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Plants of the Hamilton Marshes: A Delaware River Freshwater Tidal Wetland

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Freshwater tidal wetlands cover an estimated 500,000 to 1,000,000 ha along the Atlantic and Gulf Coast states (Odum, Dunn, and Smith 1979) where they serve as buffers between estuaries and upstream ecosystems (Simpson et al. 1983a). During our studies of plant productivity and vegetation dynamics, beginning in 1974, we observed the diversity of vascular plant species in the Hamilton Marshes (also known locally as the Trenton Marshes), the northernmost freshwater tidal wetland on the Delaware River in New Jersey. The purpose of this paper is to summarize our qualitative and quantitative data on the distribution and abundances of species. We also summarize pertinent geologic and land use information for the wetland complex.

LOCATION, PHYSIOGRAPHY, SEDIMENTS, AND GEOLOGY

The wetland-upland complex occupies an old meander on the alluvial plain of the Delaware River (Fig. 1), and covers ~500 ha of which ~260 ha are palustrine and riverine tidal wetlands (Tiner 1985). It is bounded by bluffs to the east and by the Delaware River to the west. Crosswicks Creek is the major stream in the wetland but there are numerous smaller channels, such as Watson Creek, that wend through it. The dynamic nature of Watson Creek was described by Abbott (1887: 158–159):

> The alluvial flats through which it flows are very uniform in composition; and unless lodged by trees, borne hither and thither by freshlets, have been the cause, there is nothing to show why the creek is not almost a straight line, instead of being as tortuous as a writhing serpent.
>
> That it has changed its course for many a rod, even in historic times, there is evidence in maps attached to old deeds. That it was equally erratic in prehistoric times is also demonstrable, but not with so little labor. In several tracts of the lower lying meadows ancient channels can still be traced, and when ditches have been cut, I have gathered many a curious relic of Indians, left upon what was the bank of a stream, centuries ago.

Sediments are primarily alluvial and aeolian (Wagner, Miller, and Foss 1982; Stewart 1983). Alluvial sediments were deposited from both the Delaware River and Crosswicks Creek. Those from the Delaware River are silts and clays rich in organic matter while sediments from Crosswicks Creek are typically carbonaceous sands with smaller amounts of silt and clay (Owens and Minard 1975). Aeolian sediments were deposited during periods of drought (Wagner, Miller, and Foss 1982; Stewart 1983). Carbon dating of surface sediments show that deposits date from the Pleistocene through Holocene while the deeper sediments are the unconsolidated Cretaceous clays and sands

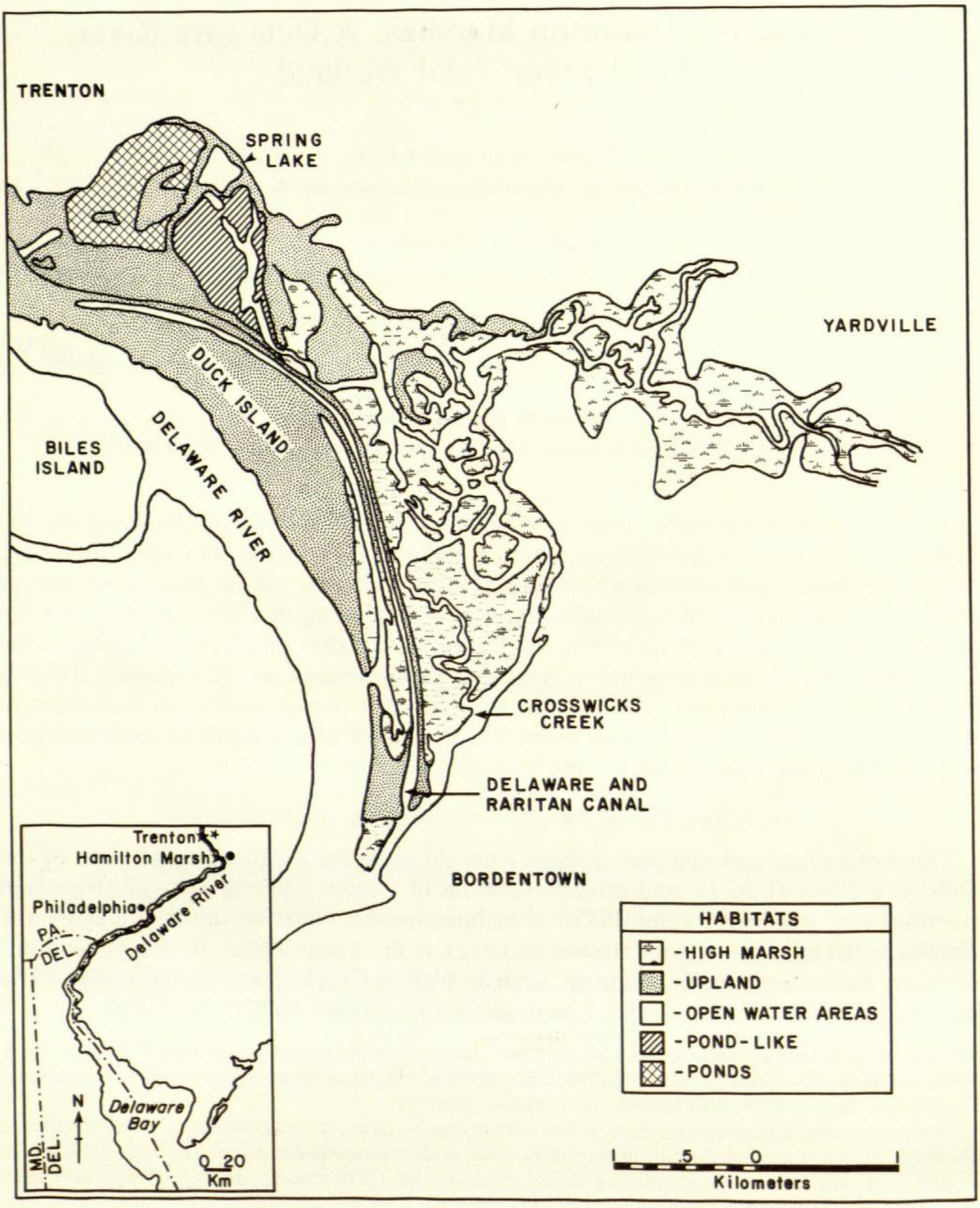

FIG. 1. Location of the Hamilton Marshes (inset) and extent of primary vegetation habitats.

of the Raritan Formation. Below these sediments the basement rocks are mostly amphibolites and gneisses (Owens and Minard 1964). Sediments of higher elevation areas within the wetland-upland complex are generally of different origin. For example, Duck Island is composed of superficial deposits that are classified as Graywacke I sediments and are interstratified sand and gravelly sand of Pleistocene origin which

may be as young as the Wisconsin Glaciation but more likely as old as the Sangamon (Owens and Minard 1975).

The older and better drained sediments along stream terraces or levees (Wagner, Miller, and Foss 1982), which were probably formed during the last ice age (see Hamblin 1985), are now relatively stable. These areas are currently forested, and have been sites of historic (as shown in aerial photographs) but not prehistoric (K. Kalb pers. comm.) agriculture.

Only in low lying areas is active sedimentation still occurring in response to regional environmental shifts such as the warming and drying that occurred during late Middle and early Late Archaic times (Wagner, Miller, and Foss 1982; Stewart 1983). Accretion rates, measured by Pb210, are currently 0.8 cm yr-1 (Simpson, Good, and Orson unpublished), but were much slower in the past. Most of the surface sediments have high organic matter content related to the high rates of production and subsequent deposition of large amounts of organic matter. The sediments in wetter areas contain 13–36% organic material and have bulk densities of 0.18–0.53 g cm-3 (Sickels and Simpson 1985).

Long-Term Vegetation History

Vegetation history of the wetland was evaluated from the analysis of sediment cores (Russell 1986; pers. comm.). Sediments from a 6 m core, taken at the base of the Lister site bluff (Fig. 2, site 9), were dated to 8580 ± 100 BP and indicate that a lake, presumably an oxbow lake, was present for a long period of time. The pollen record indicates that plant taxa, now present in the wetland, have been present for thousands of years. Over the millenia, however, various groups waxed and waned in importance depending on climatic conditions.

Land Use History

The wetland and adjacent high ground to the east (Fig. 2) have a varied and rich history as suggested by designation as the Abbott Farm National Landmark. The wetland-upland complex was the site of considerable Indian activity. Use by Woodland Indians, especially by Middle Woodland groups (Cavallo 1983), extended to the 18th century. Although the Indians must have used the wetlands extensively, as suggested by Abbott (1887), they probably had little impact on the physical environment as their activities primarily involved fishing and hunting (Cavallo 1983).

In the early 1700's when the wetland was on the edge of civilization and Trenton was known as the Falls of the Delaware, Isaac Watson owned property from the bluffs to the Delaware River (West 1954). Adjacent property, settled by John Abbott, was later the home of Charles C. Abbott (1843–1919), a well known naturalist and archeologist whose writings describe the wetland as he saw it a century ago (Abbott 1887). We have not examined maps from the colonial era to determine what types of physical alterations were effected after settlement by Europeans, but written records indicate that significant changes occurred. Natural drainage patterns were modified as parts of the wetland were diked, drained, and used for agricultural purposes (Wagner, Miller and Foss 1982). In fact, Abbott (1887) refers to "meadow ditches" and "pasture meadows" still being used in the 19th century, and aerial photographs (1930, 1940) indicate that agricultural use extended into the 20th century. These meadows were drier than at the present time (C. C. Abbott photograph ~1910). Destruction of wet-

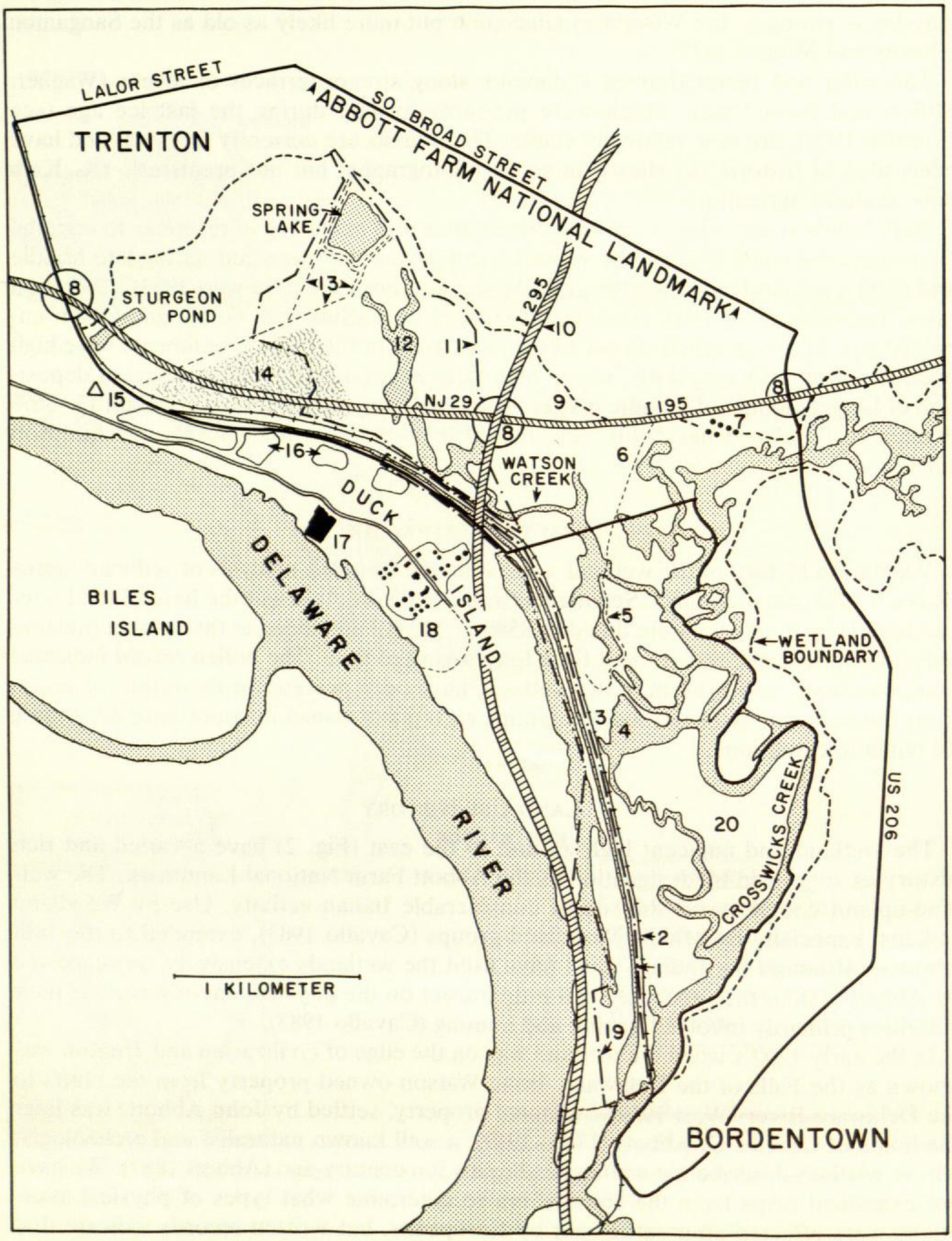

FIG. 2. Anthropogenic landmarks associated with the Hamilton Marshes. (1) Delaware and Raritan Canal, (2) Conrail (Camden and Amboy Railroad), (3) brick factory site, (4) lagoon, (5) road, (6) primary study site, (7) Hamilton Sewage disposal plant, (8) Interchange (highways and interchanges currently under construction), (9) Lister Bluff site, (10) I 195, I 295, and NJ 29, (11) Roebling Memorial Park, Mercer County Park system, (12) Rowan Lake, (13) service roads and high tension wires, (14) landfill, (15) Resource Recovery Plant, (16) Containment lagoons and other artificial landmarks, (17) Public Service Gas and Electric Co., (18) gas and oil tank farm, (19) Delaware and Raritan Canal State Park (entire length of the canal), (20) Duck Island State Recreation Area.

lands along the Delaware River during the past 50 years has caused increased runoff and an associated ~1 m rise in tide level (Sharp 1984).

From 1830–1838 the first large-scale physical alteration in the wetland occurred with construction of the Delaware and Raritan Canal (Fig. 2, site 1). At the same time the Camden and Amboy Railroad (now operated by Conrail) was constructed adjacent to the canal. This construction created Sturgeon Pond and blocked the mouth of Watson Creek, preventing it from flowing directly into the Delaware River and causing it to become a branch of Crosswicks Creek. Duck Island, which had been marsh, was altered by the changed hydrology and later by deposition of hydrofill from Delaware River navigation projects (Heite 1986). The canal and the railroad signaled the beginning of many other changes. A brick factory was built adjacent to the Canal (Fig. 2, site 3). It took advantage of coal, transported via canal, for fueling kilns and the local clay supply. A large shallow open water area adjacent to the brick factory ruins, as well as other ponds through the wetland, may be the result of digging clay for bricks (Davison 1976). Brick manufacture in the Trenton area dates to 1674 (Weiss and Weiss 1966). About 100 yrs ago Spring Lake was created by diking ~7 ha of the wetland. Aquatic grasses were harvested until about 1955 (Schmeltz per. comm.), and a well-known amusement park operated at Spring Lake until the 1940's. Since the 1930's, considerable industrialization has occurred on Duck Island; gas and oil terminals were built in the 1930's and a coal-burning power plant was built in the 1950's. The latter was accompanied by the filling of a corridor through the wetland for transmission lines, which further reduced the flow of tidal water between the areas around Spring Lake and Sturgeon Pond and the adjacent wetland. A large landfill (Fig. 2, site 14), operated between ~1960 and 1976, designated as a hazardous waste site between 1982 and 1985 by the New Jersey Department of Environmental Protection (Remington 1986), caused loss of ~23 ha of wetland. An additional ~40 ha of wetland will be destroyed by the interchange for Interstates 195 and 295 (Fig. 2, site 8), and the proposed mitigation (40 ha) will involve deforesting and excavating part of Duck Island (Remington 1986). Approximately 5 ha were filled in for the Hamilton Township sewage treatment plant and sludge lagoons between 1930 and 1960. Currently the plant adds more than 10,000,000 gal d-1 of secondarily treated wastewater to the wetland. In addition, stormwater drains of both Hamilton and Bordentown Townships terminate in the wetland and deliver significant loads of heavy metals from urban runoff into it (Simpson et al. 1981, 1983).

On a smaller scale, examination of aerial photographs (on file at the New Jersey Office of Environmental Analysis) of the wetland dating from 1930 show a variety of land use and other changes in the area most intensely studied (Fig. 2, site 6). In 1930 much of the area was agricultural, part apparently under cultivation and part meadows. What is now a forested island was the site of two prominent cultivated fields. A road, still depicted on topographic maps (United States Geological Survey, Trenton East Quadrangle 1981), extended toward the brick factory (Fig. 2, site 5). Also, ~1 km west of the road was a drainage ditch. Outlining the ditch, perhaps on spoil, were trees. A small forested island near the road was isolated and not connected to the forested bluff by shrub forest vegetation. Except for the prominant tributary of Crosswicks Creek, smaller drainage channels were not apparent. There was little change between 1930 and 1940 except for the construction of the sewage treatment plant east of the study site and increased urbanization of upland areas surrounding the wetland.

By 1951 the drainage ditch was not visible except by the position of a tiny island. The agricultural fields on the large island although open, were no longer cultivated. The

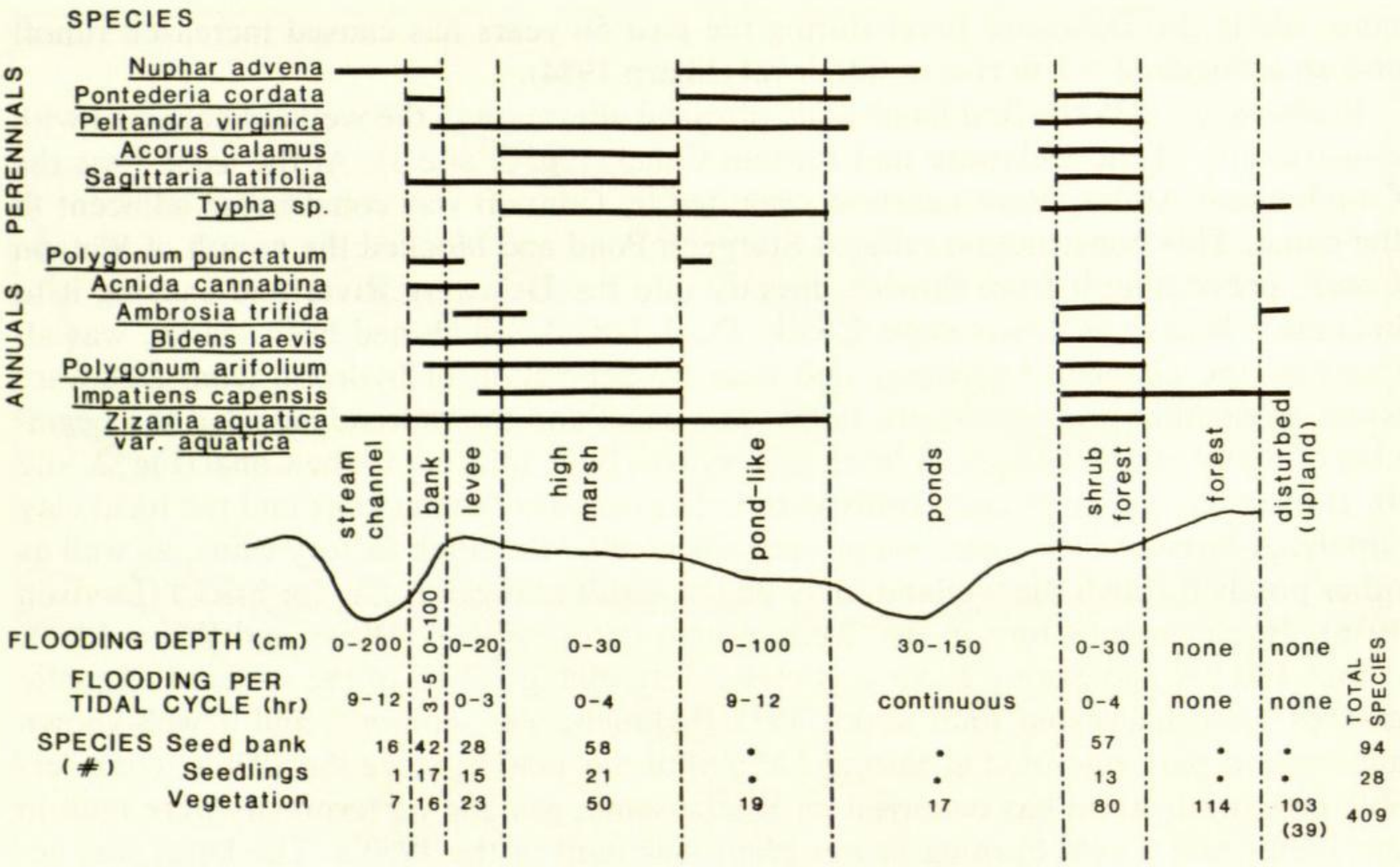

FIG. 3. Diagrammatic representation of major habitats and distribution patterns for dominant wetland species. Numbers of species located in the various habitats (Tables 1, 2) are indicated. Adapted with permission from Simpson et al. (1983).

sewage treatment facility had expanded with filling of ~5 ha of adjacent wetland. In 1961 the agricultural fields were completely forested and the smaller island appeared connected to the hillside by shrub forest vegetation.

HABITATS

The Hamilton Marshes are classed as riverine and palustrine wetlands (Tiner 1985). The major habitats and their relationship to the tidal cycle are depicted in Fig. 3. Of the major wetland habitats, we believe that the pond and pond-like habitats are the 2 in which species composition has been most strongly influenced by human activity since colonial times. Many species may be found in more than one habitat but each is usually abundant in only one habitat. Distinct species associations, however, may occur in a given habitat (Whigham and Simpson 1975; Parker and Leck 1985). In the shrub forest, for example, tidally inundated areas support species characteristic of the high marsh. This vegetation type is interspersed with hummocks containing shrubs and herbs not usually found in the tidally inundated areas. The most widespread habitat, the high marsh, is spatially quite diverse and is dominated by a mixture of annuals and perennials. Some areas, however, are dominated almost exclusively by *Typha* sp. or other species (Whigham 1974).

VEGETATION

The species list (Table 1), compiled over a period of more than 10 yrs, summarizes distribution information by habitat type. The data base for Table 1 comes from our studies of species in the seed bank, as seedlings in the field, and as mature plants in the vegetation. Seed bank data are based on greenhouse studies carried out between 1976

TABLE 1. Species list and distribution in the seed bank, in the field as seedlings, and in the vegetation of flowering plants of the Hamilton Marshes. Site abbreviations are: C = Stream channel, SB = Stream Bank, L = Levee, HM = High Marsh, PL = Pond-like, P = Pond, SF = Shrub Forest, and F = Forest. Abundance abbreviations are: r = rare, i = infrequent, f = frequent, c = common, + present, − not observed/absent. Note: the SF seed bank and field seedlings data were from tidally inundated soil, but not hummocks, whereas vegetation data included both microhabitats. See text for an explanation of abundance categories.

Species	Seed Bank					Field Seedlings					Vegetation							
	C	SB	L	HM	SF	C	SB	L	HM	SF	C	SB	L	HM	PL	P	SF	F
Acer rubrum	−	−	−	−	−	−	−	−	r	−	−	−	−	−	−	−	c	i
A. saccharinum	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	c	f
Acnida cannabina	c	c	c	f	−	−	c	c	c	−	−	c	c	i	−	−	−	−
Acorus calamus	−	−	−	−	−	−	−	−	−	−	−	i	−	c	−	−	f	−
Agrostis alba	−	r	−	−	r	−	−	−	−	−	−	−	−	−	−	−	+	−
Alisma subcordatum	−	−	−	r	−	−	−	−	−	−	−	−	−	+	−	−	+	−
Alnus rugosa	−	−	−	−	r	−	−	−	−	+	−	−	−	−	−	−	+	+
Ambrosia trifida	−	i	f	r	−	−	i	c	i	−	−	i	f	i	−	−	+	−
Andropogon virginicus	−	−	r	r	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Aster pilosus	r	r	r	r	r	−	−	−	−	−	−	−	−	−	−	−	+	+
Baccharis halimifolia	−	−	−	r	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Betula nigra	−	−	−	i	i	−	−	−	−	−	−	−	−	−	−	−	+	+
B. populifolia	−	−	−	r	−	−	−	−	−	−	−	−	−	−	−	−	−	+
Bidens frondosa	−	−	r	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−
B. laevis	i	c	c	c	c	−	c	c	c	c	−	c	c	c	−	−	+	−
Boehmeria cylindrica	−	−	−	−	c	−	−	−	−	−	−	−	−	i	−	−	c	i
Callitriche heterophylla	i	c	c	f	c	−	c	c	c	c	−	f	−	−	−	−	−	−
Cardamine bulbosa	−	−	−	−	f	−	−	−	−	−	−	−	−	+	−	−	f	−
C. pensylvanica	−	−	−	r	c	−	−	−	r	−	−	−	−	i	−	−	i	−
Carex scoparia	−	−	−	r	c	−	−	−	−	−	−	−	−	−	−	−	+	−
C. stipata	−	−	−	−	c	−	−	−	−	−	−	−	−	−	−	−	+	−
C. swanii	−	−	−	−	f	−	−	−	−	−	−	−	−	−	−	−	−	−
Carex sp.	i	f	−	f	c	−	−	−	−	−	−	−	−	−	−	−	+	−
Carya ovata	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	i
Cephalanthus occidentalis	−	r	−	−	f	−	−	−	−	−	−	−	−	i	−	−	c	−
Chelone glabra	−	−	−	−	r	−	−	−	−	−	−	−	−	−	−	−	+	−
Cicuta maculata	−	r	r	r	f	−	r	r	r	f	−	−	r	i	−	−	i	−
Cinna arundinacea	−	−	−	−	r	−	−	−	−	−	−	−	−	−	−	−	+	+
Cornus amomum	−	−	−	−	f	−	−	−	−	+	−	−	−	−	−	−	f	−

TABLE 1. Continued

Species	Seed Bank					Field Seedlings					Vegetation							
	C	SB	L	HM	SF	C	SB	L	HM	SF	C	SB	L	HM	PL	P	SF	F
Liriodendron tulipifera	–	–	–	–	i	–	–	–	–	–	–	–	–	–	–	–	–	c
Lonicera japonica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	f
Ludwigia palustris	–	i	–	i	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Lycopus virginicus	–	–	–	–	i	–	–	–	–	–	–	–	–	–	–	–	+	–
Lysimachia ciliata	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Lythrum alatum	–	–	–	–	–	–	–	–	–	–	–	–	–	i	–	–	–	–
L. salicaria	r	r	–	i	–	–	–	–	–	–	–	–	–	i	–	–	+	–
Microstegium vimineum	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Mikania scandens	–	i	i	c	c	–	–	–	–	–	–	–	–	i	–	–	+	+
Myosotis laxa	–	–	–	–	f	–	–	–	–	–	–	–	–	–	–	–	i	–
Nasturtium officinale	–	r	r	r	r	–	–	–	–	–	–	–	–	+	–	–	+	–
Nuphar advena	–	*r*	–	–	–	–	r	–	–	–	c	c	i	i	c	c	–	–
Nyssa sylvatica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	f
Panicum dichotomiflorum	–	i	–	i	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Parthenocissus quinquefolia	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	+	f
Paulownia tomentosa	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Peltantra virginica	–	r	i	c	i	–	f	i	f	–	–	i	+	c	c	c	c	–
Phalaris arundinacea	–	r	c	f	i	–	–	–	–	–	–	–	c	c	–	–	–	–
Phragmites australis	–	–	–	i	i	–	–	–	–	–	–	–	–	+	–	–	–	–
Physocarpus opulifolius	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Pilea pumila	f	c	c	c	c	–	f	c	c	c	–	f	i	i	–	–	c	c
Poa trivialis	–	–	–	r	c	–	–	–	–	c	–	–	–	+	–	–	c	–
Polygonum arifolium	c	c	c	c	c	–	c	f	c	c	–	c	c	c	–	–	c	–
P. punctatum	c	c	f	i	c	–	c	r	–	–	–	c	f	–	c	–	–	–
P. sagittatum	–	i	f	c	–	–	i	i	r	–	–	–	i	–	–	–	–	i
Pontederia cordata	–	r	–	–	–	–	–	–	–	–	+	f	–	–	f	f	f	–
Populus heterophylla	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Potamogeton crispus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	i	i	–	–
Potentilla norvegica	–	–	–	i	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Prunus serotina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	i	f
Quercus palustris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	f
Q. rubra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	c
Ranunculus sceleratus	–	–	–	c	f	–	–	–	r	–	–	–	–	+	–	–	+	–

TABLE 1. Continued

Species	Seed Bank					Field Seedlings					Vegetation							
	C	SB	L	HM	SF	C	SB	L	HM	SF	C	SB	L	HM	PL	P	SF	F
Rhus radicans	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	i
Rosa palustris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	f	–
Sagittaria latifolia	i	f	f	c	i	–	c	f	i	–	–	f	f	f	–	–	f	–
Salix spp.	–	–	–	r	r	–	–	–	–	–	–	–	–	–	–	–	+	–
S. bebbiana	–	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–
S. hybrid	–	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–
S. rigida	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	+	+
Sambucus canadensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	i
Sassafras albidum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	i
Scirpus cyperinus	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	+	+
S. fluviatilis	–	–	–	–	–	–	–	–	–	–	–	–	–	f	–	–	–	–
Scutellaria lateriflora	–	–	–	–	i	–	–	–	–	–	–	–	–	–	–	–	+	–
Sium suave	–	i	–	c	c	–	–	–	f	f	–	–	r	i	–	–	i	–
Smilax herbacea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	i
S. rotundifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	i
Solidago canadensis	–	r	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thalictrum polygamum	–	–	–	–	f	–	–	–	–	–	–	–	–	–	–	–	f	–
Tovara virginiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	i
Typha angustifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	f	–	–	–	–
T. latifolia	f	c	f	c	c	–	i	–	c	f	–	–	–	c	+	–	c	–
Ulmus rubra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	i
Veronica peregrina	–	i	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Viburnum dentatum	–	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	c	c
V. prunifolium	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	c	i
Viola sororia	–	–	–	–	r	–	–	–	–	–	–	–	–	–	–	–	+	f
Vitis aestivalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	i
Zizania aquatica	c	f	i	f	i	c	c	i	c	–	c	c	c	c	+	–	f	–
Totals 119					94					28								106

[a] *Heteranthera multiflora* and *H. reniformis* were not distinguished in this study. Both occur in Hamilton Marshes.

and 1986 (Leck and Graveline 1979; Parker and Leck 1985; Leck and Simpson 1987a and unpublished). Studies of seedling distribution in field plots, located near where soil samples had been obtained for the seed bank studies, were conducted in May of 1977 (Leck and Graveline 1979), 1983, 1984 (Leck and Simpson 1987a), and 1985 to 1987 (Leck and Simpson unpublished). They were monitored throughout the growing season in 1978 (Parker and Leck 1985). Studies of mature plants in the wetland have been conducted since 1974 (e.g. Whigham 1974; Whigham and Simpson 1975, 1976; Simpson et al. 1981, 1983b; Leck and Simpson 1987a).

For seed bank and field seedling density estimates the following were used: rare = 1–5 m^{-2}; infrequent = 6–25 m^{-2}; frequent = 26–100 m^{-2}; common = >100 m^{-2}; for the mature vegetation frequency data, based on percent of plots where a species occurred, the categories were delimited as: rare = 1–5%; infrequent = 6–25%; frequent = 26–50%; common = >50%. Because there was substantial variability from year to year for some species, the abundance category for a given species in a particular habitat, was based on the highest value for that species in that habitat. For example, for *Zizania aquatica* var. *aquatica* high marsh frequency values were 0% in 1972 and 40% in 1983. A (+) indicates that the species was present at the site. A (−) indicates that there was no observation for a species in a given habitat. This analysis for Table 1 is based on quantitative data from Whigham (1974), Leck and Graveline (1979), Parker and Leck (1985), and Leck and Simpson (1987a and unpublished).

Because the studies described above did not include any systematic floristic survey, additional species, found primarily during 1986–1987 surveys, are presented separately in Table 2. These surveys were not complete and it is expected that many more species are present. Also included are species recorded by J. Arsenault, R. Blicharz, and A. E. Schuyler, or represented by herbarium specimens at The Academy of Natural Sciences of Philadelphia. Herbarium specimens, prepared for more than half of all species, are deposited in the Rider College herbarium.

Nomenclature follows Fernald (1950) except for some species such as *Phragmites australis* and *Microstegium vimineum* which are in accordance with more recent literature (e.g. Hough 1983).

Discussion

The number of flowering plant species found in each habitat can be seen of Fig. 3. Over the more than 10 yrs of our studies, we have identified 409 species (exclusive of several unidentified graminoids and 1 dicot) (Tables 1, 2). Many more species (94) germinated from seed bank samples in the greenhouse than were observed in the field as seedlings (28) (Table 1) or established plants (24) in comparable studies (Leck, Simpson, and Parker 1988). The total (Tables 1, 2) was 426 species.

Various factors may account for the absence of many species as seedlings in the field. Soil disturbance during collection for seed bank studies may have provided dormant seeds with a stimulating light environment (Wesson and Waring 1969; Baskin and Baskin 1985). Furthermore, a favorable alternating temperature regime in the greenhouse may have elicited germination. In the field, vegetation canopy and/or litter could inhibit light-requiring species as well as those requiring specific alternating temperatures. Also, the continuously wet, and frequently inundated (<5 cm) soils found in the wetland may reduce or prevent germination (Leck and Simpson 1987a). Biotic stress, e.g. competition, would be more intense in the field (Parker and Leck 1985). Finally,

TABLE 2. Hamilton Marsh species other than those presented in Table 1. Species provided by J. Arsenault (*), R. Blicharz (**) and A. E. Schuyler, including specimens in the Academy of Natural Sciences of Philadelphia herbarium (+) are so indicated. The habitat in which each species was found is noted as: forest (F), wetland (including shrub forest) (W), and disturbed (D) or open upland (D′). Disturbed areas include road construction and other obviously man-altered sites. Open upland sites are areas where disturbance may have occurred, but are now open and sandy spots (e.g., on Duck Island and near Spring Lake). Species may also occur in habitats other than those noted here.

SEED PLANTS. *Acalypha virginica* (D), *Acer negundo* (F), *Acer platanoides* (F), *Acer pseudo-platanus* (F), *Achillea millefolium* (D), *Agastache scrophularifolia*** (F), *Ailanthus altissima* (D), *Alliaria officinalis* (F), *Allium vineale* (F), *Alnus serrulata* (W), *Ambrosia artemisiifolia* (D), *Amorpha fruticosa* (D′), *Amphicarpa bracteata* (F), *Andropogon gerardii* (D′), *Andropogon scoparius* (D′), *Andropogon virginicus* (D′), *Anthemis cotula* (D), *Apios americana* (W), *Apocynum androsaemifolium* (D′), *Apocynum cannabinum* (D), *Arabis laevigata* (Muhl.)** (F), *Arisaema triphyllum* (F), *Aristida dichotoma* (D′), *Artemesia vulgaris* (D), *Arthraxon hispidus** (D), *Asarum canadense*** (F), *Asclepias incarnata** + (W), *Asclepias syriaca* (D), *Asparagus officinalis* (D), *Aster divaricatus* (D), *Aster puniceus* (W), *Aster simplex* (D), *Aster vimineus** (D), *Berberis vulgaris* (F), *Bidens bidentoides* + (W), *Bidens comosa* + (W), *Bidens connata* + (W), *Bidens coronata* + (D), *Bidens polylepis* (W), *Broussonetia papyrifera** (D), *Cabomba caroliniana* (W), *Caltha palustris* + (W), *Capsella bursa-pastoris* (D), *Carex crinita* (W), *Carex grayii* (W), *Carex intumescens* + (W), *Carex lacustris* + (W), *Carex lupulina* (F), *Carex projecta* + (W), *Carex rosea** (F), *Carex squarrosa* + (W), *Carex straminea* (D), *Carex stricta* (W), *Carex vulpinoidea* + (W), *Carpinus caroliniana* (F), *Carya cordiformis* (F), *Cassia fasciculata* (D′), *Cassia nictitans* (D′), *Catalpa bignonioides* (D), *Celastrus scandens* (F), *Celtis occidentalis* (F), *Centaurea maculosa* (D), *Ceratophyllum demersum** + (W), *Chelidonium majus*** (F), *Chenopodium album* (D), *Chenopodium ambrosioides* (D), *Chimaphila maculata* (F), *Chrysanthemum leucanthemum* (D), *Cicuta bulbifera* (W), *Circaea quadrisulcata** (F), *Cirsium arvense* (D), *Cirsium vulgare* (D), *Claytonia virginica* (F,W), *Clematis dioscoreifolia* (F), *Clematis virginiana* (F), *Clethra alnifolia* (F), *Commelina communis* (D), *Convolvulus sepium* (W), *Cornus florida* (F), *Coronilla varia* (D), *Corydalis flavula*** (F), *Cycloloma atriplicifolium* (D), *Cyperus dentatus* (D), *Cyperus filiculmis* (D), *Cyperus ovularis* (F), *Dactylis glomerata* (D), *Daucus carota* (D), *Desmodium canescens** (F), *Desmodium cuspidatum* (D′), *Dianthus armeria* (D), *Dicentra cucullaria*** (F), *Digitaria sanguinalis* (D), *Dioscorea batatas* (D), *Diospyros virginiana* (F), *Eleocharis acicularis* + (W), *Eleocharis obtusa* (W), *Eleusine indica* (D′), *Elodea nuttallii* (W), *Elymus virginicus** (F), *Eragrostis hypnoides* + (W), *Eragrostis spectabilis* (D′), *Eriocaulon parkeri* + (W), *Erythronium americanum*** (F), *Euonymus alatus* (D), *Eupatorium hyssopifolium* (D′), *Eupatorium perfoliatum* (D), *Eupatorium rugosum* (F), *Euphorbia chamissonis* (D′), *Euphorbia corollata* (D′), *Fagus grandiifolia* (F), *Fagopyrum sagittatum*** (D), *Festuca rubra* (D), *Froelichia gracilis* (D), *Galium aparine* (W), *Galium tinctorium* (D), *Geum canadense* (W), *Geum laciniatum** (F), *Glechoma hederacea* (D), *Glyceria pallida* + (W), *Glyceria septentrionalis* (F), *Helenium autumnale* (D), *Helianthus annus*** (D), *Helianthus decapetalus*** (F), *Helianthus tuberosus* (D), *Hieracium pratense* (D′), *Hordeum jubatum* (D), *Hosta plantaginea* (D), *Houstonia caerulea* (D′), *Humulus japonicus* (D), *Hypericum mutilum* (D), *Hypericum perforatum* (D), *Hystrix patula* + (W), *Ilex opaca* (F), *Ilex verticillata* (W), *Iris versicolor* (W), *Juncus acuminatus* (D), *Jussiaea repens* (W), *Justica americana* + (W), *Krigia virginica*** (D′), *Lactuca canadensis* (D), *Lamium amplexicaule*** (D), *Laportea canadensis* (F), *Lechea villosa* (D′), *Leersia virginica* (D), *Lemna minor** (W), *Leonurus cardiaca** (D), *Lepidium* sp. (D), *Lespedeza capitata* (D′), *Lespedeza intermedia* (D′), *Ligustrum vulgare*

TABLE 2. Continued.

(D′), *Lilium* sp. (W), *Linaria canadensis*** (D′), *Lindera benzoin* (W, F), *Lindernia dubia* + (W), *Lobelia cardinalis* + (W), *Lobelia inflata* (D), *Lobelia siphilitica*** (W), *Lolium perenne* (D), *Lonicera morrowii* (D), *Lonicera xylosteum* (D′), *Ludwigia alternifolia* (D), *Luzula multiflora** (D), *Lycopus americanus** + (W), *Melilotus alba* (D), *Melilotus officinalis* (D), *Mimulus alatus* + (W), *Mimulus ringens* (D), *Mollugo verticillata* (D), *Monotropa uniflora** (F), *Morus alba* (F), *Myriophyllum heterophyllum* + (W), *Myriophyllum spicatum* (W), *Nymphaea odorata* (W), *Oenothera biennis* (D), *Orontium aquaticum* + (W), *Osmorhiza longistylis** (F), *Oxalis stricta* (F), *Panicum anceps* (F), *Panicum clandestinum* (D), *Panicum latifolium* (W), *Panicum stipitatum* + (W), *Panicum virgatum** (D′), *Penthorum sedoides* (D), *Philadelphus coronarius* (F), *Phytolacca americana* (F), *Pinus rigida* (D′), *Plantago aristata* (D), *Plantago lanceolata* (D), *Plantago rugelii* (D), *Platanus occidentalis* (F), *Poa compressa* (D), *Podophyllum peltatum* (F), *Polygonatum biflorum* (F), *Polygonum amphibium* (W), *Polygonum cespitosum* (D), *Polygonum cuspidatum* (D), *Polygonum hydropiperoides* (W), *Polygonum lapathifolium* (D), *Polygonum orientale* + (D), *Polygonum pensylvanicum* (D), *Polygonum scandens* (F), *Populus grandidentata* (D), *Populus tremuloides* (D), *Potamogeton diversifolius* + (W), *Potamogeton epihydrus* + (W), *Potamogeton pectinatus* + (W), *Potentilla simplex* (F), *Prunella vulgaris* (D), *Ptilimnium capillaceum** (W), *Pycnanthemum muticum* (F), *Pycnanthemum virginianum*** (D′), *Pyrus prunifolia* (D′), *Quercus phellos* (F), *Ranunculus abortivus* (F), *Ranunculus longirostris* + (W), *Rhexia virginica* (D), *Rhus copallina* (D′), *Rhus typhina* (D′), *Rhus glabra* (W), *Robinia pseudo-acacia* (D′), *Rosa multiflora* (DF), *Rubus pensilvanicus* (W), *Rubus phoenicolasius* (F), *Rudbeckia hirta* (D), *Rudbeckia lacinata* (W), *Rumex crispus* (D), *Rumex obtusifolius*** (F), *Sagittaria rigida* + (W), *Sagittaria subulata* + (W), *Salix fragilis** (D), *Salix humulis* (? *S. tristis*) (D), *Saponaria officinalis* (D), *Scirpus polyphyllus* (D), *Scirpus pungens* + (W), *Scrophularia marilandica** (F), *Scutellaria epilobiifolia*** (W), *Scutellaria integrifolia* (D′), *Senecio aureus* (F), *Setaria faberii* (D), *Setaria glauca* (D′), *Sisyrinchium angustifolium* (D′), *Smilacina racemosa* (F), *Solanum dulcamara* (F), *Solanum nigrum* (D), *Solidago caesia** (F), *Solidago graminifolia* (D), *Solidago juncea* (D), *Solidago rugosa* (D), *Solidago sempervirens** (W), *Sorghastrum nutans* (D′), *Sparganium americanum* + (W), *Sparganium eurycarpum* + (W), *Spartina pectinata* + (W), *Specularia perfoliata* (D), *Spergularia rubra* (D′), *Spiraea latifolia* (W), *Spirea tomentosa* (D), *Spirodela polyrhiza** (W), *Stachys palustris* + (W), *Stachys tenuifolia* var. *hispida* (W), *Stellaria longifolia* (W), *Symplocarpus foetidus* (F), *Taraxacum officinale* (D), *Taxus* sp. (D), *Teucrium canadense** (F), *Tilia americana* (F), *Trichostema dichotomum* (D′), *Trifolium agrarium* (D), *Trifolium arvense* (D), *Trifolium pratense* (D), *Trifolium repens* (D), *Triodia flava* (D′), *Utricularia intermedia* + (W), *Utricularia vulgaris* + (W), *Uvularia sessilifolia* (F), *Vaccinium corymbosum* (F), *Vallisneria americana* + (W), *Verbascum blattaria* (D), *Verbascum thapsus* (D), *Verbena urticifolia** (F), *Veronica longifolia*** (D′), *Viola kitaibeliana*** (D′), *Vitis labrusca* (F), *Vitis riparia** (F), *Vitis vulpina* (D), *Wisteria floribunda* (F), *Wolffia columbiana** (W), *Xanthium strumarium* (D).

FERNS AND HORSETAILS (see also Leck and Simpson 1987b). *Asplenium platyneuron, Athyrium felix-femina, Botrychium dissectum, Botrychium virginianum, Dennstaedtia punctilobula, Dryopteris noveboracensis, Dryopteris spinulosa, Dryopteris thelypteris, Equisetum arvense, Equisetum fluviatile, Onoclea sensibilis, Osmunda cinnamomea, Osmunda claytoniana, Osmunda regalis, Polystichum acrostichoides, Pteretis pensylvanica (Matteuccia struthiopteris), Woodwardia areolata.*

finding seedlings of graminoids, for which we have poor "search images" anyway, and of uncommon species is difficult in the field.

Seed input, distribution, and turnover are clearly important to species diversity. Most species, especially annuals, produce large numbers of seeds (e.g. Whigham and Simpson 1977; Simpson, Leck, and Parker 1985; Sickels and Simpson 1985; and unpublished data) and many have seeds which are water dispersed (e.g. West and Whigham 1976; Parker and Leck 1985). Many fewer species germinated in samples collected in June suggesting high turnover rates and short lived seeds for many seed bank species. Many species have seeds that appear not to survive for long periods; 40% of the species found in seed bank samples occur only in the surface (0–2 cm) and ~30% germinate only in March (Leck and Simpson 1987a).

Many species are very uncommon in the seed bank, yet they collectively add considerable diversity to the seed bank (Leck and Simpson 1987a). In turn, the seed bank is considerably more diverse than the wetland flora at any one time and provides for recruitment of species which germinate if conditions change within any wetland habitat (Leck, Simpson, and Parker in press).

There are also some species that occur regularly in one or more habitats but have not been found in the seed bank or in the field as seedlings. For some of these, e.g. *Acorus calamus* and *Scirpus fluviatilis,* seed production does not occur or is limited (Packer and Ringius 1984; A. E. Schuyler pers. comm.). For others dispersal may be limited. Of the 21 woody species in the seed bank, *Cornus amomum* and *Viburnum dentatum*, are bird dispersed; the other 19 are wind or water dispersed. Despite seemingly effective dispersal mechanisms, only *Cephalanthus occidentalis* was frequent in the seed bank. Various common species, such as *Rhus radicans* and *Ilex verticillata*, which have bird dispersed fruits, were not found in seed bank soil samples or as seedlings. Clearly, more information about the production, dispersal, longevity, and germination of most species is needed before we can understand existing vegetation patterns or processes responsible for temporal changes in the vegetation.

Six species, *Bidens bidentoides, Eriocaulon parkeri, Justicia americana, Populus heterophylla, Ranunculus longirostris,* and *Sagittaria subulata* are among the rare and endangered species of New Jersey (Snyder and Vivian 1981). *Populus heterophylla* was represented by a single seed bank plant; the others are herbarium records (Academy Natural Sciences of Philadelphia). Of the rare Pennsylvania species found in the Delaware River estuary (Schuyler 1986), *Acnida cannabina* (*Amaranthus cannabinus*), *Bidens bidentoides, Bidens laevis, Echinochloa walteri, Eriocaulon parkeri, Ptilimnium capillaceum, Sagittaria subulata, Scirpus fluviatilis, and Zizania aquatica* are known from the Hamilton Marshes. *Sagittaria subulata, Bidens bidentoides,* and *Eriocaulon parkeri* were collected near the mouth of Crosswicks Creek, and *Echinochloa walteri* was represented by a single seed bank plant. *Acnida cannabina, Bidens laevis,* and *Scirpus fluviatilis* are common. Of nine rare intertidal species with ranges encompassing Crosswicks Creek (Ferren and Schuyler 1980), *Bidens bidentoides, Eriocaulon parkeri, Sagittaria subulata, Scirpus fluviatilis,* and *Zizania aquatica* occur in the Hamilton Marshes.

Abbott's (1887) 19th century description of his wanderings in the wetland included reference to more than 90 species. Of these, 16 are not among those presented in Tables 1 and 2. Two of the 16, *Nelumbo lutea* (Willd.) Pers. and *Castanea pumila* (L.) Mill., are rare or endangered in New Jersey (Snyder and Vivian 1981); and only 2, *Gerardia flava* L. and *Nelumbo lutea,* are not listed for Mercer County (Hough 1983). (Evidence that

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