.2	5.3	5.7	5.2	6.7	5.1	5.9	3.4
4.0	4.2	3.7	4.7	4.5	4.5	4.6	4.8	4.7	5.0
5.6	5.8	5.3	3.3	4.1	4.3	3.8	2.8	3.2	2.0
8.2	8.8	7.0	6.1	6.5	7.0	5.6	5.8	7.0	3.7

of species that are encountered frequently within the coastal sandplain communities (Figure 2; Table 1). We have attached informal names that describe distinctive features of most groups, which also are distinguished by Roman numerals, letters, and numbers to differentiate hierarchical levels in the dichotomies.

Distinguishing grasslands and heathlands. The first TWINSPAN division separates the samples into two groups that reflect graminoid-dominated sandplain grasslands (Group I, with 228 relevés) and shrub-dominated heathlands (Group II, with 134 relevés). Three of the five species that occur most frequently in the grasslands are graminoids, including *Schizachyrium scoparium, Carex pensylvanica*, and *Danthonia spicata*, whereas four of the top five species in heathlands are woody, including *Quercus ilicifolia, Gaylussacia baccata, Arctostaphylos uva-ursi,* and *Vaccinium angustifolium*. Nevertheless, there is significant overlap in species composition between these communities; seven of the ten most frequent species in each community are the same, and these species occur in over 60 percent of the relevés. These include *A. uva-ursi, C. pensylvanica, S. scoparium, Q. ilicifolia, Aster linariifolius, Myrica pensylvanica,* and *V. angustifolium*.

Overall, the grasslands are considerably more species-rich than the heathlands; on average, 37 percent more species occur in the former (26.5 vs. 19.4 spp./relevé; Table 1). This richness is contributed largely by forbs, which are nearly twice as abundant in the grasslands than in the heathlands (11.4 vs. 6.1 spp./relevé; Table 1). Species considered to be endangered, threatened, or of special concern by the Massachusetts Natural Heritage and Endangered Species Program (1992) have similar frequencies in both grassland and heathland relevés, occurring in 58% and 57% of the relevés, respectively. Thirteen of the 22 endangered, threatened, special concern, or watch list species found in grasslands or heathlands in Massachusetts were encountered in the relevés (Table 2). Grasslands also tend to have more introduced species than heathlands (1.6 vs. 0.1 spp./relevé; Table 1). Of the 45 species of non-native taxa found in the relevés, only 10 occurred in heathlands, and all of these were much more abundant in grasslands. Relevés in Nantucket grasslands and heathlands tend to have more rare species (1.0 $\pm$ 0.9) than those from either Cape Cod or Martha's Vineyard (0.3 $\pm$ 0.5; 0.7 $\pm$ 0.7). They also tend

Table 2. Rare native plants occurring in coastal sandplain grasslands and heathlands. Species rank within Massachusetts (Mass. Nat. Her. & End. Spp. Prog. 1990, 1992): E = Endangered, T = Threatened, SC = Special Concern, WL = Watch List. Species preceded by > were present in relevés in this study. Occurrence data based on this study and personal records. G = Predominantly sandplain grasslands, H = Predominantly heathlands, G-H = Found in both grasslands and heathlands, ! = Exclusively in one community, * = Relevé occurrences predominantly in HDN Sandplain Grassland (Group A2b).

Species	Rank	Occurrence
Agalinis acuta (Sandplain Gerardia)	E	G!
>*Amelanchier nantucketensis* (Nantucket Shadbush)	SC	G-H
Aristida purpurascens (Purple Needlegrass)	T	G
Asclepias purpurascens (Purple Milkweed)	T	G
>*Asclepias tuberosa* (Butterflyweed)	WL	G
>*Aster concolor* (Eastern Silvery Aster)	E	G-H*
>*Cirsium horridulum* (Yellow Thistle)	WL	G-H*
>*Corema conradii* (Broom Crowberry)	SC	H
Panicum commonsianum (Commons' Panic-grass)	SC	G
Gnaphalium purpureum (Purple Cudweed)	E	G!
>*Helianthemum dumosum* (Bushy Rockrose)	SC	G-H
Hypericum stragulum (St. Andrew's Cross)	E	G-H
Lactuca hirsuta var. *sanguinea* (Hairy Wild-lettuce)	T	G
Lechea minor (Thyme-leaved Pinweed)	WL	G-H
>*Liatris scariosa* var. *novae-angliae* (New England Blazing-Star)	SC	G-H*
>*Linum intercursum* (Sandplain Flax)	SC	G*
>*Lupinus perennis* (Wild Lupine)	WL	G
>*Polygala nuttallii* (Nuttall's Milkwort)	WL	G
>*Quercus stellata* (Post Oak)	WL	G-H
>*Scleria pauciflora* (Papillose Nut-sedge)	E	G
>*Sisyrinchium fuscatum* (Sandplain Blue-eyed Grass)	SC	G*
Spiranthes vernalis (Early Ladies'-tresses)	SC	G

to have fewer non-native species (0.4 ± 0.7 vs. 2.4 ± 3.7 on Cape Cod, and 2.4 ± 2.9 on Martha's Vineyard).

The abundance of shrubs, particularly heath species, in the grasslands is noteworthy. There is little difference between grasslands and heathlands in terms of the average number of ericads (4.1 vs. 5.3 spp./relevé; Table 1) or other shrubs (4.6 vs. 4.7). Comparisons of the percentage of relevés in which many of the smaller heath species occur illustrate this. Species such as *Arctostaphylos uva-ursi* (76 vs. 84%), *Vaccinium angustifolium* (61 vs. 77%), and *Hudsonia ericoides* (46 vs. 57%) are similarly com-

Table 3. Characteristics of grassland and heathland soils on Nantucket. Only vegetation types from which soil samples were collected are included. Values ± 1 SD.

	n	pH	Sand (%)	Clay (%)
GRASSLANDS				
All grasslands (Group I)	44	3.52 ± 0.20	90.4 ± 5.8	4.4 ± 1.9
Pennsylvania Sedge GL (Group A2a)	24	3.55 ± 0.20	88.8 ± 7.0	5.0 ± 1.8
HDN Sandplain GL (Group A2b)	12	3.55 ± 0.15	89.7 ± 1.4	5.2 ± 0.8
Heathy Grassland (Group B1)	8	3.37 ± 0.21	96.3 ± 0.4	1.7 ± 1.0
HEATHLANDS				
All heathlands (Group II)	36	3.30 ± 0.24	91.0 ± 4.5	4.3 ± 0.8
Low Shrub (Group C)	8	3.17 ± 0.22	92.5 ± 2.7	3.8 ± 0.3
Huckleberry-Scrub Oak (Group D1)	28	3.35 ± 0.24	90.6 ± 5.0	4.4 ± 0.8

mon in both vegetation types. However, the dominance of taller shrub species in heathlands is pronounced, as demonstrated by the percent frequencies of several taxa in grasslands versus heathlands: *Quercus ilicifolia* (63 vs. 90%), *Gaylussacia baccata* (57 vs. 87%), *Quercus prinoides* (25 vs. 63%), *Comptonia peregrina* (19 vs. 52%), and *Aronia arbutifolia* (14 vs. 26%). This pattern also is reflected in another measure, the average of dominance values, which is generally higher for these shrubs in the heathlands (e.g., *Gaylussacia baccata* (d.v. = 2.2 vs. 3.2), *Quercus ilicifolia* (d.v. = 1.5 vs. 2.3).

Samples collected from Nantucket suggest that heathland soils tend to be more acidic (pH 3.30 vs. 3.52, $p < 0.005$) and have higher organic C:N ratios (31.5 vs. 24.8, $p < 0.005$) than grasslands (Table 3).

Types of sandplain grasslands. Within the group of grassland relevés (Figure 2; Table 1), the first dichotomy separates those in which *Deschampsia flexuosa* is a major component (Group B–Hairgrass Grasslands) from those in which *Schizachyrium scoparium* is the primary dominant grass (Group A–

Table 3. Extended.

Silt (%)	Mg (ppm)	Ca (ppm)	Na (ppm)	K (ppm)	C:N
5.3 ± 4.1	6.3 ± 4.0	19.0 ± 14.0	2.7 ± 1.6	6.9 ± 3.9	24.8 ± 4.7
6.2 ± 5.5	6.2 ± 4.0	16.9 ± 13.0	2.8 ± 1.8	7.3 ± 4.3	24.4 ± 5.4
5.1 ± 1.0	6.4 ± 4.4	15.1 ± 10.8	3.2 ± 1.2	7.0 ± 3.4	23.3 ± 2.4
3.0 ± 0.0	6.2 ± 3.5	30.3 ± 17.2	1.6 ± 0.7	5.3 ± 3.1	28.2 ± 3.0
5.9 ± 4.5	7.0 ± 4.1	23.5 ± 16.7	2.5 ± 1.1	7.1 ± 3.7	31.5 ± 4.6
3.7 ± 2.4	9.2 ± 4.0	36.3 ± 19.2	2.8 ± 0.9	9.1 ± 3.4	34.4 ± 4.3
6.5 ± 4.9	6.9 ± 4.8	22.5 ± 20.1	2.3 ± 1.1	6.4 ± 3.6	30.1 ± 4.4

Little Bluestem Grasslands). Although *Schizachyrium scoparium* is common in both groups (84% in Group B vs. 96% in Group A), *Deschampsia flexuosa* is not (88% in Group B vs. 25% in Group A). In general, the Hairgrass Grasslands tend to have fewer vascular species than the Little Bluestem Grasslands (21.7 vs. 29.6 spp./relevé), a pattern which is most noticeable among the forbs (8.2 vs. 13.5 spp./relevé). The frequencies of many rare species also are lower in the Hairgrass Grasslands: *Sisyrinchium fuscatum* (4 vs. 22%), *Helianthemum dumosum* (27 vs. 43%), *Amelanchier nantucketensis* (7 vs. 17%), *Linum intercursum* (0 vs. 12%), *Asclepias tuberosa* (0 vs. 5%), and *Liatris scariosa* var. *novae-angliae* (2 vs. 6%). Hairgrass Grasslands are well represented on Cape Cod and Nantucket, but appear to be scarce on Martha's Vineyard, where two relevés were collected of this type (Table 4).

Many Hairgrass Grasslands are dominated by a mixture of graminoids and heath species. The TWINSPAN dichotomy that subdivided Group B distinguished a large subgroup of relevés, termed Heathy Grasslands (Group B1; Figure 2; Table 1), that had high frequencies of grasses (*Schizachyrium scoparium*–93%;

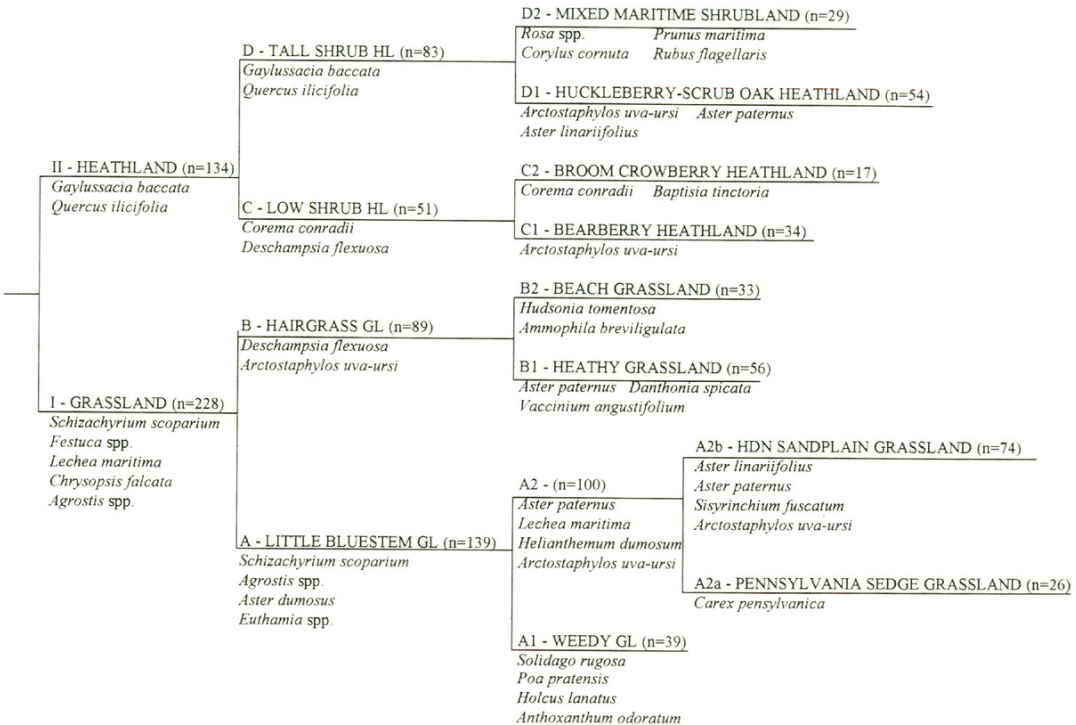
I - GRASSLAND (n=228)
Schizachyrium scoparium
Festuca spp.
Lechea maritima
Chrysopsis falcata
Agrostis spp.
II - HEATHLAND (n=134)
Gaylussacia baccata
Quercus ilicifolia
A - LITTLE BLUESTEM GL (n=139)
Schizachyrium scoparium
Agrostis spp.
Aster dumosus
Euthamia spp.
B - HAIRGRASS GL (n=89)
Deschampsia flexuosa
Arctostaphylos uva-ursi
C - LOW SHRUB HL (n=51)
Corema conradii
Deschampsia flexuosa
D - TALL SHRUB HL (n=83)
Gaylussacia baccata
Quercus ilicifolia
A1 - WEEDY GL (n=39)
Solidago rugosa
Poa pratensis
Holcus lanatus
Anthoxanthum odoratum
A2 - (n=100)
Aster paternus
Lechea maritima
Helianthemum dumosum
Arctostaphylos uva-ursi
A2a - PENNSYLVANIA SEDGE GRASSLAND (n=26)
Carex pensylvanica
A2b - HDN SANDPLAIN GRASSLAND (n=74)
Aster linariifolius
Aster paternus
Sisyrinchium fuscatum
Arctostaphylos uva-ursi
B1 - HEATHY GRASSLAND (n=56)
Aster paternus Danthonia spicata
Vaccinium angustifolium
B2 - BEACH GRASSLAND (n=33)
Hudsonia tomentosa
Ammophila breviligulata
C1 - BEARBERRY HEATHLAND (n=34)
Arctostaphylos uva-ursi
C2 - BROOM CROWBERRY HEATHLAND (n=17)
Corema conradii Baptisia tinctoria
D1 - HUCKLEBERRY-SCRUB OAK HEATHLAND (n=54)
Arctostaphylos uva-ursi Aster paternus
Aster linariifolius
D2 - MIXED MARITIME SHRUBLAND (n=29)
Rosa spp. Prunus maritima
Corylus cornuta Rubus flagellaris

Table 4. Summary of relevés by vegetation type from Nantucket, Cape Cod, and Martha's Vineyard. % = Number of relevés in each vegetation type sampled in a particular region divided by the total number of relevés sampled in all regions for that vegetation type.

	Nantucket (n = 243)		Cape Cod (n = 91)		Martha's V. (n = 28)		Total (n = 362)
	No.	%	No.	%	No.	%	No.
Heathland (Group II)	116	87	16	12	2	1	134
Tall Shrub (Group D)	81	98	0	0	2	2	83
Mixed Maritime (Group D2)	29	100	0	0	0	0	29
Huckleberry-Scrub Oak (Group D1)	52	96	0	0	2	4	54
Low Shrub (Group C)	35	69	16	31	0	0	51
Broom Crowberry (Group C2)	14	82	3	18	0	0	17
Bearberry (Group C1)	21	62	13	38	0	0	34
Grassland (Group I)	127	56	75	33	26	11	228
Hairgrass (Group B)	41	46	46	52	2	2	89
Beach (Group B2)	0	0	31	94	2	6	33
Little Bluestem (Group A)	86	62	29	21	24	17	139
HDN Sandplain (Group A2b)	70	95	0	0	4	5	74
Pennsylvania Sedge (Group A2a)	15	58	7	27	4	15	26
Weedy (Group A1)	1	3	22	56	16	41	39

Carex pensylvanica–93%; *Danthonia spicata*–91%; *Deschampsia flexuosa*–80%), ericoids (*Arctostaphylos uva-ursi*–100%; *Hudsonia ericoides*–73%; *Vaccinium angustifolium*–71%), and other common heathland plants. Soil samples from sites within this subgroup (Group B1; Table 3) are significantly sandier, have a lower pH, and have lower exchangeable Mg:Ca and Na:K ratios than the other grasslands ($p < 0.005$).

The other branch of the Hairgrass Grassland dichotomy identified a smaller subgroup of relevés we termed the Beach Grasslands (Group B2; Figure 2; Table 1). These grasslands often occur close to the coast in areas that receive some input of eolian sand

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Figure 2. TWINSPAN dendrogram of coastal sandplain relevé groupings. Informal names describe major distinguishing features of grassland (GL) and heathland (HL) vegetation types. Species identified by TWINSPAN to be "indicator species" are listed under each dichotomy. (n = number of relevés comprising group).

and usually include such species as *Ammophila breviligulata* (64%), *Hudsonia tomentosa* (82%), *Lechea maritima* (91%), and several species of *Cladonia* and *Cladina* lichens. This group had the lowest diversity of any of the grassland types and generally did not contain any rare species.

Little Bluestem Grasslands (Group A) include several types of coastal sandplain vegetation that were distinguished in the TWINSPAN ordination. Weedy Grasslands (Group A1) are characterized by the greatest number of non-native species, with an average of 5.3 spp./relevé (16% of the vascular plants), compared to 1.6 spp./relevé (6% of the vascular plants) for all grasslands (Group I). Common non-native species include grasses such as *Festuca ovina* (72%), *Anthoxanthum odoratum* (41%), *Poa pratensis* (44%), *Holcus lanatus* (33%), and *Phleum pratense,* and forbs such as *Hypochoeris radicata* (41%), *Rumex acetosella* (46%), *Hieracium piloselloides* (28%), and *Hypericum perforatum* (26%). Weedy Grasslands also tend to have fewer heath species than any other grasslands (3.0 vs. 4.1 ericads/relevé). Two native grasses, *Schizachyrium scoparium* and *Agrostis* species, are also common. These grasslands are frequent on Cape Cod and Martha's Vineyard, but only one of the Nantucket relevés was of this type (Table 4).

The dichotomy that distinguished subgroups within the Little Bluestem Grasslands contrasted the Weedy Grassland samples with a group of relevés (Group A2) that is noteworthy for the presence of *Helianthemum dumosum,* a species listed as "Special Concern" in Massachusetts (Mass. Natural Heritage and Endangered Species Program 1992). This species is found in both coastal grasslands and heathlands, and occurred in over 50% of the relevés in this group. Group A2, which might be considered as the "non-weedy" Little Bluestem Grasslands, is best described by examining the two distinct subgroups of which it is comprised. Group A2a, Pennsylvania Sedge Grasslands, contains abundant *Carex pensylvanica,* occurring in 100 percent of the relevés with an average d.v. = 3.7. This type is more common on Nantucket and Cape Cod, with only a couple of locations sampled on Martha's Vineyard (Table 4). The second group (Group A2b) includes the largest number of native grassland species (28 spp./relevé), the most rare species (1.3 spp./relevé), and the fewest non-native species (0.9 spp./relevé) in any of the Little Bluestem Grasslands. We refer to it as High Diversity Native (HDN) Sandplain Grass-

land, because it provides the most diverse expression of the native grasslands, with a rich flora of rare species and few introduced taxa. In addition to the greater dominance of *Carex* in Group A2a than in Group A2b, these two grassland types also can be distinguished from one another by the greater frequency of ericads (4.9 vs. 4.0 spp./relevé) and forbs (13.8 vs. 10.3 spp./relevé) in the HDN Sandplain Grasslands. This type was found most frequently on Nantucket, with only a few examples on Martha's Vineyard, and none on Cape Cod (Table 4).

Types of coastal heathlands. The first dichotomy within the heathland relevés (Figure 2; Table 1) separates those dominated by tall (>0.7 m) shrubs (Group D–Tall Shrub Heathlands) from others that are generally of low stature (Group C–Low Shrub Heathlands). *Gaylussacia baccata* and *Quercus ilicifolia* are common in both groups, but both are more dominant in Group D (d.v. = 3.7 and 2.6) than in Group C (d.v. = 2.3 and 1.9). Most other tall shrubs found in these coastal habitats, including such species as *Rosa virginiana* and *Rubus flagellaris,* also occur with a greater frequency in Tall Shrub Heathlands than in any other types.

Tall Shrub Heathlands (Group D) are divided into Mixed Maritime Shrublands (Group D2) and Huckleberry-Scrub Oak Heathlands (Group D1). The samples in our study come primarily from Nantucket, although both vegetation types occur frequently throughout the coastal sandplains of Cape Cod and Martha's Vineyard. Many tall, non-ericaceous species are found most frequently in Group D2, including *Aronia arbutifolia, Corylus cornuta, Prunus maritima,* and *Rubus flagellaris.* This group tends to be the most species-poor of all heathlands (14.1 spp./relevé) and contains the lowest numbers of ericads (3.4 spp./relevé), graminoids (2.0 spp./relevé), and forbs (3.7 spp./relevé). Unlike other heathland types, where *Quercus ilicifolia* occurs in >86% of the relevés, oak is much less frequent in Mixed Maritime Shrublands (62%). As the name implies, Mixed Maritime Shrublands are extremely variable in composition; quite different associations of shrub species may be lumped into this group. In many places, they probably would not be considered to be types of heathlands. However, the relevés that comprise Group D2 mostly include *Gaylussacia baccata* and *Vaccinium angustifolium* as dominants, and thus are arguably heathlands. The other Tall Shrub Heathland subtype, the Huckleberry-Scrub Oak Heathlands (Group D1), is

noteworthy in having the greatest dominance of both *Quercus ilicifolia* (d.v. = 2.8) and *Gaylussacia baccata* (d.v. = 3.7) of any heathland type. In some cases, this type approaches the composition, structure, and appearance of many scrub oak barrens.

The other main group of heathlands, Low Shrub Heathlands (Group C), is dominated by *Arctostaphylos uva-ursi* (100% frequency, d.v. = 3.6), *Hudsonia ericoides* (75%, d.v. = 2.4), and a diversity of other low ericoid shrubs, such as *Corema conradii* and *Vaccinium angustifolium*. Compared to the Tall Shrub Heathlands, both grasses (4.1 vs. 2.8 spp./relevé) and forbs (6.5 vs. 5.8 spp./relevé) are more frequent in this vegetation type. Low Shrub Heathlands are well developed on Nantucket and Cape Cod, but are infrequent on Martha's Vineyard (Table 4).

Low Shrub Heathlands were divided into two types. *Arctostaphylos uva-ursi* is extremely dominant (d.v. = 3.9) in the Bearberry Heathlands (Group C1). Although bearberry occurs in most heathlands and many grasslands, it reaches its greatest abundance in this type. Many examples exist within the Cape Cod National Seashore and on Nantucket. Broom Crowberry Heathlands (Group C2) have many of the same species as Bearberry Heathlands, but are strongly dominated by the rare shrub *Corema conradii* (100%, d.v. = 4.0). This vegetation type is most common on Cape Cod, with several sites on Nantucket (Table 4).

DISCUSSION

The results of a TWINSPAN classification of relevés from grasslands and heathlands on Cape Cod, Martha's Vineyard, and Nantucket highlight the compositional variability of the shrub, grass, and forb-dominated vegetation types found in this region. The fact that seven of the ten most frequent taxa are shared by both communities emphasizes the degree of overlap in these vegetation types. While some sites are relatively distinct, others incorporate so many taxa from both communities that it may be arbitrary into which type they are classified.

The inclusion of samples from other coastal grasslands and heathlands in the Northeast would further clarify the taxa that define the communities described in this classification. Data from such well-known sites as the Hempstead Plains and Montauk in New York (Taylor 1923; Conard 1935; Reschke 1990), as well as lesser-known examples from Rhode Island and Connecticut,

would likely expand the number of types beyond those we have described. Even within Massachusetts, some types were not represented in our samples, including the *Panicum virgatum* grasslands of Noman's Land and Cuttyhunk (Elizabeth Islands) and the *Smilax-Gaylussacia* heathlands and *Myrica pensylvanica* shrublands elsewhere in the Elizabeth Islands (pers. obs.).

The distribution and extent of grasslands and heathlands on Nantucket, Martha's Vineyard, and Cape Cod can be evaluated from various vegetation maps of these areas (Harshberger 1914; Robertson 1973; MacConnell et al. 1984; Nature Conservancy 1995). However, the different vegetation types identified in these studies make it difficult to compare the grassland and heathland types we describe. On 1980 aerial photos, MacConnell et al. (1984) delineated "heath plant community" acreages that amounted to about 576 ha on Cape Cod, 280 ha on Martha's Vineyard, and 3638 ha on Nantucket. Their definition appears to have lumped most of the grassland and heathland vegetation types we sampled. MacConnell et al.'s Nantucket figure compares favorably with a total of 3239 ha reported in a GIS study by The Nature Conservancy (1995) based on 1978 aerial photographs.

Although our selection of relevé sites was neither random nor exhaustive, we collected data from most major native grasslands and heathlands on Cape Cod, Martha's Vineyard, and Nantucket (Dunwiddie et al. 1993). The number of relevés sampled in each of the three regions is similar to the relative acreages reported by MacConnell et al. (1984). Thus our relevé data from different vegetation types, summarized by region (Table 4), may provide a general indication of the occurrence and abundance of these communities in southeastern Massachusetts. These data suggest that most types of grassland and heathland are found throughout the areas sampled, but that significant regional variation exists. For example, the grassland type with the greatest concentration of rare species (HDN Sandplain Grassland, Group A2b) occurs primarily on Nantucket. Weedy Grasslands (Group A1), in contrast, are more prevalent on Cape Cod and Martha's Vineyard. Hairgrass Grasslands appear most frequently on Cape Cod, and are uncommon on Martha's Vineyard.

The great variability in the composition and distribution of these communities presents an intriguing and difficult problem in understanding the origin, maintenance, and dynamics of the coastal sandplain vegetation. Why grasslands develop in some

areas while heathlands and maritime shrublands predominate in others, or why some sites appear to be relatively stable while others succeed to forests within a few decades, are questions that may have several answers in different places. A combination of factors probably is important in most areas, including differences in climate, substrate, disturbance and land use history, and initial floristic composition.

Proximity to the ocean was considered as one factor that might affect the distribution of vegetation types. Wind and salt spray play an evident role in suppressing arboreal species near the coast (Boyce 1954), which may explain the prevalence of both grasslands and heathlands within a few miles of the shoreline. However, we could find no clear relationship between the occurrence of different vegetation types identified in our study and their distance from the ocean. For example, Bearberry Heathlands are abundant on coastal bluffs on Cape Cod, while Little Bluestem Grasslands flourish close to the Nantucket shore. Only the Beach Grassland (Group B2) showed a tendency to occur primarily within a few hundred meters of the shore.

We also examined whether grassland and heathland types occur preferentially on different substrates. However, a categorization of sites as located on either glacial moraine or outwash revealed no correlation; the different vegetation types occur on both types of deposits. Comparisons of soils collected from some Nantucket grasslands or heathlands showed no significant differences in available cations or particle size (Table 3), also suggesting that underlying parent material composition is not controlling the distribution of these vegetation types. Additional soil samples from Cape Cod, Martha's Vineyard, and other coastal grassland and heathland sites are needed to determine whether these patterns can be generalized throughout the region.

Several differences in soil characteristics are worth noting. The significantly higher organic C:N ratios in heathland soils than in grasslands may largely result from biotic activity. Grassland species tend to have a higher percent N in tissues (lower C:N ratio), generally producing soils with relatively high exchangeable N; perennial woody species often produce litter with a lower percent N in tissues, giving rise to soils with a higher organic C:N ratio and lower N availability.

Within the grassland samples, the data provide some evidence that the occurrence of at least one of the grassland types may

relate to soil parameters. The samples from the Heathy Grasslands subgroup (Group B1) are significantly sandier, more acid, and have lower Mg:Ca and Na:K ratios than the other grassland samples. The other grassland type in the Hairgrass group (Beach Grasslands, Group B2) might also be expected to have a similar pattern of occurrence on droughty, low nutrient soils. Both of these grassland types have lower species diversity than the relatively species-rich Little Bluestem Grasslands.

Our results suggest that substrate and geographic location play roles in the distribution of some of the coastal vegetation types. However, clear environmental correlates do not emerge to explain many of the patterns of grassland and heathland distribution we observed. Instead, we hypothesize that much of the variation in composition and distribution of coastal sandplain grasslands and heathlands reflects differences in the disturbance and successional histories of sites, rather than resulting from differences in the physical or environmental characteristics of sites. According to this hypothesis, the mosaic of current vegetation on the coastal sandplain documented in our relevés is largely attributable to disturbances of different types and intensities occurring at different times and frequencies. Each disturbance acts upon a unique assemblage of species that is continually reshaped at each site. A similar situation has been described in midwestern prairies, where sites that have a recent history of fire and grazing support different communities than comparable sites where these disturbances are absent (Curtis 1959).

This hypothesis needs to be examined using sites with a long and detailed land use history. Such an examination would be difficult, however, as most grasslands and heathlands in southeastern Massachusetts are many decades removed from the period when grazing, fires, and agriculture were actively shaping the vegetation. Records of 18th and 19th century fires, land use, and vegetation that are tied to specific sites are scant, and were unobtainable for most of our relevé sites. While it is likely that all of these coastal sites received some degree of livestock grazing during the last 300 years, plowing histories may differ considerably between locations. Unfortunately, we did not collect data on the presence of plow horizons and other evidence of past soil tillage.

In the absence of detailed, site-specific land use histories for the relevé sites, we have drawn upon photographic studies on Nantucket (Dunwiddie 1992), Martha's Vineyard (Dunwiddie

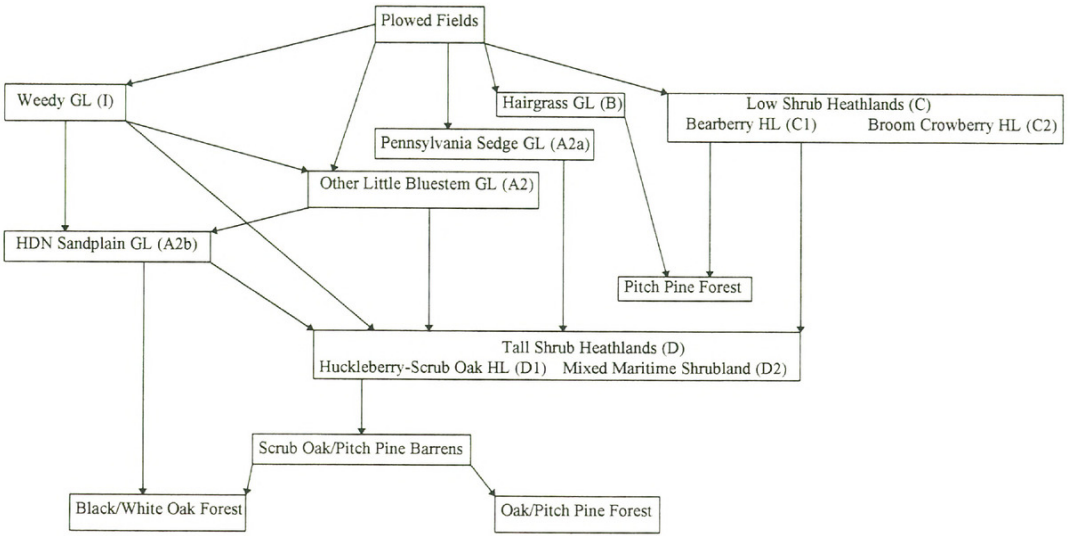

Figure 3. Proposed successional relationships of major coastal sandplain vegetation types. GL = Grassland; HL = Heathland.

1994), and Cape Cod (Dunwiddie and Adams 1994) to provide anecdotal information on how different vegetation types have changed over time in this region. Combining this information with our observations of the distribution of sites and a regional knowledge of past land use, we developed a model of the successional relationships among coastal vegetation types (Figure 3).

Agriculture was widespread throughout the coastal sandplain, and many sites no doubt were plowed, at least for a while. Thus our model depicts several successional pathways beginning with plowed fields. Factors that determine which pioneering communities develop on bare ground may include the type and extent of disturbance creating the bare ground, the composition of both the prior and surrounding vegetation, the current land use, and differences in substrate. For example, many agricultural fields and improved pastures develop into some form of the Weedy Grassland (Group A1), especially if they have received additions of lime and fertilizer and have been cultivated for sufficient time to eliminate much of the native seed bank. These areas may increasingly resemble the other Little Bluestem Grassland types (Group A2) if sources of native seed are available, and fires, salt spray, grazing, or other factors prevent extensive shrub encroachment. Otherwise, they may succeed to various Tall Shrub Heathlands (Group D).

Weedy Grasslands are less likely to develop in agricultural sites that received little or no nutrient or lime amendments and in pastures that were created by clearing open woodland or shrubland and were never plowed. Instead, these sites may develop

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Figure 4. (a) The intermingling of sandplain grassland and heathland vegetation on Nantucket is visible in the photograph, taken about 1890. Light areas are dominated by *Deschampsia flexuosa* and *Schizachyrium scoparium*. Small dark cushions in the foreground are *Hudsonia ericoides*; dark patches in the distance are primarily *Gaylussacia baccata* clones. Heavy grazing by sheep and other livestock had declined in this area about 40 years earlier, although occasional animals may have continued to graze when this photo was taken (reprinted courtesy of the Nantucket Historical Association). (b) Photograph taken from the same location a century later, showing an increase in taller woody plants, especially *Quercus ilicifolia*. Many areas of Nantucket, Cape Cod, and Martha's Vineyard have experienced much more rapid succession of shrubs and trees into the grasslands and heathlands than depicted in these photographs.

other types of grassland or Low Shrub Heathland. Old photographs and some contemporary examples of unimproved grazing land on Nantucket, Martha's Vineyard, and the Elizabeth Islands suggest that they frequently develop into types of Little Bluestem Grassland (Group A; Dunwiddie 1992, 1994). The high diversity HDN Sandplain Grasslands (Group A2b) may develop from these sites if they are not overtaken by woody plants. On Cape Cod, Hairgrass Grasslands (Group B) appear to have developed more frequently in pastured land than in the other locales. It is not clear under what conditions the Pennsylvania Sedge dominated (Group A2a) type develops, although it may be related to particularly heavy grazing. The high organic C:N ratios observed in Low Shrub Heathlands suggest that nitrogen may be particularly limiting in these sites; Broom Crowberry (Group C2) and Bearberry Heathlands (Group C1) often appear to develop in areas where the topsoil is removed, and the subsoil is widely exposed.

Tall Shrub Heathlands (Group D) develop from both grasslands and Low Shrub Heathlands (Group C; Figure 4). The factors that determine which of the different tall shrub vegetation types may develop are unclear, although seed availability and land use history probably play major roles. Huckleberry-Scrub Oak Heathland (Group D1) often replaces Low Shrub Heathland, but where it succeeds grassland types, low ericaceous shrubs are generally already common. Mixed Maritime Shrublands (Group D2) often develop from grasslands and less often from Low Shrub Heathlands.

In some cases, tall shrub stages may be bypassed and succession directly to forest can occur. Many of the pitch pine forests on Cape Cod are replacing Low Shrub Heathlands and Hairgrass Grasslands (Dunwiddie and Adams 1994). On Martha's Vineyard, forests of black, white, and post oaks have developed in Little Bluestem Grasslands in many areas during the last 80–100 years, with no intervening shrub stage (Dunwiddie 1994). The loss of grassland and heathland to scrub oak, pitch pine, and other taller woody plant associations often is very rapid (Dunwiddie 1992). MacConnell et al. (1984) reported a 30 percent loss of heathland on Martha's Vineyard and Nantucket between 1951 and 1971 as a result of succession of these species.

Our model does not attempt to describe disturbances that arrest or reverse succession. Such events usually would correspond to a different set of arrows in the reverse direction in Figure 3. While

the model begins with plowed fields, succession following other disturbances, such as fire, livestock grazing, and forest clearance, is also likely to follow similar pathways. However, the starting point of these successional sequences would vary, depending on the initial species composition and the nature of the disturbance.

Most of the maritime grasslands and heathlands of southeastern Massachusetts are dominated by native species, including a diversity of rare taxa. In many places, these vegetation types may have been created by plowing or grazing. In other cases, agricultural practices modified the composition of existing natural grasslands or heathlands. Today, many organizations are focusing their efforts on preserving the remaining examples of these vegetation types. The classification presented here provides a means of identifying more clearly how particular sites compare to the compositional range of grasslands and heathlands in the region. Furthermore, it can provide the basis for ranking sites to establish priorities for acquisition and management (Dunwiddie et al. 1993).

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