Biological Report 12
June 1993

Ecology of Red Maple Swamps in the Glaciated Northeast: A Community Profile

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By

Francis C. Golet, Aram J. K. Calhoun,
William R. DeRagon, Dennis J. Lowry,
and Arthur J. Gold

James A. Allen, Project Officer
U.S. Fish and Wildlife Service
National Wetlands Research Center
700 Cajundome Boulevard
Lafayette, Louisiana 70506

U.S. Department of the Interior
Fish and Wildlife Service
Washington, D.C. 20240

Preface

In many areas of the glaciated northeastern United States, forested wetlands dominated by red maple (*Acer rubrum*) cover more of the landscape than all other nontidal wetland types combined. Yet surprisingly little of their ecology, functions, or social significance has been documented. Bogs, salt marshes, Atlantic white cedar swamps, and other less common types of wetlands have received considerable attention from scientists, but, except for botanical surveys, red maple swamps have been largely ignored. This report conveys what is known about these common wetlands and identifies topics most in need of investigation.

Red maple swamps are so abundant and so widely distributed in the Northeast that their physical, chemical, and biological properties range widely as well, and their values to society are diverse. The central focus of the U.S. Fish and Wildlife Service community profile series is the plant and animal communities of wetlands and deepwater habitats. However, the abiotic environment, particularly hydrogeologic setting and water regime, is also of critical importance because it largely determines the structure and species composition of the biota and controls major wetland functions and values. The importance of abiotic factors is given especially strong emphasis in this profile.

For most aspects of red maple swamp ecology, significant research has been limited to one or two studies; in some cases, there are no studies at all. For that reason, we have consciously avoided broad generalizations in this report. Instead, we frequently present detailed results from isolated studies, particularly where they were comprehensive or quantitative works. We hope such in-depth review will shed light on the characteristics and functions of red maple swamps in other parts of the Northeast, and even outside of the region.

Through our field research and work on this report, we have found red maple swamps to be highly diverse, productive, aesthetically pleasing ecosystems that are of great significance to society. However, our understanding of these wetlands is only beginning. We hope that the obvious information gaps identified in our report will stimulate more investigation into the ecology of this valuable resource.

This community profile is one in a series coordinated by the U.S. Fish and Wildlife Service's National Wetlands Research Center. Questions or comments concerning this publication or others in the community and estuarine profiles series should be directed to:

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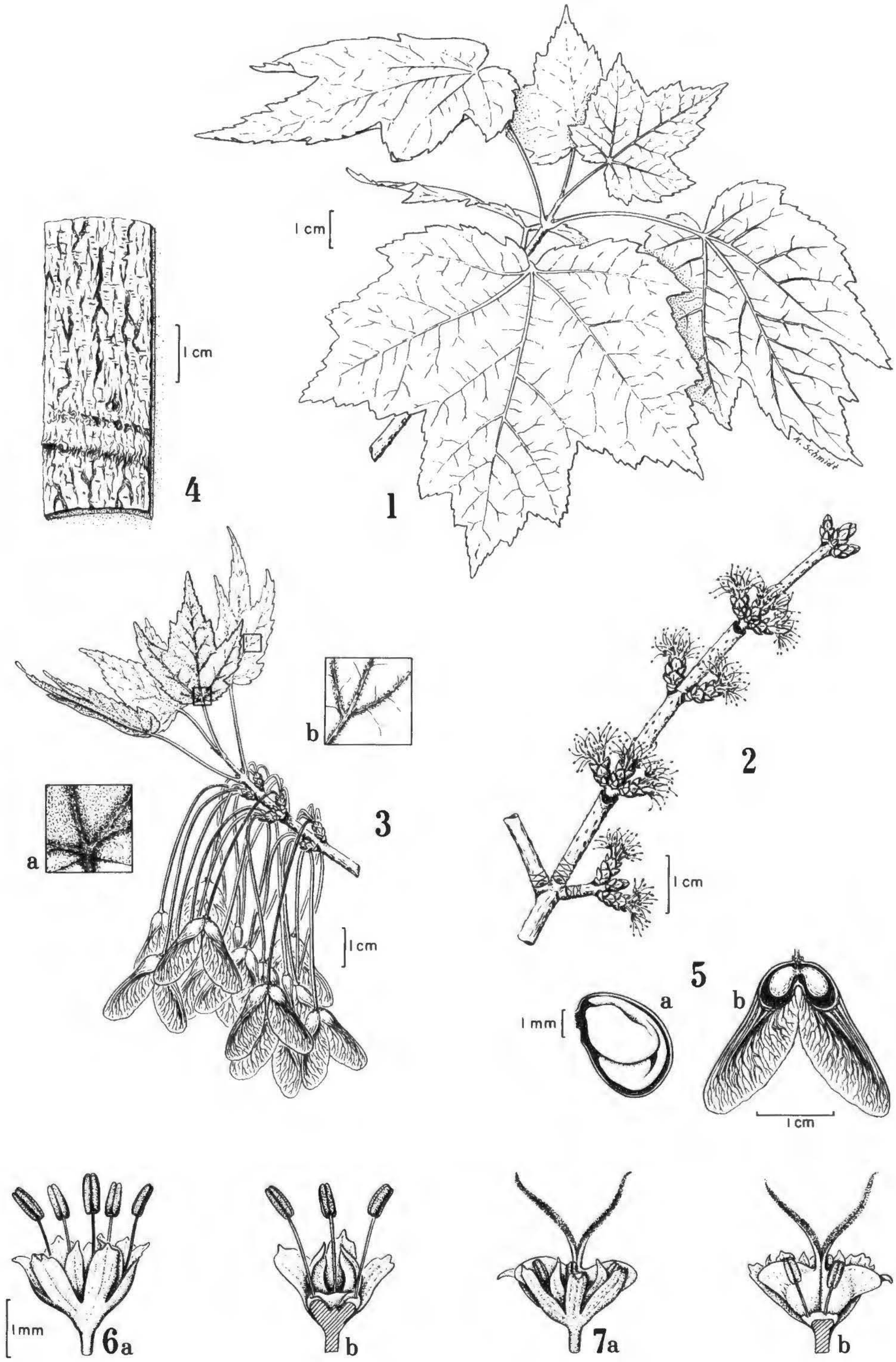
Conversion Table

Metric to U.S. Customary

Multiply	By	To obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (L)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre–feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (° C)	1.8 (° C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre–feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (BTU)	0.2520	kilocalories
Fahrenheit degrees (° F)	0.5556 (° F - 32)	Celsius degrees



Acer rubrum (red maple) diagnostic features. 1. leaves, 2. flowering branch with male flowers, 3. fruiting branch, 3a. lower leaf surface, 3b. upper leaf surface, 4. bark, 5a. seed, 5b. fruit, paired samaras, 6a., b. male flowers, 7a., b. bisexual flowers. *Drawing by K. Schmidt.*

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Ecology of Red Maple Swamps in the Glaciated Northeast: A Community Profile

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Francis C. Golet, Aram J.K. Calhoun, and
William R. DeRagon

Department of Natural Resources Science
University of Rhode Island
Kingston, Rhode Island 02881

Dennis J. Lowry

IEP/Fugro-McClelland, Inc.
Northborough, Massachusetts 01532

and

Arthur J. Gold

Department of Natural Resources Science
University of Rhode Island
Kingston, Rhode Island 02881

Abstract. This report is part of a series of profiles on the ecology of wetland and deepwater habitats. This particular profile addresses red maple swamps in the glaciated northeastern United States. Red maple (*Acer rubrum*) swamp is a dominant wetland type in most of the region; it reaches its greatest abundance in southern New England and northern New Jersey, where it comprises 60–80% of all inland wetlands. Red maple swamps occur in a wide variety of hydrogeologic settings, from small, isolated basins in till or glaciofluvial deposits to extensive wetland complexes on glacial lake beds, and from hillside seeps to stream floodplains and lake edges. Individual swamps may be seasonally flooded, temporarily flooded, or seasonally saturated, and soils may be mineral or organic. As many as five distinct vegetation layers may occur in these swamps, including trees, saplings, shrubs, herbs, and ground cover plants such as bryophytes and clubmosses. On a regional scale, red maple swamps support at least 50 species of trees, more than 90 species of shrubs and vines, and more than 300 species of nonwoody plants. These swamps also provide habitat for a rich faunal community, including several wetland-dependent species. In areas that are becoming urbanized, these wetlands often constitute critical habitat for facultative species as well. Red maple swamps also are important sites for flood storage, water quality improvement, recreation, scenic beauty, and open space.

Key words: Swamp, red maple, *Acer rubrum*, forested wetlands, deciduous forest, northeastern United States.

Chapter 1. Introduction

Wetland Forests of the Northeast

Classification

Forested wetland is the most abundant class of wetland throughout the northeastern United States. According to Cowardin et al. (1979), this class includes all wetlands with at least 30% cover of trees (i.e., woody plants 6 m or more in height). Wetland forests are distinguished from upland forests by a predominance of hydrophytes (plants adapted for life in water or in saturated soil) and the presence of undrained hydric soil, as defined by the U.S. Soil Conservation Service (U.S. Soil Conservation Service 1991). Northeastern forested wetlands are contained within the palustrine system, which includes all inland wetlands dominated by persistent vegetation (e.g., trees, shrubs, persistent emergents) and all other inland wetlands not contained in river channels or lake basins (Cowardin et al. 1979). The three major subclasses of palustrine forested wetlands in the Northeast are needle-leaved deciduous, needle-leaved evergreen, and broad-leaved deciduous.

Needle-leaved deciduous forested wetlands, dominated by tamarack (*Larix laricina*), are relatively uncommon. They are generally limited to northern New England and the higher elevations of New York, western Massachusetts, and northeastern Pennsylvania, where spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) forests dominate the upland landscape. Needle-leaved evergreen forested wetlands are common throughout most of the Northeast. They are the predominant subclass in the spruce–fir regions, where black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and balsam fir are the principal wetland tree species. Within 80 to 150 km of the Atlantic coast, from Massachusetts southward, Atlantic white cedar (*Chamaecyparis thyoides*) forested wetlands are common; isolated cedar swamps are found as far north as southern Maine (Laderman et al. 1987). Scattered throughout the Northeast are wetland forests dominated by a variety of other needle-leaved evergreens, chiefly eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), and pitch pine (*Pinus rigida*).

Broad-leaved deciduous forested wetlands are the predominant subclass in the Northeast. Abundant in all parts of the region except for the spruce–fir zones, broad-leaved deciduous wetland forests occur in a variety of settings. On major river floodplains, dominant species typically include silver maple (*Acer saccharinum*), eastern cottonwood (*Populus deltoides*), ashes (*Fraxinus* spp.), black willow (*Salix nigra*), sycamore (*Platanus occidentalis*), pin oak (*Quercus palustris*), elms (*Ulmus* spp.), and river birch (*Betula nigra*) (Teskey and Hinckley 1978a; Holland and Burk 1984; Metzler and Damman 1985; Tiner 1985). Broad-leaved deciduous forested wetlands also occur in isolated upland depressions, at the headwaters of streams, along the shores of lakes and high-gradient perennial watercourses, and as wet expanses in broad valleys and coastal lowlands. In all of these nonfloodplain settings, and in the wetter parts of many floodplains as well, the dominant species throughout the Northeast almost invariably is red maple (*Acer rubrum*) (Fig. 1.1). This community profile describes the ecology of red maple forested wetlands in the glaciated portion of the northeastern United States.

Red Maple Forested Wetlands

In red maple forested wetlands, red maple is the dominant overstory species—the "dominance type" of Cowardin et al. (1979). In many broad-leaved deciduous forested wetlands in the glaciated Northeast, red maple composes more of the canopy cover than all other tree species combined. In southern New England, where red maple forested wetlands most closely approach a pure type, red maple commonly composes more than 90% of the cover (Lowry 1984). Toward the northern and western limits of the region, subordinate species such as black ash (*Fraxinus nigra*), green ash (*F. pennsylvanica*), American elm (*Ulmus americana*), and swamp white oak (*Quercus bicolor*) assume relatively greater importance; pin oak, black gum (*Nyssa sylvatica*), and sweet gum (*Liquidambar styraciflua*) are more important in southern areas. Red

Fig. 1.1. Broad-leaved deciduous forested wetland dominated by red maple (*Acer rubrum*).

maple forested wetlands are commonly referred to as red maple swamps (Golet and Larson 1974), and that more familiar term will be used interchangeably with "forested wetland" in this report.

For our purposes, the southern limit of the glaciated Northeast coincides with the maximum extent of the most recent, or Wisconsin, glaciation (Flint 1971). The region includes New England, all of New York except for a small area along the Pennsylvania border in the western part of the state, northeastern and northwestern Pennsylvania, and northern New Jersey (Fig. 1.2). While red maple swamps occur

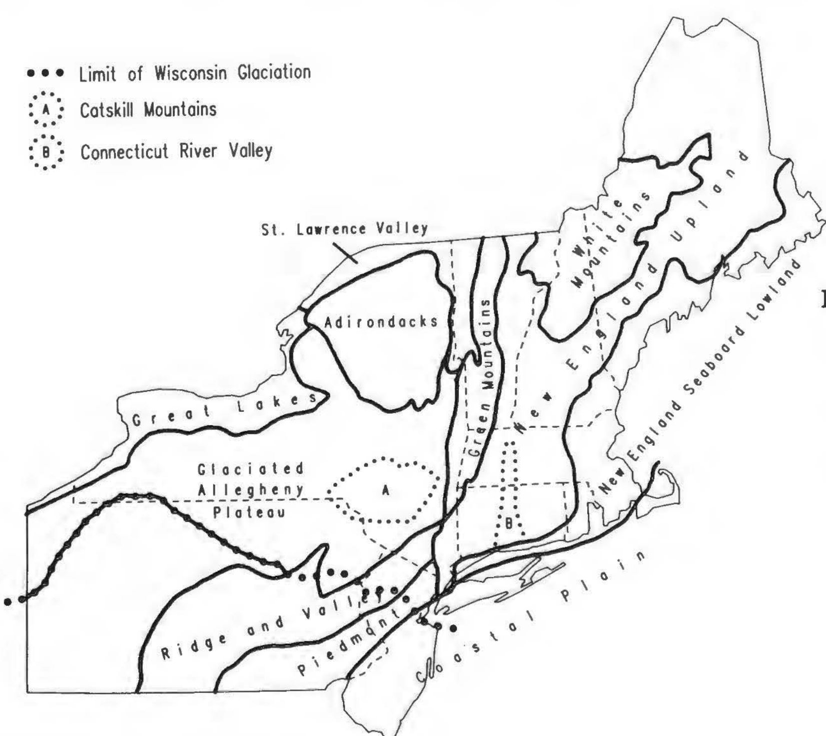

Fig. 1.2. Physiographic regions of the glaciated Northeast (adapted from Lull 1968 and Fenneman 1938). The Catskill Mountains and Connecticut River valley are shown for reference pusposes, but are not considered separate regions.

throughout the glaciated Northeast, their size, abundance, typical landscape positions, edaphic characteristics, flora, and fauna all vary as a result of the physiographic and climatic diversity of the region. The following section outlines the regional setting or context within which northeastern red maple swamps are found.

Regional Setting

Physiography

The physiography of the glaciated Northeast is extremely varied (Fig. 1.2, Table 1.1). Elevations range from sea level in the Coastal Plain and New England

Table 1.1. *Synoptic outline of the physiographic regions of the glaciated Northeast (based on Fenneman 1938, Lull 1968, and Cunningham and Ciolkosz 1984).*

Region	Elevation above sea level (m)	Salient features	Geology
New England Seaboard Lowland	< 150	Narrow, low-lying coastal zone with varied shoreline, including rocky shores, barrier spits and islands, and sand beaches	Granite and schist in Maine, granite, sedimentary, and metamorphic rocks elsewhere; abundant stratified drift in southern New England
New England Upland	150–450	Elevated plain with rolling hills, narrow valleys, numerous lakes; also contains Connecticut River valley (elev. ≤120 m)	Granite, gneiss, schist, slate, shale, some Triassic sandstone in Connecticut River valley; diverse glacial deposits dominated by till
White Mountains	450–1,800	White Mountains and adjacent elevated lands formed by massive granite intrusion; steep slopes and narrow valleys	Intrusive igneous rocks, mainly granite, overlain by till
Green Mountains	250–1,200	Low mountain ranges, including Green Mountains and Taconic Range, separated by a narrow valley	Slate and schist in mountains, limestone and marble in lowland between ranges
St. Lawrence Valley	< 150	Low-lying plain along St. Lawrence River and in Lake Champlain basin; scattered drumlins up to 30 m high	Glacial drift and marine clays and sands over sandstone, limestone, and shale
Adirondacks	600–1,500	Broad plateau (elevation approximately 600 m) in western portion, mountains in east; more than 2,000 lakes	Precambrian igneous rocks, primarily granite, overlain by till
Great Lakes	30–90	Low-lying region between Finger Lakes and Lakes Erie and Ontario	Limestone, sandstone, and shale overlain by glacial lake deposits and other drift
Glaciated Allegheny Plateau	370–600 (average)	Broad, uplifted plain west of Appalachians; elevations drop to 120 m in river valleys and climb to 1,200 m in Catskill Mountains	Limestone, sandstone, shale, and conglomerate; diverse glacial deposits
Ridge and Valley	400–600	Long, narrow, flat-topped ridges and deep valleys on western slope of Appalachians; most of region is unglaciated	Ridges: sandstone and conglomerate; valleys: shale and limestone
Piedmont	60–90	Region of gentle slopes (relief < 15 m) except in river valleys; small segment of large, mainly unglaciated region	Triassic sandstone, shale, and conglomerate; extensive glacial lake deposits in northern New Jersey
Coastal Plain	< 60 (average)	Coastal strip limited to Cape Cod, Mass., Long Island, N.Y., and northeastern N.J.; part of much larger, primarily unglaciated, region	Glacial end moraines and outwash over Cretaceous and Tertiary sedimentary rocks

Seaboard Lowland regions to more than 1,500 m in the White Mountains and Adirondacks. Coastal areas (including the Great Lakes region) generally are relatively flat, while mountainous regions are characterized by steep slopes and narrow valleys. The bulk of the Northeast falls within the New England Upland and Glaciated Allegheny Plateau regions, where moderate elevations (150-600 m), rolling hills, and narrow river valleys predominate.

Bedrock types include primarily igneous and metamorphic rocks through most of New England and in the Adirondack Mountains and limestone, sandstone, and shale in much of the rest of the Northeast (Table 1.1). Unstratified glacial deposits, more commonly known as till, predominate in the region. Stratified deposits are found in abundance in lowlands near the glacial limit, especially in southern New England (Seaboard Lowland) and northern New Jersey (Coastal Plain and Piedmont), but also in deep preglacial valleys of central New York and in low-lying areas within the Great Lakes and St. Lawrence Valley physiographic regions. Marine sediments occur in parts of the New England Seaboard Lowland and St. Lawrence Valley (Fenneman 1938; Lull 1968; Cunningham and Ciolkosz 1984).

Climate

Climate in the Northeast is highly varied because of the wide range of physiographic conditions and the influence of the Atlantic Ocean and Great Lakes (Cunningham and Ciolkosz 1984). Variability in time and space is probably the most conspicuous aspect of the region's climate. There are wide ranges in daily and annual temperatures, wide variations in temperature and precipitation for the same month or season in different years, and marked fluctuations in weather conditions over short periods (Ruffner 1985).

Throughout the glaciated Northeast, precipitation is evenly distributed over the year. Total annual precipitation ranges from more than 135 cm in certain areas of the White Mountains, Green Mountains, and Catskills to less than 75 cm in the Great Lakes region and the Lake Champlain basin (Moody et al. 1986). Mean annual precipitation values for the various northeastern states are similar, however, generally averaging 102–122 cm. Total snowfall varies greatly over the glaciated Northeast. Annual amounts range from less than 81 cm on the Coastal Plain to as much as 400 cm in parts of the White Mountains (Lull 1968).

Mean annual air temperatures range from less than 4° C in northern New England to 10° C in parts of southeastern New England, northern New Jersey, and northeastern Pennsylvania (Cunningham and Ciolkosz 1984). Average daily minimum temperatures in January are below freezing throughout the glaciated Northeast, ranging from −18° C in northern New England to −3° C along the Atlantic coast (Lull 1968). Average daily maximum temperatures in July range from 21° to 30° C. The length of the freeze-free period varies from less than 90 days in parts of the White Mountains, Green Mountains, and Adirondacks to 180–210 days in coastal areas of southern New England (Lull 1968). Table 1.2 summarizes climatic

Table 1.2. *Climatic data for the northeastern United States, by physiographic region (from Lull 1968).*

Region	Mean annual precipitation (cm)	Mean annual snowfall (cm)	Mean daily air temp. (° C) Jan. min.	July max.	Mean freeze-free period (days)
New England Upland	107	188	−13	27	128
New England Seaboard Lowland	109	145	−9	27	157
White Mountains	102	257	−16	26	112
Green Mountains	107	188	−12	27	111
Adirondacks	107	272	−14	27	114
Great Lakes[a]	84	190	−10	28	148
Glaciated Allegheny Plateau	102	163	−9	28	127
Ridge and Valley[b]	102	84	−6	29	159
Piedmont[b]	112	66	−4	31	172
Coastal Plain[b]	114	46	−3	29	192

[a] Includes climatic data from the St. Lawrence Valley region described in this report.

[b] Includes data from unglaciated states (West Virginia, Maryland, and Delaware) and from unglaciated portions of Pennsylvania and New Jersey.

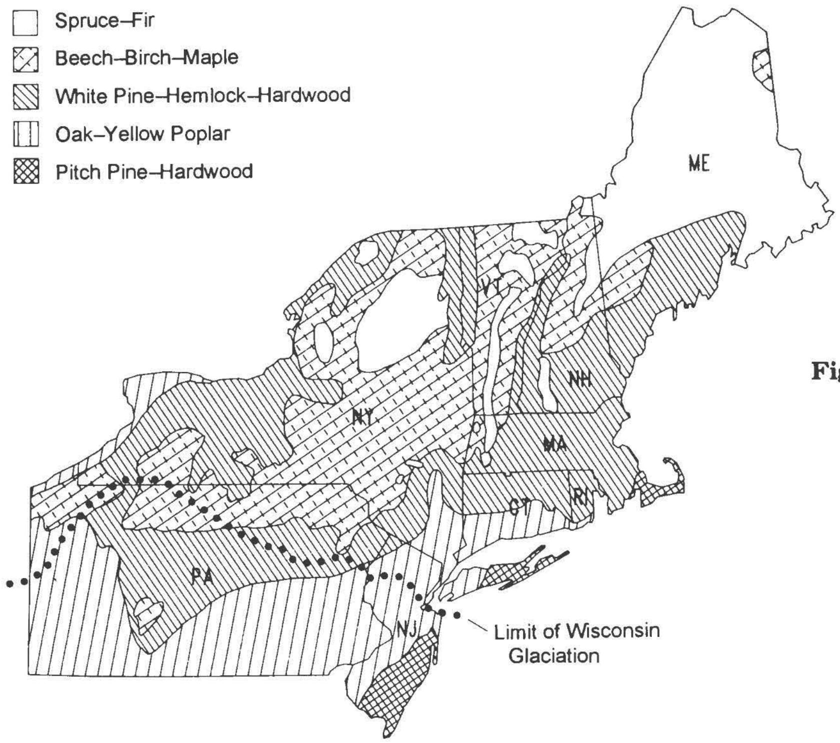

Fig. 1.3. Major forest regions of the glaciated Northeast (after Lull 1968 and Little 1979).

data for each physiographic region in the Northeast.

Major Forest Regions

The forests of the glaciated Northeast can be divided into five major regions (Fig. 1.3), which are differentiated according to the forest associations that dominate the upland landscape: spruce–fir, beech–birch–maple, white pine–hemlock–hardwood, oak–yellow-poplar, and pitch pine–hardwood. As comparison of Figs. 1.2 and 1.3 suggests, the configuration of the various forest regions is determined largely by physiography and related climatic factors.

Table 1.3 identifies the most common tree species found on upland and wetland sites in the five forest regions. Red maple swamps occur throughout the Northeast, but their relative abundance and floristic composition vary with physiography and forest region. Generally, these wetlands are most abundant in the white pine–hemlock–hardwood region and least abundant in the spruce–fir region.

Ecology and Distribution of Red Maple

Red maple is an extremely broadly adapted species that occurs in both wetland and upland habitats throughout the eastern United States (Fowells 1965). It is found virtually everywhere east of the 100th meridian where precipitation is adequate to support tree growth (Fig. 1.4). It occurs on dry, moist, and wet soils derived from a wide variety of bedrock types, ranging from acidic granites and gneisses to basic sedimentary rocks such as limestone. It grows on dry mountain ridges, in seasonally flooded depressions with organic or mineral soils, in mesic hardwood forests, in boreal conifer forests, and in southern bottomlands. Both northern and southern wetland studies characterize red maple as a moderately flood-tolerant tree (Hall and Smith 1955; Teskey and Hinckley 1978a, 1978b; McKnight et al. 1981; Theriot 1988) that is most common on sites that are intermediate in wetness between permanent flooding and temporary or intermittent flooding (Buell and Wistendahl 1955; Satterlund 1960; Monk 1966; Sollers 1973; Dabel and Day 1977; Conner and Day 1982; Huenneke 1982). In the glaciated Northeast, red maple predominates in swamps where soils are saturated or flooded from late fall through early summer in most years.

The Society of American Foresters (SAF) currently recognizes 90 forest cover types in the eastern United States (Eyre 1980). Red maple is a major component (i.e., composes at least 20% of total stand basal area) in five of these types and is listed as an associated species in 63 others. It is a major or associated species in 41 of the 43 forest cover

Table 1.3. *Principal tree species in upland and wetland forests of the glaciated Northeast, by forest region (based primarily on Lull 1968; names modified after Little 1979).*

Forest region	Upland forests	Wetland forests
Spruce–fir	Red spruce White spruce Black spruce Balsam fir American beech Yellow birch Sugar maple	Black spruce Tamarack Northern white cedar Balsam fir Red maple Black ash
Beech–birch–maple[a]	American beech Yellow birch Sugar maple Eastern hemlock Black birch Red maple Basswood White ash Northern red oak	Northern white cedar Black spruce Tamarack Red maple Black ash
White pine–hemlock–hardwood	White pine Eastern hemlock Northern red oak American beech Yellow birch Sugar maple Other oaks Yellow-poplar Hickories Red maple	Red maple Ashes Eastern hemlock White pine Atlantic white cedar
Oak–yellow/poplar	White oak Northern red oak Black oak Scarlet oak Chestnut oak Hickories Yellow-poplar	Red maple Atlantic white cedar Black gum
Pitch pine–hardwood	Pitch pine Bear oak	Red maple Black gum Atlantic white cedar

[a] Also frequently referred to as northern hardwoods.

types occurring in the glaciated Northeast. Of the five forest cover types in which it is a major component, three (white pine–northern red oak–red maple, gray birch–red maple, and black cherry–maple) are upland forest types, one (black ash–American elm–red maple) is a wetland type, and one (red maple) may occur on either wetland or upland sites. So, while red maple is the dominant tree in the vast majority of broad-leaved deciduous wetland forests in the Northeast, it is classified as a facultative species, that is, one that occurs in wetlands from one-third to two-thirds of the time (Reed 1988).

The distribution of red maple forested wetlands generally coincides with the combined distributions of the black ash–American elm–red maple cover type (SAF type no. 39) and the red maple type (no. 108). The former type is found throughout the glaciated Northeast and the Great Lakes States, and from southern Manitoba to Newfoundland (Eyre 1980). In the Great Lakes States, black ash may be as abundant as elm and red maple in this cover type, but elsewhere it usually composes a small percentage of the stand. American elm has greatly declined in abundance due to Dutch elm disease, so red maple has become the dominant species in the black ash–American elm–red maple type throughout the Northeast.

The red maple cover type (SAF no. 108) is most common in New England, the Middle Atlantic States, the Upper Peninsula of Michigan, and northeastern Wisconsin. Toward the western and southern limits of its range, this type generally occurs on wetland soils; in New England and the Upper Peninsula of Michigan, it is found both in wetlands and on dry, sandy, or rocky upland sites. In Pennsylvania, most red maple stands are found on mesic to dry upland sites (Eyre 1980).

The SAF established the red maple forest cover type in 1980; before that, red maple was merely listed as a codominant or associated species in a number of other types. The dramatic increase in the proportion of red maple in many stands since the previous SAF classification (SAF 1954) has been attributed to disturbances such as logging and fire and the progressive elimination of American elm by Dutch elm disease (Eyre 1980). Production of heavy seed crops nearly every spring, rapid seed germination, and vigorous sprouting from stumps and damaged seedlings give red maple a competitive advantage over associated species on a wide variety of disturbed sites.

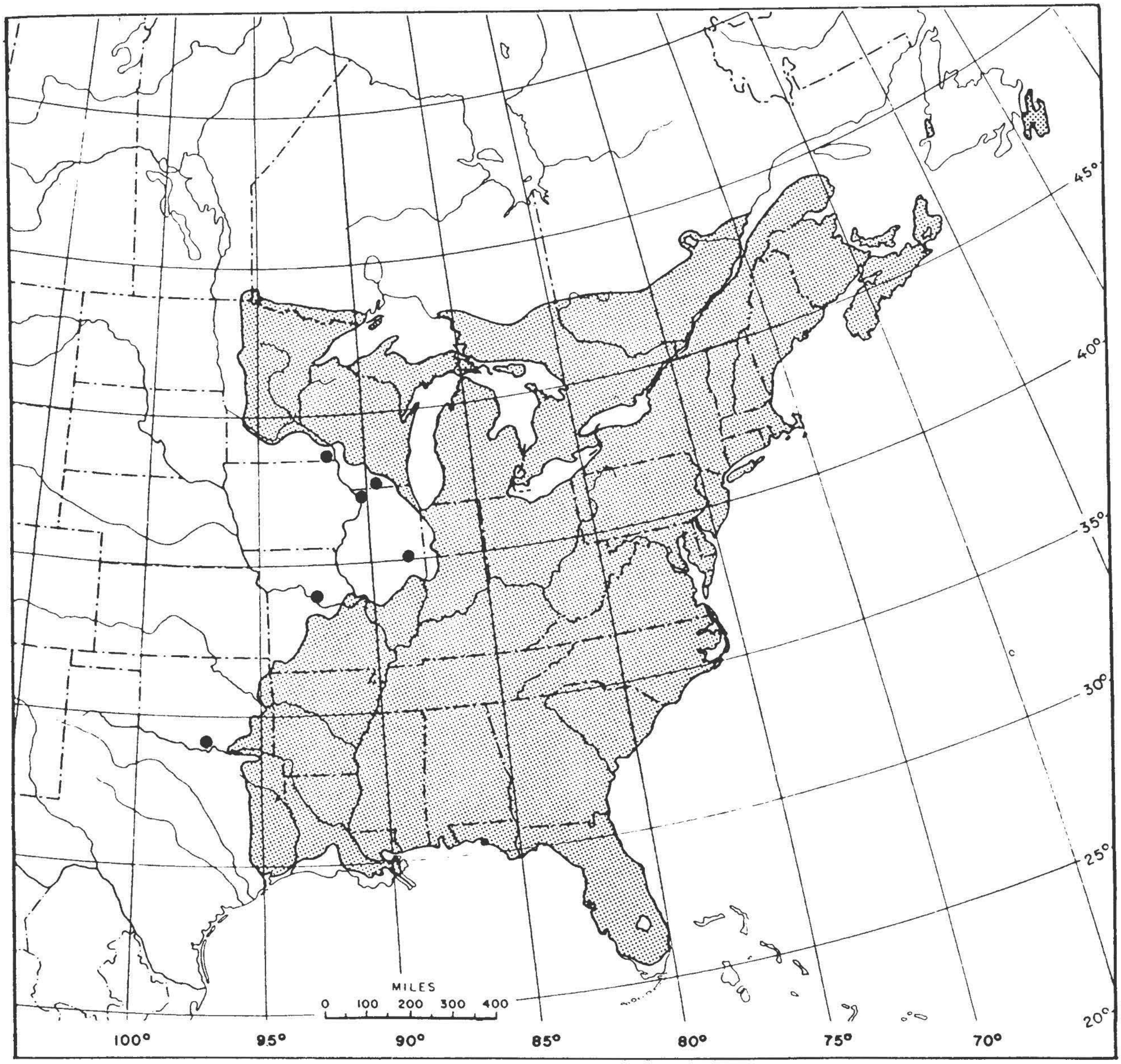

Fig. 1.4. The range of red maple (after Fowells 1965). *Dots* along the western edge of the range represent isolated or disjunct occurrences of the species.

Relative Abundance of Red Maple Swamps

Statewide Wetland Inventory Statistics

The most comprehensive statistics on the areal extent of wetlands in the glaciated Northeast have been compiled by the U.S. Fish and Wildlife Service's (FWS) National Wetlands Inventory (NWI). As of this writing, statewide area statistics have been published for New Jersey and Rhode Island (Tiner 1985, 1989b) and are also available for Vermont, Connecticut, and Massachusetts (R. Tiner, U.S. Fish and Wildlife Service, Newton Corner, Mass., personal communication). National Wetlands Inventory data also have been compiled for 105 towns along coastal Maine (Fefer 1980) and, on a sample basis, for the state of Pennsylvania (Tiner and Finn 1986; Tiner 1989a). While the NWI does not provide area statistics for red maple swamps specifically, in most cases it does give totals for the broad-leaved deciduous forested wetland subclass. For our purposes, these two categories are considered synonymous, and NWI statistics for broad-leaved deciduous forested wetlands are taken to represent the abundance of red maple swamps in the states listed above.

Table 1.4. *Relative abundance of forested wetland and broad-leaved deciduous (BLD) forested wetland in the glaciated northeastern United States (based on National Wetlands Inventory and New York State Wetlands Inventory data[a]).*

State	Total palustrine wetland (ha)	Forested wetland (%)	BLD forested wetland (%)	BLD forested wetland (ha)
Rhode Island	23,120	83	77	17,874
New Jersey[b]	42,148	68	68	28,644
Massachusetts	188,714	71	64	121,067
Connecticut	61,454	64	60	36,863
Maine[c]	76,802	64		
Pennsylvania[d]	90,900	56		
New York	360,905	48	34	123,934
Vermont	88,514	55	27	23,728

[a] National Wetland Inventory (NWI) data were used for all states but New York. All NWI statistics except for Rhode Island (Tiner 1989b), New Jersey (Tiner 1985), and Maine (Fefer 1980) are unpublished and were provided by R. Tiner, U.S. Fish and Wildlife Service, Newton Corner, Mass. Statistics for New York were generated by the New York State Wetlands Inventory (O'Connor and Cole 1989).

[b] Data are from eight northern counties that are at least 50% glaciated: Sussex, Passaic, Bergen, Essex, Hudson, Warren, Morris, and Union.

[c] Data are from 105-town coastal zone only (Fefer 1980).

[d] Data are from glaciated regions of state only: Middle Western Upland Plain, Northern and Southern Poconos, and Other Glaciated Northeast Pennsylvania. See Tiner (1989a) for region locations.

National Wetlands Inventory mapping has not been completed in New York, but comparable statewide wetland area statistics have been generated by the New York State Wetlands Inventory, which was conducted by the state's Department of Environmental Conservation in the 1970's (Hardy and Johnston 1975; O'Connor and Cole 1989). Those data have been used in this profile to estimate the abundance of red maple swamps in New York. Statewide wetland inventory statistics are currently unavailable for New Hampshire and Maine.

In the six states for which statewide NWI statistics are available, forested wetland constitutes from 55% (Vermont) to 83% (Rhode Island) of all palustrine wetland (Table 1.4). In New York, the estimate is 48%, and in coastal Maine, 64%. Widoff (1988) estimated an area of about 2 million hectares of palustrine wetland in Maine as a whole, of which 1.2 million (60%) are forested.

The broad-leaved deciduous subclass of forested wetland predominates in all areas of the glaciated Northeast except for the spruce–fir regions. In the southern New England–northern New Jersey area, broad-leaved deciduous forested wetlands compose from 60 to 77% of all palustrine wetland (Table 1.4). In the colder parts of the Northeast, particularly in northern New England and the Adirondacks, broad-leaved deciduous wetland forests decline in abundance, while needle-leaved evergreen wetland forests increase markedly. In Vermont, for example, broad-leaved deciduous swamps constitute only 27% of all palustrine wetland; needle-leaved evergreen swamps account for 24% of the total. According to NWI statistics, the total area of broad-leaved deciduous forested wetland ranges from 18,000 ha in Rhode Island to 121,000 ha in Massachusetts (Table 1.4). New York has at least 124,000 ha (O'Connor and Cole 1989).

Physiographic Variation in Wetland Abundance

The size and relative abundance of inland wetlands (and red maple swamps) vary markedly from one part of the glaciated Northeast to another, chiefly as a result of differences in topographic relief, surficial geology, and related surface drainage. Wetlands are especially abundant wherever topographic and geologic conditions prevent water from freely infiltrating soils or flowing off the land surface. In central and eastern Maine, where shallow soils and a rolling, bedrock-controlled landscape provide an abundance of moisture at the surface year-round, wetlands have been estimated to cover 9–12% of the landscape (Widoff 1988). In southeastern New England, broad lowlands, high regional groundwater tables, and generally congested surface drainage also lead to a

Table 1.5. *Percentage of total land area in each glaciated northeastern state covered by palustrine wetland and by forested wetland (based on National Wetlands Inventory [NWI] and New York State Wetlands Inventory data).*[a]

State	Total land area (ha)	Palustrine wetland (%)	Forested wetland (%)	BLD[b] forested wetland (%)
Rhode Island	274,130	8.4	7.0	6.5
Massachusetts	2,027,368	9.3	6.6	6.0
Maine[c]	835,375	9.2	5.9	
New Jersey[d]	534,534	7.9	5.4	5.4
Connecticut	1,262,267	4.9	3.1	2.9
Pennsylvania[e]	2,049,348	4.4	2.3	
Vermont	2,402,712	3.7	2.0	1.0
New York	12,240,809	2.9	1.4	1.0

[a] NWI data were used for all states but New York. All NWI statistics except for Rhode Island (Tiner 1989b), New Jersey (Tiner 1985), and Maine (Fefer 1980) are unpublished and were provided by R. Tiner, U.S. Fish and Wildlife Service, Newton Corner, Mass. Statistics for New York were generated by the New York State Wetlands Inventory (O'Connor and Cole 1989). NWI data are not available for New Hampshire.

[b] BLD = broad-leaved deciduous.

[c] Data are from 105-town coastal zone only (Fefer 1980).

[d] Data are from eight northern counties that are at least 50% glaciated (see Table 1.4 for list).

[e] Data are from glaciated regions of state only (Table 1.4).

great abundance of wetlands. In northern New Jersey, large wetland complexes overlie the deposits of former glacial lakes Passaic and Hackensack (Tiner 1985). National Wetlands Inventory statistics indicate that palustrine wetlands cover 8–9% of the land area of Rhode Island, Massachusetts, and glaciated New Jersey; broad-leaved deciduous forested wetlands cover 5–6% of the land in those states (Table 1.5).

In the White Mountains, Green Mountains, Adirondacks, and Catskills, more rugged relief results in a lesser abundance and smaller size of wetlands. Broad-leaved deciduous wetland forests are often limited to narrow streamside bands and isolated depressions in those areas. In New York and Vermont, palustrine wetlands occupy only 3-4% of the landscape, and broad-leaved deciduous wetland forests only 1% (Table 1.5). U.S. Forest Service statistics suggest that red maple forested wetland covers no more than 1% of Maine (Powell and Dickson 1984) and New Hampshire (Frieswyk and Malley 1985) as well.

Marked differences in wetland abundance are apparent even within individual states. For example, in the eastern (Seaboard Lowland) part of Massachusetts (Fig. 1.2), red maple swamps cover from 8 to 16% of the various counties (U.S. Fish and Wildlife Service, National Wetlands Inventory, Newton Corner, Massachusetts, unpublished data). In Worcester County, located in the central (New England Upland) part of the state, red maple swamps cover 6% of the land surface. West of the Connecticut River valley, in the Green Mountains (Berkshire Hills) physiographic region, less than 3% of the land supports red maple swamps. Similarly, the coverage of red maple swamps ranges from 3 to 10% in the various counties of Rhode Island (Tiner 1989b) and northern New Jersey (Tiner 1985).

Heeley (1973) demonstrated that Massachusetts wetlands are relatively more abundant on stratified glacial deposits and postglacial alluvium than on till and bedrock, but the variation in wetland abundance appears to be more a function of physiography than surficial geology per se. In Massachusetts, stratified drift and alluvium predominate in lowland areas of the landscape where the land surface is relatively flat, surface water from upstream areas collects, and regional water tables are relatively high. Till and bedrock generally occur at higher elevations where relief is greater, groundwater tables are deeper, and surface water is scarce. In other areas of the Northeast, where stratified drift is less common and till blankets the lowlands as well as the hills, swamps may still be numerous and extensive. For example, Jordan (1978) tallied more than 4,000 wetlands on the 5,100-km2 Tug Hill Plateau, an elevated plain lying between the Adirondack Mountains and Lake Ontario in New York. More than 90% of those wetlands were located on till. In northwestern Connecticut (Green Mountains physiographic region), Messier (1980) calculated that 5-7% of the land was wetland; of this, 95% was underlain by till.

Chapter 2. The Physical Environment

Surficial Geology

Most of the unconsolidated geologic deposits covering the northeastern landscape were laid down during the Wisconsin continental glaciation (Flint 1971). Since the retreat of the glacier 12,000–18,000 years ago, glacial deposits, often referred to as drift, have been eroded, weathered, and, in some instances, buried by postglacial windblown (aeolian) or water-carried (alluvial) material. The physiographic diversity that is so characteristic of the glaciated Northeast results from highly varied preglacial bedrock-controlled topography, as well as glacial and postglacial erosion, transport, and deposition. This combination of geologic conditions and hydrology controls the size, distribution, and, to a large extent, the form and functions of northeastern wetlands. The influence of bedrock on wetlands is largely hydrologic (e.g., perching of groundwater) and chemical. While some wetlands in the region occur directly on bedrock, most red maple swamps have developed in unconsolidated surficial deposits. For this reason, we place major emphasis on surficial geology.

The surficial geologic deposits of the glaciated Northeast can be broadly categorized as follows:

- A. Glacial deposits
  - 1. Till
  - 2. Stratified drift
    - a. Glaciofluvial deposits
    - b. Glaciolacustrine deposits
    - c. Glaciomarine deposits
- B. Postglacial Deposits
  - 1. Stream terrace deposits
  - 2. Modern fluvial deposits (alluvium)
  - 3. Aeolian deposits

The origin and characteristics of the three principal types of surficial deposits—till, stratified drift, and alluvium—are outlined below; their relative positions on the landscape are illustrated in Fig. 2.1. Glaciomarine deposits, which include stratified drift laid down in marine or estuarine environments; stream terrace deposits, which represent historic floodplains; and aeolian deposits, which consist of a thin mantle of fine sand or silt deposited by wind shortly after deglaciation, are of limited extent in the Northeast and thus are rarely associated with red maple swamps. Unless otherwise indicated, the following descriptions follow Flint (1971).

Till

Till is a heterogeneous mixture of particles, ranging in size from clay to boulders, that was laid down directly by the glacier as it moved or as it melted. Material deposited beneath the glacier is often fine grained and exceedingly compact due to the weight of the overlying ice. This "lodgement till" is commonly encountered as a dense, low-permeability soil layer. Till dropped during melting of the ice, often referred to as ablation till, is frequently lighter and thus more permeable. In general, however, the poor sorting of particles in till results in permeabilities that are far lower than those found in most stratified drift deposits (Motts and O'Brien 1981). Lodgement till typically exhibits hydraulic properties comparable to clay or bedrock. The thickness of till deposits in the Northeast ranges from a few meters, where bedrock is close to the surface, to tens of meters. Till and bedrock are generally exposed in topographically high areas of the landscape; in lowland areas, they are commonly buried beneath stratified drift or postglacial deposits.

Stratified Drift

This category of glacial deposits includes material laid down in glacial streams or lakes. Following maximum glacial advance, some 18,000–21,000 years ago in the Northeast, the ice front receded in pulses over several thousand years. As the glacier retreated, meltwater issuing from beneath the ice deposited stratified sediments in low areas of the landscape (Koteff 1974).

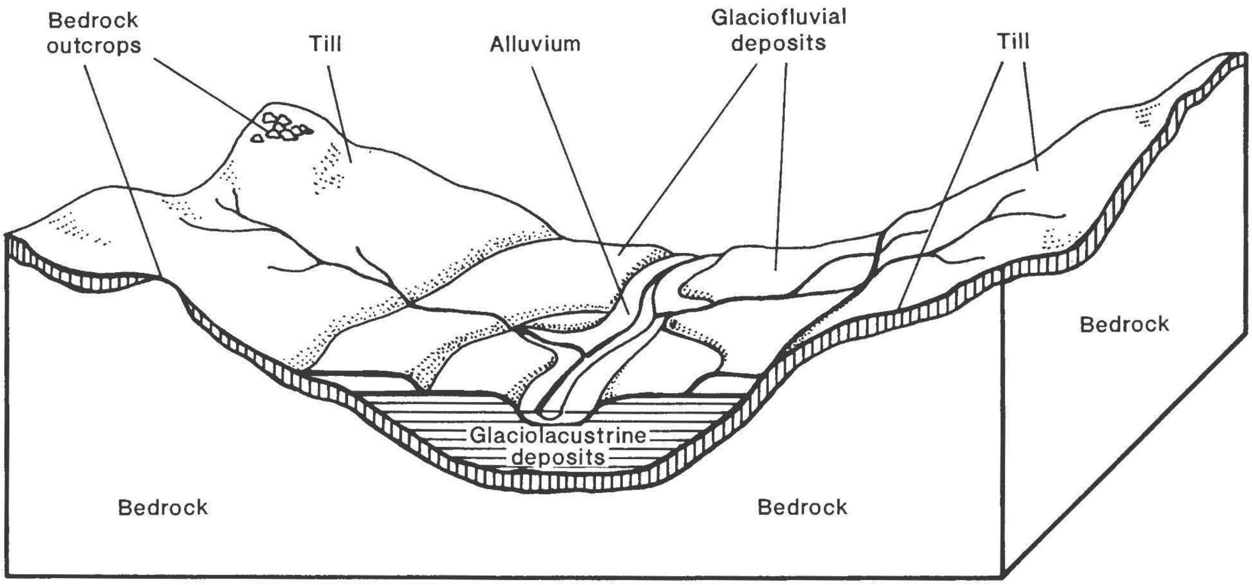

Fig. 2.1. Relative landscape positions of the principal types of surficial geologic deposits (modified after Morrissey 1987).

Glaciofluvial Deposits

Stratified materials deposited by flowing meltwaters, either in contact with the ice (ice-contact deposits) or beyond the margin of the glacier (proglacial deposits), are referred to as glaciofluvial deposits. Particle size and the degree of sorting of glaciofluvial deposits are largely a function of transport distance and energy levels in the depositional environment. Fluvial deposits laid down beneath, alongside, or on top of the ice typically consist of coarse sands and gravels with poor sorting, and they sometimes include bodies of till that have slumped off the melting ice. Proglacial deposits, also known as outwash, are generally better sorted and become finer grained with increasing distance from the glacial front. Because of their sorting and coarse texture, many glaciofluvial deposits have high permeability, and where sufficient thicknesses occur, as in deep preglacial valleys, the deposits constitute aquifers capable of supplying municipal wells (Motts and O'Brien 1981).

Glaciolacustrine Deposits

Sediments deposited in the standing water of glacial lakes generally are referred to as glaciolacustrine deposits. These deposits include fine sand, silt, and clay that settle out of the water column, as well as coarser material that is deposited by currents flowing down the face of lake deltas. Till dropped from melting blocks of glacial ice may also be incorporated in these deposits. Glaciolacustrine deposits are generally of low permeability, although highly permeable horizons may occur (Motts and O'Brien 1981). Where glaciofluvial and glaciolacustrine deposits are laid down more or less contemporaneously and in close association, they are often referred to as a morphological sequence (Koteff 1974). Several such sequences may be laid down during deglaciation in a given locale, and in some cases these interrelated fluvial and lacustrine deposits are mapped as a single surficial geologic unit.

Alluvium

The silt, sand, and gravel deposited by modern streams, either in the channels or on their floodplains during overbank flooding, are collectively referred to as alluvium. On surficial geology maps, these deposits typically appear only along large, low-gradient perennial streams; along small streams, alluvium is commonly discontinuous or too thin or narrow to be mapped.

Hydrogeologic Settings of Red Maple Swamps

Red maple swamps occur in many different locations on the landscape, from small, isolated basins in till or glaciofluvial deposits to extensive wetland complexes on glaciolacustrine deposits, and from

Table 2.1. *Hydrogeologic classification of northeastern inland wetlands (after Hollands and Mulica 1978).*

I. Wetlands directly associated with bedrock
   A. Wetlands fed by groundwater discharging from fracture porosity (joints, fractures sheeting) in bedrock
   B. Wetlands fed by groundwater discharging from faults
   C. Wetlands created by perched water tables on bedrock created by glacial erosion or differential weathering
   D. Wetlands bordering and in streams flowing through predominantly bedrock valleys
II. Wetlands associated with thick till deposits[a]
   A. Wetlands created by perched water tables in till basins
   B. Wetlands created by perched water tables on till slopes
   C. Wetlands associated with streams flowing in predominantly till valleys
   D. Wetlands associated with local or regional water tables discharging in till areas
III. Wetlands associated with glacial stratified deposits
   A. Glaciofluvial wetlands
      1. Kettles
      2. Wetlands associated with groundwater discharging at the ice-contact slope of a head of outwash
      3. Wetlands associated with meltwater channels on the surface of the morphological sequence
      4. Wetlands associated with streams flowing on the morphological sequence
      5. Wetlands associated with the intersection of the water table and the morphological sequence surface
   B. Glaciolacustrine wetlands
      1. Kettles
      2. Wetlands associated with groundwater discharging from ice-contact slopes
      3. Wetlands associated with streams flowing on a delta surface
      4. Wetlands associated with meltwater channels on a delta surface
      5. Wetlands associated with groundwater discharge at the distal edge of deltaic deposits
      6. Wetlands associated with groundwater discharging from bottomset beds
      7. Wetlands associated with perched water tables on bottomset beds
      8. Wetlands associated with streams flowing over bottomset beds
      9. Wetlands associated with the intersection of the water table and the delta surface
IV. Wetlands associated with glacial or postglacial stream terrace deposits
   A. Wetlands perched on stream terrace deposits
   B. Wetlands associated with abandoned stream channels on stream terrace deposit surface
   C. Wetlands created by the intersection of the water table with the stream terrace deposit surface
V. Wetlands associated with recent alluvial deposits and floodplains
   A. Wetlands associated with perched water tables
   B. Areas subject to flooding (1- to 2-year storm frequency)
   C. Wetlands created by the intersection of the water table with alluvial or floodplain surfaces
   D. Wetlands associated with abandoned stream channels, oxbows, and point bar deposits
   E. Wetlands consisting of the stream or river and its channel but not having a 1- to 2-year floodplain

[a]The transition from bedrock- to till-controlled wetlands may be vague.

hillside seeps at the headwaters of streams to stream floodplains and lake edges. Some swamps are fed primarily by groundwater, some mainly by surface runoff, and some by stream or lake overflow. Taken together, the geologic and hydrologic features of a particular site may be referred to as its hydrogeologic setting. While there has been relatively little research on this aspect of red maple swamps, it is clear that hydrogeologic setting is a primary determinant of water regimes, water chemistry, plant community structure and floristics, and groundwater recharge and discharge relationships.

Table 2.1 details the great variety of situations in which northeastern inland wetlands occur in association with bedrock, till, glaciofluvial deposits, glaciolacustrine deposits, stream terrace deposits, and recent alluvium or floodplain deposits. Within each of these geologic settings, wetlands may differ in the nature of the hydrologic system. For example, wetlands located over bedrock or till may be hydrologically isolated from the local or regional groundwater table by the rock or by low-permeability layers within the till; they may be fed directly by groundwater discharging from bedrock or till; or they may be associated with streams flowing over the surface of these materials. Wetlands may occur in any of a wide variety of settings on stratified drift as well, ranging from fluvial ice-contact sites to proglacial lacustrine situations. Red maple swamps are found in virtually all of the hydrogeologic settings listed in Table 2.1.

Novitzki (1979a, 1982) created a hydrologic classification for wetlands in Wisconsin that is applicable throughout the glaciated Northeast and is particularly useful for a functional analysis of wetland hydrology. His approach emphasizes the source of the water feeding each wetland and the resulting hydrologic processes. Depending upon whether the wetland is fed primarily by surface water or groundwater, and whether it is located in a depression or on a slope, it is placed into one of the following four classes: surface-water depression, surface-water slope, groundwater depression, or groundwater slope. While some wetlands are intermediate in characteristics between two or more of these classes, most fit reasonably well into one of the four categories. Red maple swamps occur in all of these hydrologic situations; however, most are either groundwater depression wetlands or groundwater slope wetlands. The basic characteristics of each hydrologic class, taken from Novitzki (1982), are outlined below.

Surface-water Depression Wetlands

In these wetlands, precipitation and overland flow (surface runoff) collect in a depression where there is little or no groundwater discharge (Fig. 2.2). Water leaves the wetland principally by evapotranspiration and infiltration (groundwater recharge). The wetland hydrologic system lies above the local or regional groundwater system and is isolated from it by an unsaturated zone; thus, it is said to be "perched." In the glaciated Northeast, surface-water depression wetlands are most likely to form over bedrock or till deposits in topographically elevated areas of the landscape; however, they may develop in lowland kettles or ice-block basins that formed in glaciolacustrine or fine-textured glaciofluvial deposits. Because surface-water depression wetlands are characteristically underlain by a low-permeability layer that causes water to accumulate above it, groundwater recharge through that layer may be limited. The relative wetness of the basin depends upon the volume of overland flow entering it, the degree of permeability of underlying strata, and basin depth. Water level fluctuation may be great in small surface-water depression wetlands that receive much surface runoff.

Surface-water Slope Wetlands

These wetlands are located along the edge of a stream or lake or on the sloping surface of a floodplain. They may occur on till or stratified drift but are commonly found on alluvium. While these wetlands are also fed by precipitation and overland flow, the principal source of water is the overflow of the adjacent water body (Fig. 2.2). The sloping surface of the wetland permits water to drain readily back to the lake or river as its stage falls. As was the case with the previous class, the wetland surface usually lies well above the local water table, so groundwater discharge to the wetland is negligible or nonexistent. Groundwater recharge from the wetland is possible, depending on the permeability of underlying surficial deposits, but because much of the infiltrating water may remain in the soil only briefly before discharging back into the lake or river, it is commonly considered "bank storage" rather than recharge. Water levels tend to fluctuate more rapidly in streamside wetlands than in lakeside wetlands.

Groundwater Depression Wetlands

These wetlands occur where a basin intercepts the local groundwater table, so that the wetland is fed by groundwater discharge as well as precipitation and overland flow (Fig. 2.2). Classic groundwater depression wetlands have no surface drainage leaving the site; however, occasional streamflow out may occur from basin overflow. Groundwater inflow may be continuous or seasonal, depending upon the depth of the basin and the degree of fluctuation of the local water table. During those periods when the wetland water level is higher than the local groundwater table (e.g., after major precipitation events in dry seasons), groundwater recharge may occur. Groundwater may enter the wetland basin from all directions, or it may discharge in one area and recharge in another. In the glaciated Northeast, groundwater depression wetlands are most likely to occur in stratified drift, particularly in coarse-textured glaciofluvial deposits where relatively rapid movement between groundwater and surface water can occur. Water levels decline throughout the growing season, but at a slower rate than in surface-water depression wetlands because groundwater inflow replaces some of the water lost

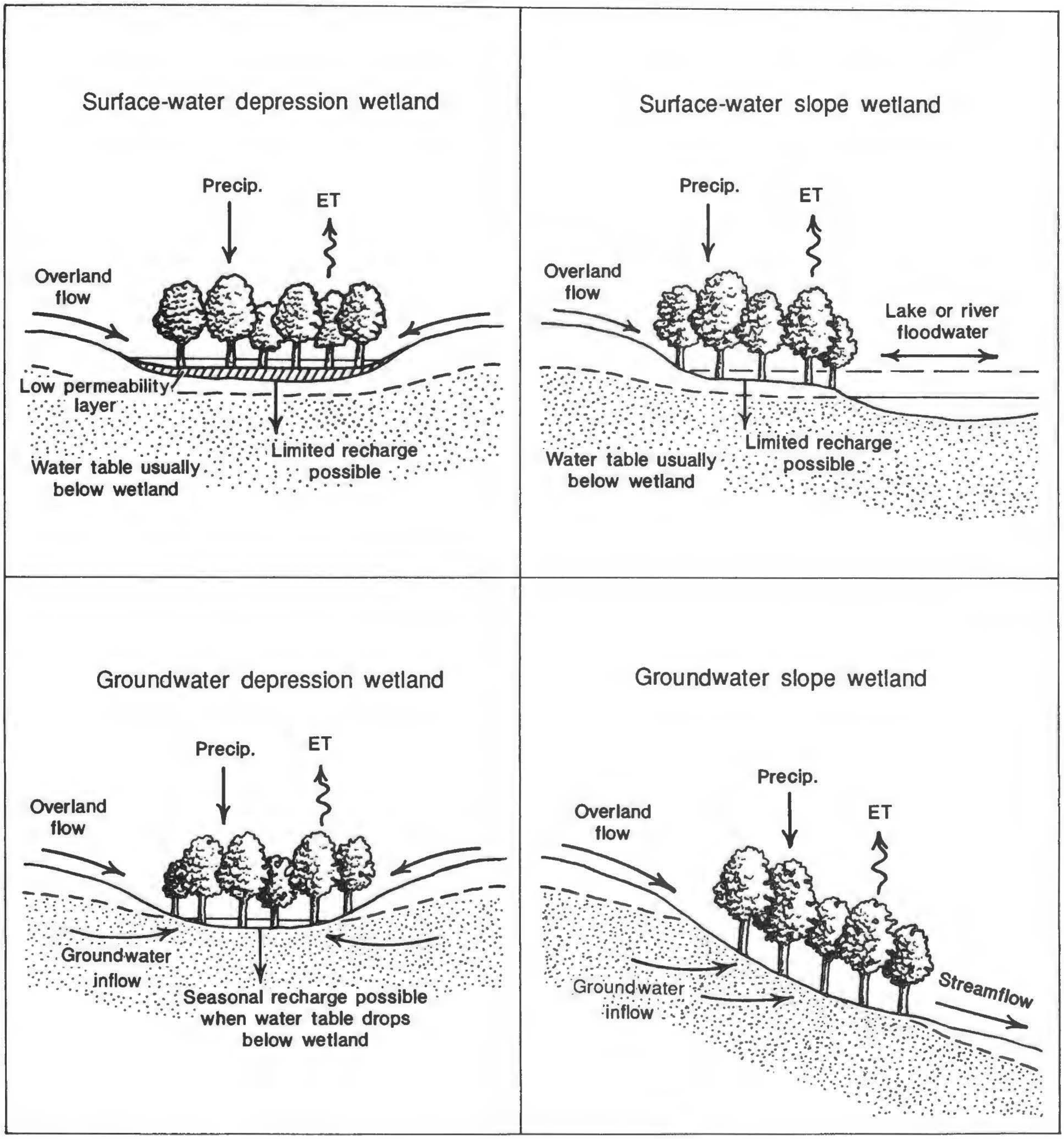

Fig. 2.2. Inland wetland hydrologic classes (based on Novitzki 1979a, 1982). The *shaded area* is the groundwater zone; its upper surface is the water table.

Fig. 2.3. Red maple swamp in the groundwater depression hydrologic class.

by evapotranspiration. Continuing groundwater inflow may cause wetland water levels to rise in the fall, when evapotranspiration declines, often in excess of direct precipitation inputs. The red maple swamp shown in Fig. 2.3 is a groundwater depression wetland.

Groundwater Slope Wetlands

These wetlands occur where groundwater discharges as springs or seeps at the land surface and drains away as streamflow (Fig. 2.2). Most commonly, these wetlands occur on hillsides over till deposits (Fig. 2.4) or at the base of hills where stratified drift and till come into contact. The great majority of red maple swamps located at the headwaters of streams are groundwater slope wetlands. The local water table slopes toward the wetland surface. Where groundwater inflow is continuous, the soil remains saturated. At many sites, however, groundwater inputs cease during late summer or early fall as evapotranspiration depletes soil moisture in the root zone, in which case the soil is only seasonally saturated. Permanent ponding of water is prevented by the sloping land surface, but water may collect temporarily in isolated depressions. Precipitation and overland flow provide additional water to the wetland on an intermittent basis. Groundwater recharge may occur in the wetland after such events, but amounts are likely to be negligible, especially where wetland soils have formed over dense lodgement till deposits. Where such deposits are present, groundwater slope wetlands may be fed primarily by shallow groundwater systems perched above the regional system.

Messier (1980) is one of the few researchers to describe the hydrologic settings of northeastern red maple swamps specifically; he also addressed the influence of setting on water regime, soil fertility, and swamp floristics. In his survey of northwestern Connecticut wetlands, Messier found red maple swamps in three distinctly different hydrologic settings; he referred to them as perched swamps, spring swamps, and valley swamps. Perched swamps, found in isolated basins over bedrock and compact till deposits, are equivalent to Novitzki's (1982) surface-water depression wetlands. Dormant season water levels in these wetlands were well above the ground surface (20–30 cm or more) and relatively stable. During the growing season, water levels fluctuated widely; they rose sharply after major rain events, but typically dropped below the surface by late summer due to evapotranspiration and the absence of significant groundwater inflow. Spring swamps, which correspond to Novitzki's groundwater slope wetlands, were

Fig. 2.4. Red maple swamp in the groundwater slope hydrologic class. This swamp is located on a hillside over till deposits; the boulders are glacial erratics.

most commonly found at the bases of hills where groundwater running downslope over bedrock or dense till layers discharged at the surface during early spring. By late August, water levels had dropped as much as 60 cm. Valley swamps appear to be intermediate between groundwater slope and groundwater depression wetlands. They occurred in level or gradually sloping valley bottoms composed of till or, less commonly, glaciofluvial deposits. They received large amounts of both surface runoff and groundwater from adjacent till slopes. As a result, some valley swamps held a meter or more of surface water during early spring and still had water levels within 10 cm of the surface in early July. While water levels were below the surface for more than half the growing season, they did not drop as far as in the perched swamps. Valley swamps were commonly drained by streams.

Hydrologic Budgets in Red Maple Swamps

The possible avenues of water inflow and outflow in a red maple swamp are summarized in Fig. 2.5. As shown in the previous paragraphs, the hydrologic setting of each wetland determines how many of the possible components are in its water budget and how large each component is. Over one or more years, the input–output equation can be expected to balance; during any given year, inputs generally equal or exceed outputs during the dormant season, while outputs (primarily evapotranspiration) predominate during the growing season. Hence, in northeastern red maple swamps, water levels are normally highest during the winter and spring, and lowest during late summer or early fall.

O'Brien (1977) developed the most detailed water budget analysis for red maple swamps in the glaciated Northeast. Although his data were gathered from only two wetlands during a single relatively dry year (annual precipitation 20% below normal), the study provides valuable information on relative inflows and outflows in different geologic settings, and it describes seasonal changes characteristic of a large proportion of the red maple swamps in this region. The two red maple forested wetlands studied by O'Brien were located 1.6 km apart, about 22 km northwest of Boston, Mass. Small streams arose within, and drained, each wetland, but neither site had streams entering (i.e., both were groundwater

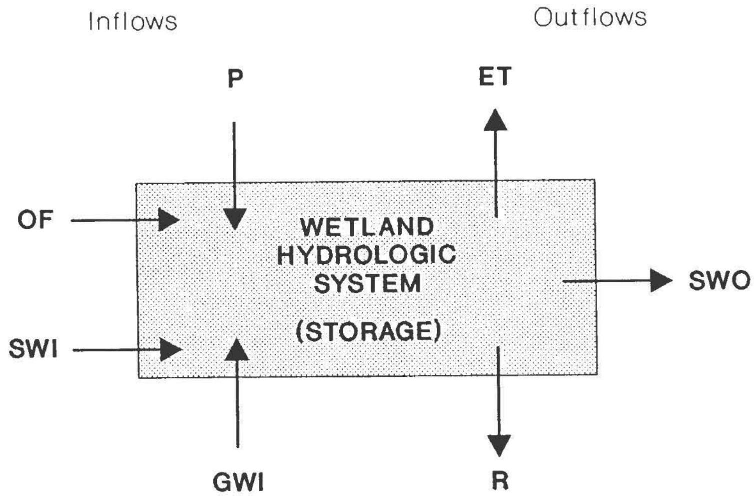

Fig. 2.5. Inflow-outflow components and water budget equation for a red maple swamp (based on Novitzki 1982).

Water Budget Equation: P + OF + SWI + GWI = ET + SWO + R

where:
P = precipitation falling on the wetland
OF = overland flow into the wetland
SWI = streamflow into the wetland
GWI = groundwater flow into the wetland
ET = evapotranspiration out of the wetland
SWO = streamflow out of the wetland
R = recharge from wetland to groundwater

slope wetlands). Other pertinent information on the two wetlands is given in Table 2.2.

Total surface-water discharge from each wetland amounted to approximately 48% of precipitation. The spring months (March–May) accounted for 70–75% of the total annual discharge at both sites. By analyzing well and stream hydrographs, O'Brien determined that nearly 93% of the total discharge from both wetlands originated as groundwater inflow. The discharge of groundwater was relatively rapid, however, and O'Brien surmised that there was insufficient storage to maintain perennial streamflow. While both red maple swamps were primarily zones of groundwater discharge, the Conant Road wetland recharged the groundwater system for 6 weeks in the late summer and early fall. During this dry period of the year, the volume of groundwater recharge from the wetland was several orders of magnitude greater than surface-water discharge.

Low vertical permeability in the well-decomposed organic soil at the Route 2 wetland caused artesian conditions to exist at that site for most of the year; groundwater was prevented from discharging at the surface of the wetland by the organic soils. High horizontal permeability in these soils allowed groundwater to discharge laterally along the edges of stream channels. Where the channels had cut through the entire organic deposit, exposing the underlying sands, groundwater discharge was considerable. The artesian pressure beneath the organic material was relieved by discharge of groundwater into the stream channels instead of to the wetland surface; consequently, the surface was relatively dry during much of the growing season.

Woo and Valverde (1981) reported similar findings from a study of a perched red maple swamp in southern Ontario. During 1 year of detailed hydrologic measurements, they found that water

Table 2.2. *General characteristics of red maple forested wetlands studied by O'Brien (1977).*

Feature	Route 2 wetland	Conant Road wetland
Surficial geology	Glaciofluvial	Till
Wetland size (ha)	85	72
Watershed size (ha)	319	290
Soil[a]	1 m sapric	3 m hemic-fibric

[a] Sapric refers to well-decomposed organic soil, while hemic and fibric refer to moderately well decomposed and poorly decomposed organic soils, respectively.

in the 1-m-thick organic soils was rapidly depleted by evapotranspiration. During the study period (April to November), total evapotranspiration from the wetland was roughly equal to rainfall, and streamflow out of the swamp was maintained by streamflow in. Water storage in the peat was insufficient to sustain flows in tributary channels throughout the year, but the swamp soils absorbed much of the rainfall from summer storms, thereby temporarily maintaining flow in some of the wetland streams.

In light of the great variety of hydrogeologic settings in which red maple swamps occur, the results reported by O'Brien (1977) and Woo and Valverde (1981) probably represent only a fraction of the hydrologic variability to be encountered in this wetland type. The magnitude of the various components in the water budget of individual wetlands can be expected to vary with topographic and hydrogeologic setting, watershed size, soil composition, relative development of surface-water drainage systems, and other site factors. Until detailed water-balance studies are conducted in red maple swamps in a wide variety of settings, relationships between these wetlands and associated groundwater and surface-water systems can be described only in general terms.

Table 2.3. *Water regimes of northeastern red maple swamps.*

Water regime	Definition
Seasonally flooded[a]	Surface water is present for extended periods, especially early in the growing season, but is absent by the end of the season in most years; when surface water is absent, the water table is often near the land surface
Temporarily flooded[a]	Surface water is present for brief periods during the growing season, but the water table usually lies well below the soil surface for most of the season
Seasonally saturated[b]	The soil is saturated to the surface, especially early in the growing season, but unsaturated conditions prevail by the end of the season in most years; surface water is absent except for groundwater seepage and overland flow

[a] Definition according to Cowardin et al. (1979).
[b] Definition by the authors of this community profile.

Water Regimes

Definitions and Key Characteristics

The net result of all inflow and outflow of water to and from a wetland at any point in time is indicated by the position of the water level in the wetland. The elevation and degree of fluctuation of the water table with respect to the land surface over time is referred to as the wetland's water regime (Golet and Lowry 1987). Because of the wide variation in water levels among years in many wetlands, water-regime descriptions are most meaningful, particularly from an ecological standpoint, when expressed as the condition to be expected in most years.

Cowardin et al. (1979) recognized eight nontidal water regimes, two of which accurately depict the hydrologic conditions found in northeastern red maple swamps (Table 2.3). Most red maple forested wetlands located in basins and fed by groundwater as well as overland flow (i.e., groundwater depression wetlands) are seasonally flooded (see Fig. 2.6). The temporarily flooded regime occurs primarily in surface-water depression wetlands and surface-water slope wetlands, where groundwater inflow is minimal and overland flow or overbank flooding by streams and lakes provides the principal source of water for the wetland. Red maple is found in temporarily flooded situations, but frequently the duration of flooding and soil saturation at such sites during the growing season is so brief that species better adapted to those conditions predominate. In southern Rhode Island, for example, pin oak and swamp white oak commonly dominate the temporarily flooded zone of surface-water depression wetlands located in till. On northeastern stream floodplains, a variety of tree species, including silver maple, ashes, cottonwood, black willow, boxelder (*Acer negundo*), American elm, and sycamore, usually dominates the temporarily flooded zone, while red maple is found mainly in seasonally flooded depressions, where soils are saturated for longer periods. In rare instances, red maple swamps located along tidal fresh rivers may be tidally influenced (e.g., McVaugh 1958).

Red maple swamps on hillsides fed by groundwater discharge (i.e., groundwater slope wetlands) are not flooded, in the strict sense, but are best

Fig. 2.6. Seasonally flooded red maple swamp. Surface water is present during the dormant season and for the early part of the growing season in most years.

described as representing the "saturated" water regime of Cowardin et al. (1979). However, this water-regime modifier was developed primarily to address permanently saturated, nonflooded wetlands such as bogs; therefore, its application to hillside seeps and other nonflooded wetlands, where the soil is saturated mainly during the early part of the growing season, is not entirely satisfactory. For this reason, we prefer to use the term "seasonally saturated" (Table 2.3) to describe the water regime of these swamps (Fig. 2.4).

Although the broad water regimes listed in Table 2.3 are useful for wetland classification and mapping, more precise, quantitative measures of water level activity are needed for examination of the influence of hydrology on the structure and functions of red maple swamps. Some pertinent water level measures, which may be expressed on a growing season, annual, or multiyear basis, include the following: average water levels, water level fluctuation (i.e., range), frequency of flooding, hydroperiod (i.e., duration of surface flooding), and flood-free period (i.e., duration of surface drawdown). Accurate portrayal of a wetland's water regime requires measurements of such hydrologic features during a period of several years. Unfortunately, these data are scarce for most wetland types in the United States, red maple swamps included.

Water Levels in Rhode Island Swamps

The most extensive data on water regimes in red maple swamps come from two studies conducted in southern Rhode Island. In the first study, reported by Lowry (1984), water levels were monitored for 7 years in six relatively wet swamps containing organic soils ranging in depth from 0.5 to 4.8 m. The second study focused on the relationships among hydrology, soils, and vegetation in the transition zones between three red maple swamps and adjacent upland forests (Davis 1988; Allen 1989; Allen et al. 1989; Sokoloski 1989). In the latter study, 3 years of water level data were gathered from a broad range of wetland soils: very poorly drained organic soils, very poorly drained mineral soils, and poorly drained mineral soils. Somewhat poorly drained and moderately well-drained upland soils were sampled as well (see Table 2.4 for descriptions of soil drainage classes). The results of these two studies provide the only

Table 2.4. *Soil drainage classes (after Wright and Sautter 1979).*

Drainage class	Characteristics
Excessively drained	Brightly colored; usually coarse-textured; rapid permeability; very low water-holding capacity; subsoil free of mottles[a]
Somewhat excessively drained	Brightly colored; rather sandy; rapid permeability; low water-holding capacity; subsoil free of mottles
Well drained	Color usually bright yellow, red, or brown; drain excess water readily, but contain sufficient fine material to provide adequate moisture for plant growth; subsoil free of mottles to a depth of at least 91 cm
Moderately well drained	Generally any texture, but internal drainage is restricted to some degree; mottles common in the lower part of the subsoil, generally at a depth of 46–91 cm; may remain wet and cold later in spring; generally suited for agricultural use
Somewhat poorly drained	Remain wet for long periods of time due to slow removal of water; generally have a slowly permeable layer within the profile or a high water table; mottles common in the subsoil at a depth of 20–46 cm
Poorly drained	Dark, thick surface horizons commonly; gray colors usually dominate subsoil; water table at or near the surface during a considerable part of the year; mottles frequently found within 20 cm of the soil surface
Very poorly drained	Generally thick black surface horizons and gray subsoil; saturated by high water table most of the year; usually occur in level or depressed sites and are frequently ponded with water

[a] See the section on soils in this chapter for a discussion of the significance of mottles.

detailed account of water level activity in seasonally flooded and seasonally saturated red maple swamps. The following discussion of water levels is based on their findings.

General Patterns

Water levels in red maple swamps are highly dynamic; marked variations among seasons, years, and swamps are typical. Figure 2.7 shows the general pattern of water level activity in seasonally flooded red maple swamps, based on Lowry's (1984) study. From an annual high in the spring (April–May), water levels at all six sites declined to their lowest points in late summer or early fall. The low point commonly occurred in September, but ranged from July to October, depending on the amount and distribution of precipitation in the particular year. High water levels ranged from 20 cm above the surface to 20 cm below in most years, but low water levels were far more variable. In the wettest year of the study (1979), three of the swamps had water at or above the surface during the entire measurement period (mid-April to mid-December); water levels at the other sites remained within 30 cm below the surface in that year. In the driest years of the study (1980, 1981), water levels at all sites dropped more than 50 cm below the surface, and at some sites a subsurface depth of 1 m was exceeded.

Differences in water levels among sites were greatest at the end of the summer, when water levels were lowest (Fig. 2.7). The greatest differences were observed in the driest years. Lowry (1984) concluded that these differences in low water levels resulted from differing amounts of groundwater inflow at the various sites, a factor determined by hydrogeologic setting and soil type (Bay 1967; O'Brien 1977). In nearly every year, water levels were clearly influenced not only by total precipitation, but also by distinct weather patterns or unusual events (e.g., heavy rains associated with Hurricane Belle in August of 1976; exceptionally high rainfall in May of 1978 and June of 1982; abnormally high, well-distributed rainfall in 1979; and consistently low rainfall throughout 1980 and 1981).

Inspection of the water level hydrographs (Fig. 2.7) revealed that most of the sites studied by Lowry (1984) met the definition of seasonally flooded (Table 2.3), while the others were seasonally saturated. The soils at all of those sites were very poorly drained. In the transition-zone study, all of the wetland stations—poorly drained and very poorly drained—were seasonally saturated; except for brief rainfall events, surface water was absent during the growing season in most years.

Figure 2.8 provides a 3-year record of water levels at 2 of the 54 wetland stations monitored

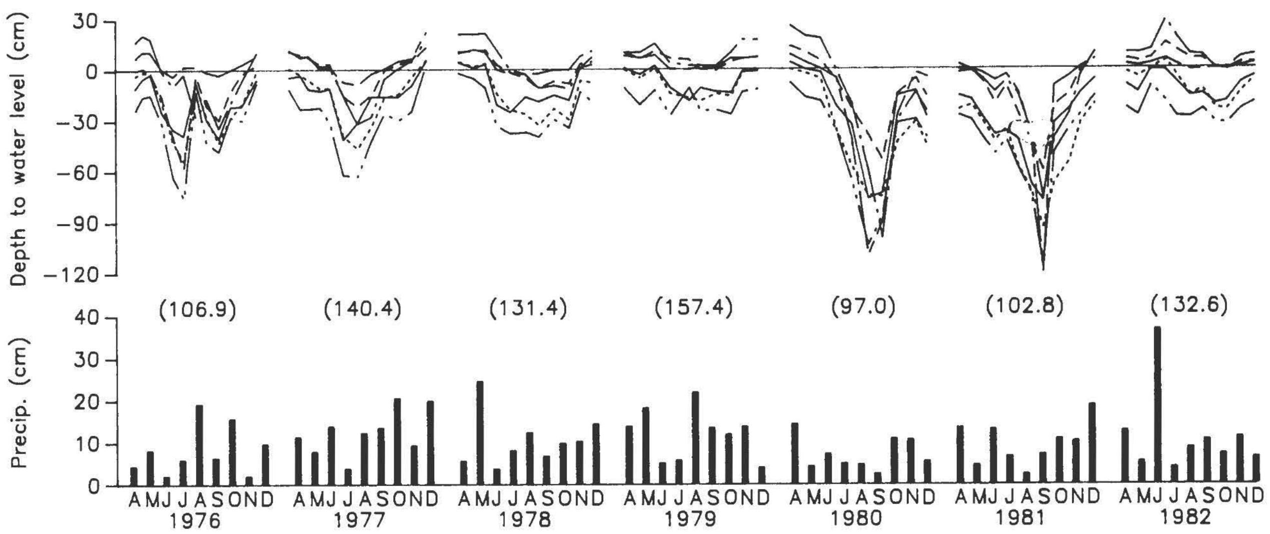

Fig. 2.7. Water levels in six Rhode Island red maple swamps during a 7-year period. Annual precipitation values are shown in parentheses. Mean annual precipitation for 1951–80 was 123.2 cm (data from Lowry 1984).

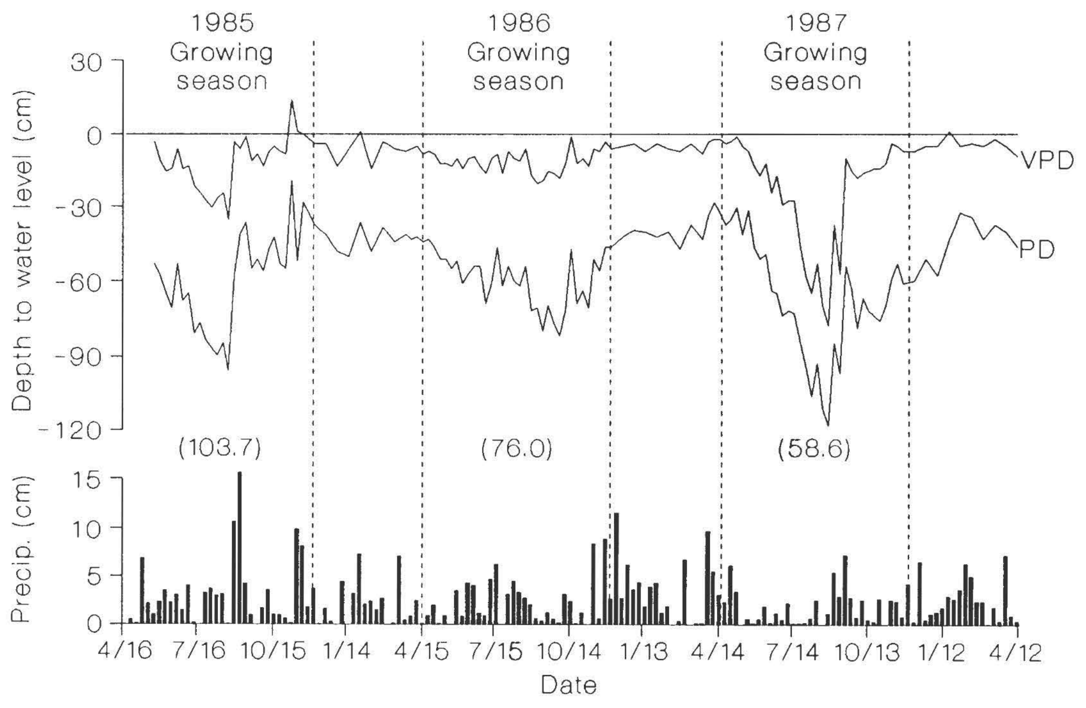

Fig. 2.8. Groundwater levels in very poorly drained (VPD) and poorly drained (PD) soils in Rhode Island red maple swamps during a 3-year period. Each curve represents a single monitoring station selected to portray average conditions for that drainage class. Both stations had a seasonally saturated water regime. Growing season precipitation totals are shown in parentheses (F. C. Golet, unpublished data).

during the transition-zone study. The stations are representative of average water level activity in a very poorly drained mineral soil (Scarboro series, a Histic Humaquept) and a poorly drained mineral soil (Walpole series, an Aeric Haplaquept). Although water levels at the two stations differed by 30–60 cm, seasonal and annual patterns were similar. At both stations, there were large variations between years in growing-season water levels; however, dormant-season water levels at each station were similar in the 3 years of observations.

Mean monthly precipitation in southern Rhode Island ranges from about 7.5 cm in June and July to 11.8 cm in March and November, while evapotranspiration ranges from 16.5 cm in July to essentially zero during the dormant season (University of Rhode Island Weather Station, Kingston). Monthly evapotranspiration is relatively constant from year to year. Thus, water level fluctuation within each year is due primarily to seasonal variations in evapotranspiration rates, whereas yearly differences in water levels are caused by annual variations in precipitation. The response of water levels to annual variations in precipitation in seasonally saturated swamps (Fig. 2.8) closely mirrored the response of water levels in the seasonally flooded swamps (Fig. 2.7). Growing-season precipitation was 41% above the 30-year mean in 1985, roughly equal to the mean in 1986, and 20% below the mean in 1987.

Specific Hydrologic Attributes

A comparison of data gathered by Lowry (1984) and values generated by the Rhode Island transition-zone project (Table 2.5) indicates that, during a period of several years, growing-season water levels in Rhode Island red maple swamps averaged about 15–25 cm below the surface for very poorly drained soils and 60 cm below the surface for poorly drained soils. The extent of annual water level fluctuation varied widely among years, but was remarkably similar from one swamp to another, particularly at Lowry's sites (Fig. 2.7). In both studies, water level fluctuation at individual sites ranged from less than 10 cm in wet years to more than 1.2 m in dry years. On the average, water levels fluctuated 35–50 cm each year in very poorly drained soils and about 70 cm in poorly drained soils. Water levels dropped more than 80 cm below the surface at the majority of the poorly drained stations at some time each year.

The duration of surface flooding varied widely as well. At the seasonally flooded sites, surface water was present from late November or December into June in most years. The 7-year mean hydroperiod at these sites ranged from less than 10% to about 50% of the growing season (Lowry 1984). At the transition-zone sites, very poorly drained soils had surface water less than 2% of the growing season, on the average, while poorly drained soils were never flooded during the 3-year study (Table 2.5).

Table 2.5. *Hydrologic characteristics of seasonally saturated soils from Rhode Island red maple swamps during the growing season (15 April–30 November) (data from Allen et al. 1989 and Department of Natural Resources Science, University of Rhode Island, Kingston, unpublished data).*

	Very poorly drained soil		Poorly
	Organic	Mineral	drained soil
Characteristic[a]	(n = 6)[b]	(n = 19)[b]	(n = 14)[b]
Mean water level (cm)	-18.7	-22.4	-59.0
(Range)	(-10.7 to -32.6)	(-4.6 to -45.6)	(-34.3 to -88.8)
Water level fluctuation (cm)	33.9	47.5	71.2
(Range)	(16 to 56)	(9 to 98)	(21 to 121)
Hydroperiod (% of growing season)	0.6	1.4	0
(Range)	(0 to 3.8)	(0 to 11.1)	
Water level duration within 30 cm of surface (% of growing season)	87.1	72.6	7.8
(Range)	(46.9 to 100)	(24.2 to 100)	(0 to 36.4)

[a] Based on weekly measurements at three swamps during 3 years.
[b] n = total number of monitoring stations at three study sites.

The duration of soil saturation has been shown to influence plant species distribution (Huffman and Forsythe 1981; Paratley and Fahey 1986) and soil morphology (Zobeck and Ritchie 1984; Evans and Franzmeier 1986). Because most of the tree, shrub, and herb roots in red maple swamps are located within 30 cm of the ground surface, the percentage of the growing season during which the water table is within that zone may be of considerable significance. In the transition-zone study, water levels at the very poorly drained stations were within 30 cm of the surface for more than 70% of the growing season, on the average; at the poorly drained stations, however, water levels were within that zone less than 10% of the time (Table 2.5). These figures might suggest that poorly drained soils are too dry to support wetland vegetation; however, anaerobiosis (depleted oxygen conditions), not soil saturation, defines the wetland soil environment. Anaerobiosis occurs when oxygen consumption by plants, soil microbes, and chemical reactions in the root zone exceeds oxygen diffusion from the surface. Meeks and Stolzy (1978) suggested that when air-filled pores constitute less than 10–20% of the total soil volume, many of the narrow soil pore spaces become blocked by water, and direct gas exchange with the atmosphere is eliminated.

In the Rhode Island transition-zone study, air-filled porosity at various soil depths was determined through the use of field tensiometers and complementary laboratory studies (Allen 1989). Although the water table at the poorly drained stations was within 30 cm of the soil surface for only brief periods during the growing season, air-filled porosities at a depth of 30 cm were at or below 15% for 49% of the season (Table 2.6). As might be expected, average periods of restricted aeration in the root zone were longer at the very poorly drained stations (91–100% of the growing season). By comparison, restricted aeration was evident at the 30-cm depth for less than 15% of the growing season at the somewhat poorly drained and moderately well drained (nonwetland) stations adjacent to the swamps.

Table 2.6. *Percentage of the growing season during which air-filled porosity at a 30-cm depth was 15% or less in soils from Rhode Island red maple swamps and adjacent upland forests, based on weekly measurements at three sites during 3 years, 1985–1987 (data from Allen 1989).*

Soil drainage class[b]	n[c]	Percentage of growing season[a] Mean	Range[d]
Red maple swamps			
Very poorly drained			
Organic soil	6	99.6	97.8–100.0
Mineral soil	18	91.4	69.6–100.0
Poorly drained	14	49.4	17.4–88.0
Upland forests			
Somewhat poorly drained	7	13.0	7.5–24.7
Moderately well drained	9	3.8	2.2–6.5

[a] 15 April through 30 November.
[b] See Table 2.4 for drainage class definitions.
[c] n = number of sampling stations per soil category.
[d] Includes the lowest and highest 3-year percentages recorded at any stations in a particular soil category.

Soils

Data compiled by the U.S. Soil Conservation Service (U.S. Soil Conservation Service National Hydric Soils and SOI-5 Data Bases, Iowa State University, Ames) indicate that red maple occurs on over 200 hydric (wetland) soil series or phases in the glaciated Northeast. The number of hydric soils on which red maple is the dominant tree is unknown. A few studies have described soil properties in red maple swamps specifically (Laundre 1980; Messier 1980; Huenneke 1982; Lowry 1984; Paratley and Fahey 1986; Sokoloski 1989), but in light of the great diversity of soils found in this wetland type, discussion of data from isolated studies would be inappropriate. This section outlines the more general features of red maple swamp soils.

Basic Types: Organic and Mineral

Two basic categories of soils are found in red maple swamps: organic soils and mineral soils. Organic soils, also known as Histosols, are readily identified by an organic surface layer at least 40 cm thick. Mineral soils have less than 40 cm of organic material on the surface. Organic material is soil material that is composed of at least 12–20% organic carbon (20–35% organic matter) by weight (Soil Survey Staff 1990). Organic material is divided into three categories—fibric, hemic, and sapric—based on the degree of decomposition of the plant tissues. In fibric material, three-fourths or more of the soil volume after rubbing consists of plant fibers. The fiber content of sapric material after rubbing is less than one-sixth of the soil volume. Hemic material is intermediate in fiber content between fibric and sapric materials.

Generally, the proportion of organic material in a wetland soil is determined by soil temperature and the duration of anaerobic conditions, both of which regulate microbial decomposition rates (Bowden 1987). In red maple swamps, where soil saturation is seasonal, anaerobic conditions occur near the soil surface during only a portion of the growing season; organic matter is more readily decomposed during aerobic periods. As a result, the organic material in the soils of red maple swamps is predominantly sapric (well decomposed) or, less commonly, hemic (moderately well decomposed). Often, sapric and hemic horizons alternate in the same soil profile (Lowry 1984), suggesting that a swamp's water regime may shift over time.

Hydric Soil Drainage Classes

As noted previously, swamp soils also can be distinguished by drainage class. Descriptions of the basic soil drainage classes appear in Table 2.4. In the glaciated Northeast, hydric soils include (1) very poorly drained and poorly drained soils where the water table lies within 15–45 cm of the surface for more than 2 weeks during the growing season, the minimum depending on soil texture and permeability; (2) somewhat poorly drained soils that have a water table within 15 cm of the surface for more than 2 weeks during the growing season; and (3) soils that are frequently ponded or flooded for at least 7 consecutive days during the growing season (U.S. Soil Conservation Service 1991). As indicated earlier, northeastern red maple swamps have primarily very poorly drained or poorly drained soils. Very poorly drained soils typically occur in seasonally flooded basins, although they are sometimes found on slopes where groundwater inflow keeps the soil wet for extended periods during the growing season. Poorly drained soils are saturated seasonally, but seldom have standing surface water. A red maple swamp with both of these soil drainage classes is shown in Fig. 2.9.

Soil Type and Wetland Setting

Unless the natural hydrology of a swamp has been altered, its soil type (organic or mineral) is usually a direct indication of relative site wetness.

Fig. 2.9. Seasonally saturated red maple swamp containing poorly drained (*foreground*) and very poorly drained (*midground*) soils. These wetlands are common along upland drainageways throughout the glaciated Northeast.

Organic soils are always very poorly drained, while mineral soils may occur in any drainage class. As is the case with plant community composition, the organic matter content of a soil changes continuously along a moisture gradient. The wettest red maple swamps frequently have peat depths exceeding 1 m; depths of more than 6 m have been recorded (W. A. Niering, Connecticut College, New London, personal communication). Carlisle muck, a Typic Medisaprist with at least 1.3 m of organic material, is one of the most common soil series in red maple swamps throughout the Northeast. Swamps with organic soils most often occupy well-defined basins in the lowest areas of the landscape, where they are fed by the regional groundwater system, as well as by surface runoff and streamflow in some cases. Cold air drainage into such wetlands from surrounding upland areas also contributes to reduced organic matter decomposition rates. Swamps with mineral soils generally occur at the edge of organic swamps, on stream floodplains, or on hillsides where soil moisture is depleted earlier in the summer by evapotranspiration. Poorly drained mineral soils usually have surface organic matter accumulations of less than 20 cm; very poorly drained mineral soils may have up to 40 cm.

Physical and Morphologic Properties

Below the organic layer in swamp soils there is often a dark gray or black highly organic mineral horizon, followed by increasingly lighter "low-chroma" horizons, some of which also may contain orange or yellow "high-chroma" mottles (Tiner and Veneman 1987). Mottles are streaks, spots, or blotches different in color from the predominant color of the soil matrix. Permanent or prolonged saturation often produces bright-gray or blue-gray "gleyed" horizons, whereas alternating saturation and aeration, caused by water table fluctuation, produces mottles. The depth to gleying or mottling is one of the primary criteria for the identification of both soil drainage classes (Table 2.4) and hydric soils (Federal Interagency Committee for Wetland Delineation 1989).

The texture of mineral horizons may vary widely, from clay to coarse sand, depending on the nature of the surficial deposit from which the soil formed. In some swamps, organic deposits are underlain by marl (calcium carbonate) layers that were originally deposited in freshwater lakes (see Hutton 1972). Mottling and gleying are most obvious in silty or clayey soils such as those that develop from till, glaciolacustrine deposits, or alluvium. Mineral horizons that develop from glaciofluvial material are usually relatively coarse. While mottling is not often apparent in sandy soils, organic matter may accumulate immediately below low-chroma horizons from which it has been leached by water table fluctuation, marking the position of the low-water table.

In Rhode Island, Sokoloski (1989) found that the presence of pale brown mottles (chroma ≤3) within 30–40 cm of the mineral soil surface was a useful indicator of the upland limit of red maple swamps in sandy soils. Comprehensive field criteria for distinguishing wetland soils from upland soils are described in the *Federal Manual for Identifying and Delineating Jurisdictional Wetlands* (Federal Interagency Committee for Wetland Delineation 1989).

Base Status and pH

Throughout most of the glaciated Northeast, the soils of red maple swamps are acidic and low in available plant nutrients. Anaerobic decomposition of organic material creates organic acids that may lower soil pH. The pH of wetland soils may be neutral or alkaline in areas with high base saturation, where groundwater carries calcium and magnesium from the surrounding landscape to the wetland. (Base saturation is the percentage of a soil's cation exchange capacity that is saturated with exchangeable bases such as calcium and magnesium.) Most of the glaciated Northeast is characterized by bedrock and surficial deposits with low base content. These materials do not provide sufficient quantities of calcium and magnesium to groundwater to neutralize or markedly raise the base content of the soils in red maple swamps. Figure 2.10 identifies the major areas in the Northeast with high base saturation; these are the areas most likely to have alkaline wetland soils. Occasionally, even where wetland soils form directly over calcareous materials such as limestone or marl, the organic surface horizons may be acidic (Malecki et al. 1983; Paratley and Fahey 1986). In such cases, mineral-poor layers become functionally isolated from mineral-rich layers below, thereby affecting nutrient availability and the floristic composition of the plant community.

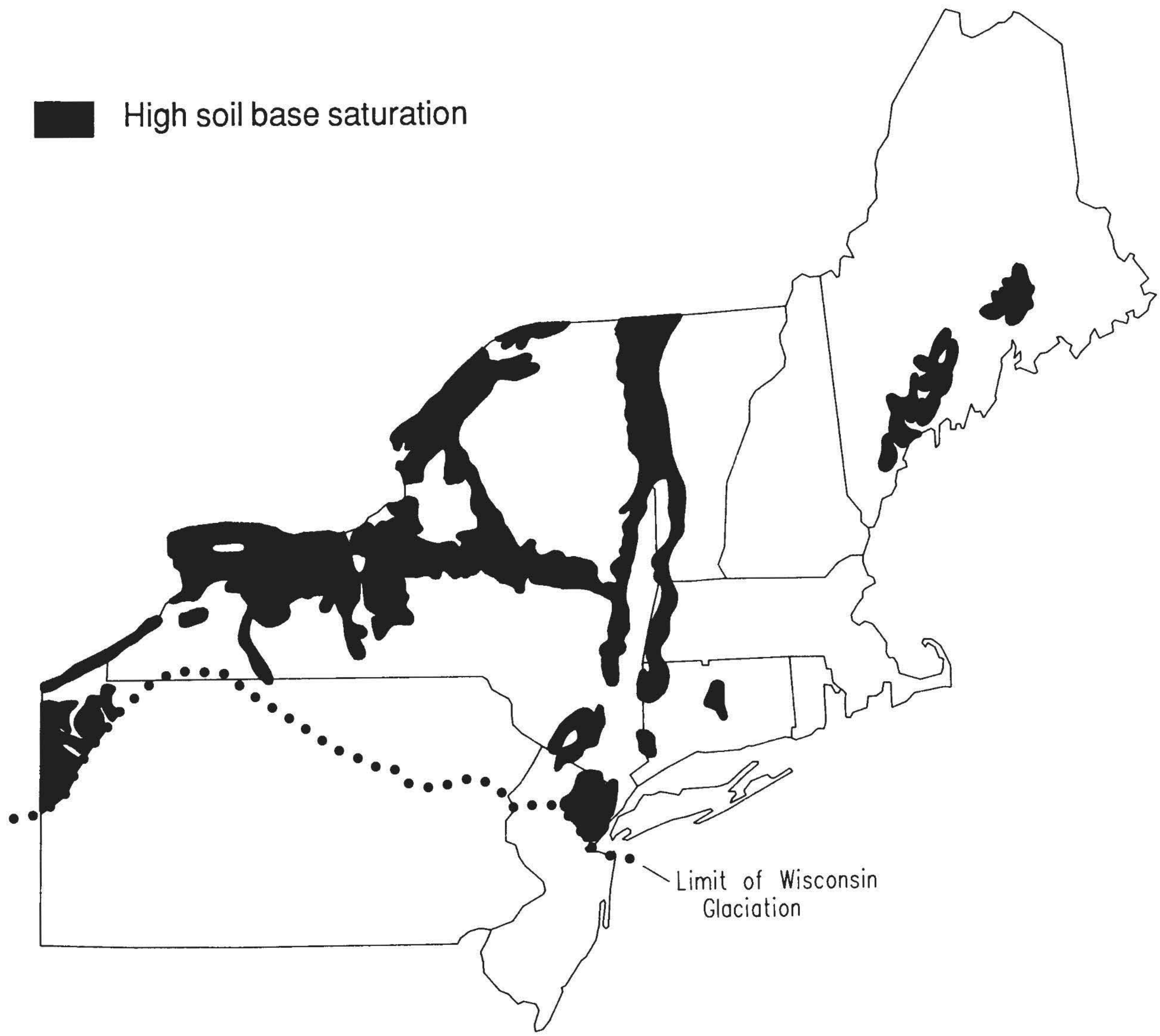

Fig. 2.10. Major areas of the glaciated Northeast with high soil base saturation. These areas are depicted on the *General Soil Map of the Glaciated Northeastern United States* (Smith 1984) as Alfisols or as Inceptisols with Eutrochrepts as the dominant soil map component. Soils with high base saturation occur in other parts of the region as well, but are too limited in area to map at this scale.

Chapter 3. The Plant Community

The two most fundamental aspects of the plant community in red maple swamps are community structure and floristic composition. Community structure refers to the physical composition of the plant community in terms of vegetation height, density, percent cover, and similar characteristics, and the relative development of various life-form layers. Structure is of special importance because of its relation to certain wetland functions and values, such as wildlife habitat, flood flow alteration, and forest biomass production. The floristic composition of a swamp, like its structure, may be a valuable indicator of the prevailing water regime, nutrient status, microclimate, or land-use history. Changes in either species composition or structure over time may reflect significant changes in these or other environmental conditions.

Descriptions of the plant community of northeastern red maple swamps come primarily from surveys of natural areas and preserves (Goodwin 1942; Niering 1953; Niering and Goodwin 1962, 1965; Egler and Niering 1967, 1971; Kershner 1975; Profous and Loeb 1984), statewide wetland surveys (Metzler 1982; Tiner 1985, 1989b; Metzler and Tiner 1992), research on green-timber impoundments (Reed 1968; Golet 1969; Malecki et al. 1983), and studies of individual and often unusual swamps (Wright 1941; Baldwin 1961; Eaton 1969; Fosberg and Blunt 1970; Vogelmann 1976). The most detailed floristic information has been gathered in plant community surveys conducted as a basis for wetland classification or for purely descriptive purposes (Nichols 1915, 1916; Conard 1935; Spurr 1956; Damman and Kershner 1977; Greller 1977; Messier 1980; Huenneke 1982). The majority of these surveys were carried out in Connecticut or on Long Island, New York. Only a few studies (Cain and Penfound 1938; Vosburgh 1979; Laundre 1980; Braiewa 1983; Lowry 1984; Swift et al. 1984) have been designed specifically to examine some aspect of red maple swamp ecology. Quantitative studies have been limited primarily to southern New England (Anderson et al. 1980; Messier 1980; Braiewa 1983; Lowry 1984) and New York (Stewart and Merrell 1937; Goodwin 1942; Huenneke 1982; Malecki et al. 1983; Paratley and Fahey 1986).

Figures 3.1–3.5 illustrate some of the more common members of the red maple swamp plant community.

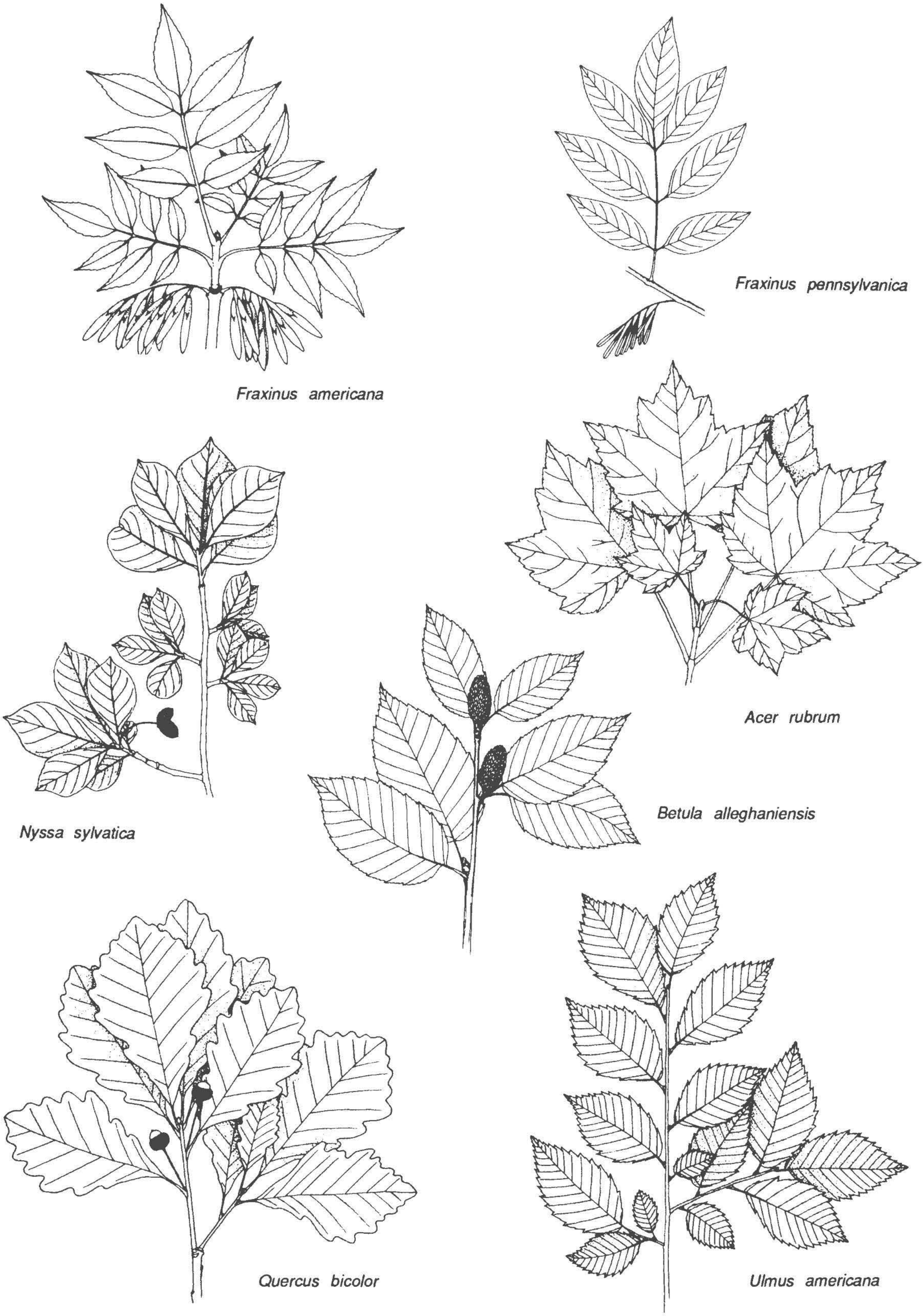

Fig. 3.1. Common broad-leaved deciduous trees of northeastern red maple swamps. See text and Table 3.3 for the relative importance and occurrence of these and other species in various sections of the glaciated Northeast. *Drawings by A. Rorer.*

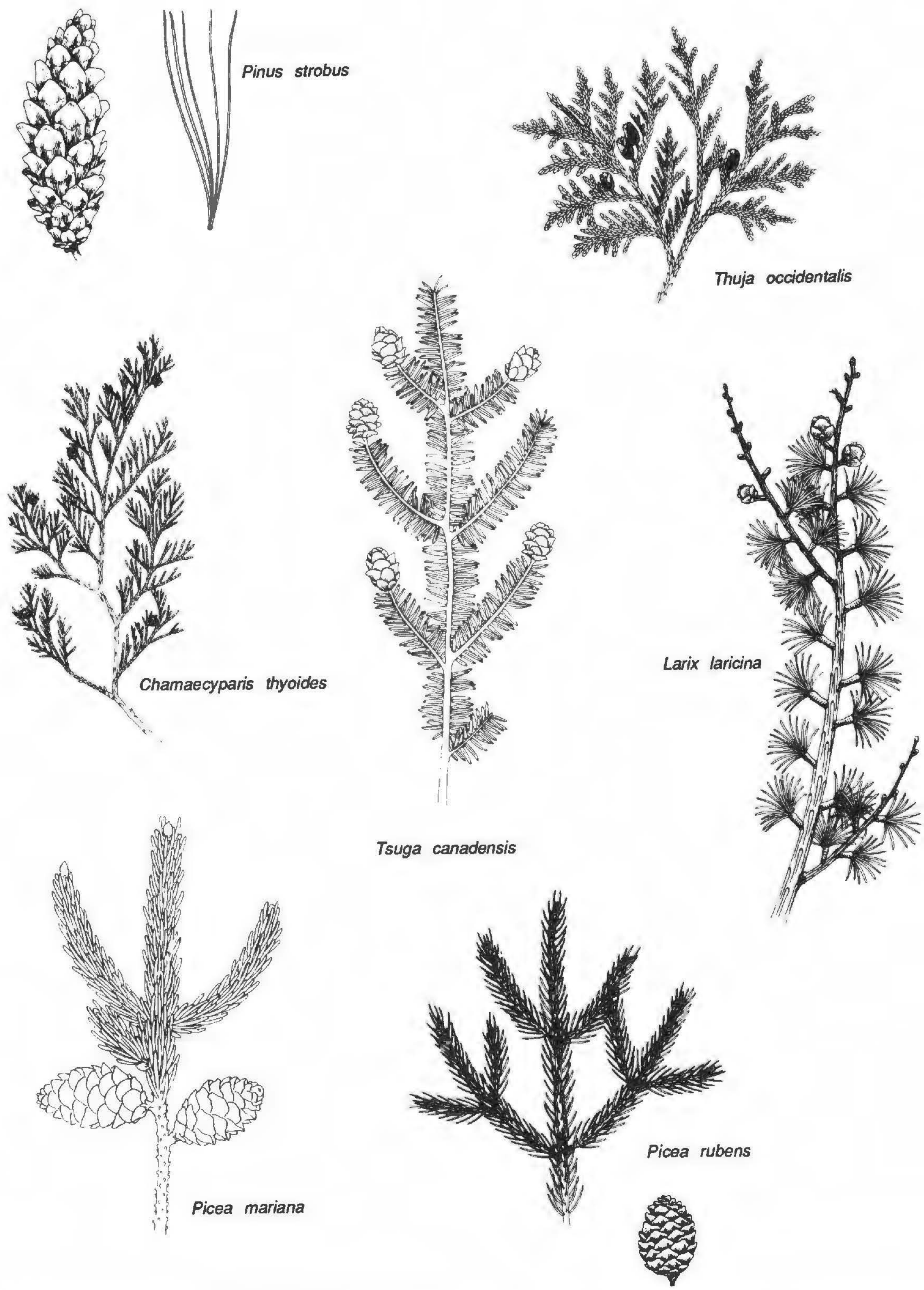

Fig. 3.2. Common needle-leaved trees of northeastern red maple swamps. See text and Table 3.3 for the relative importance and occurrence of these and other species in various sections of the glaciated Northeast. *Drawings by A. Rorer.*

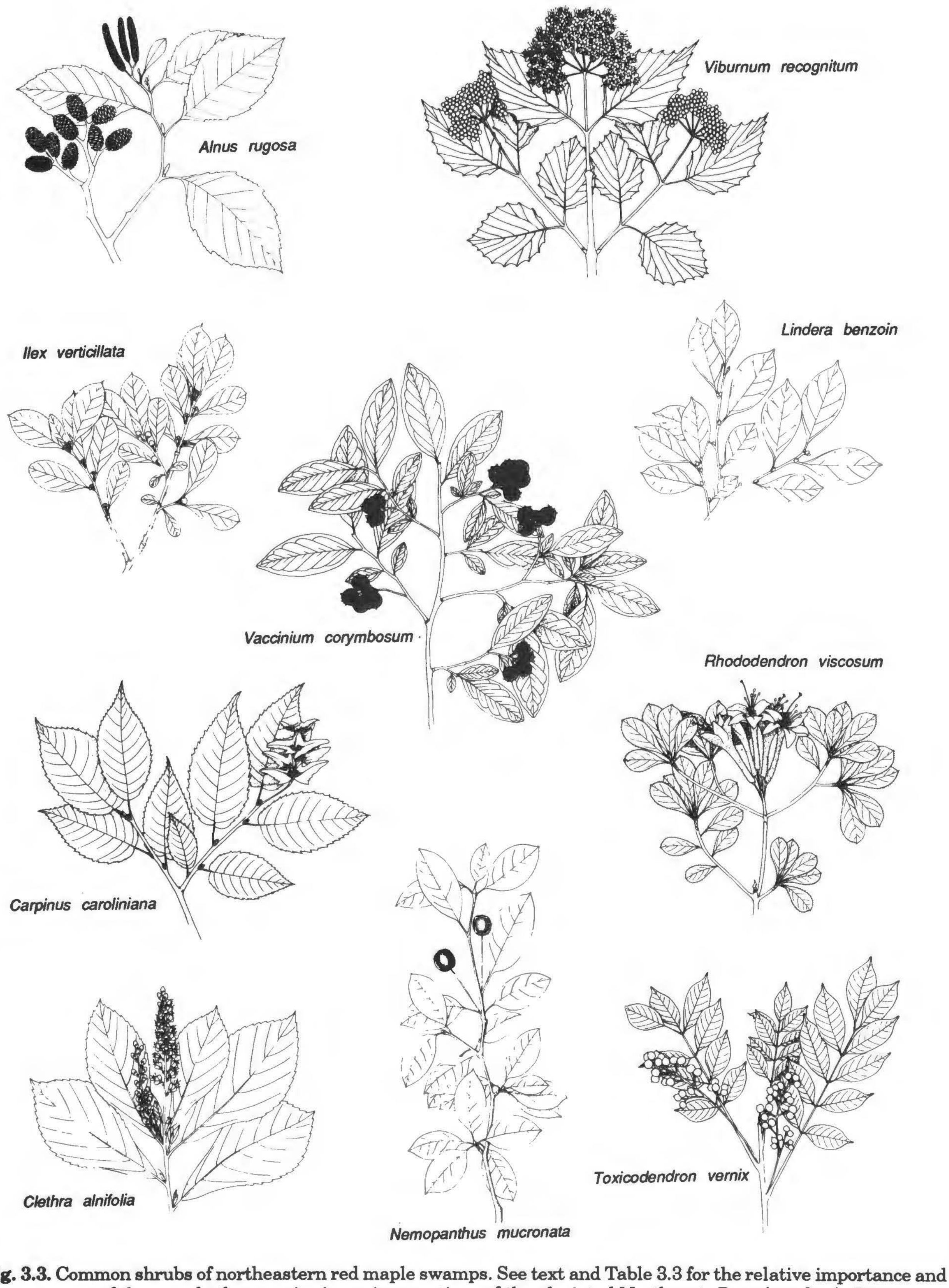

Fig. 3.3. Common shrubs of northeastern red maple swamps. See text and Table 3.3 for the relative importance and occurrence of these and other species in various sections of the glaciated Northeast. *Drawings by A. Rorer.*

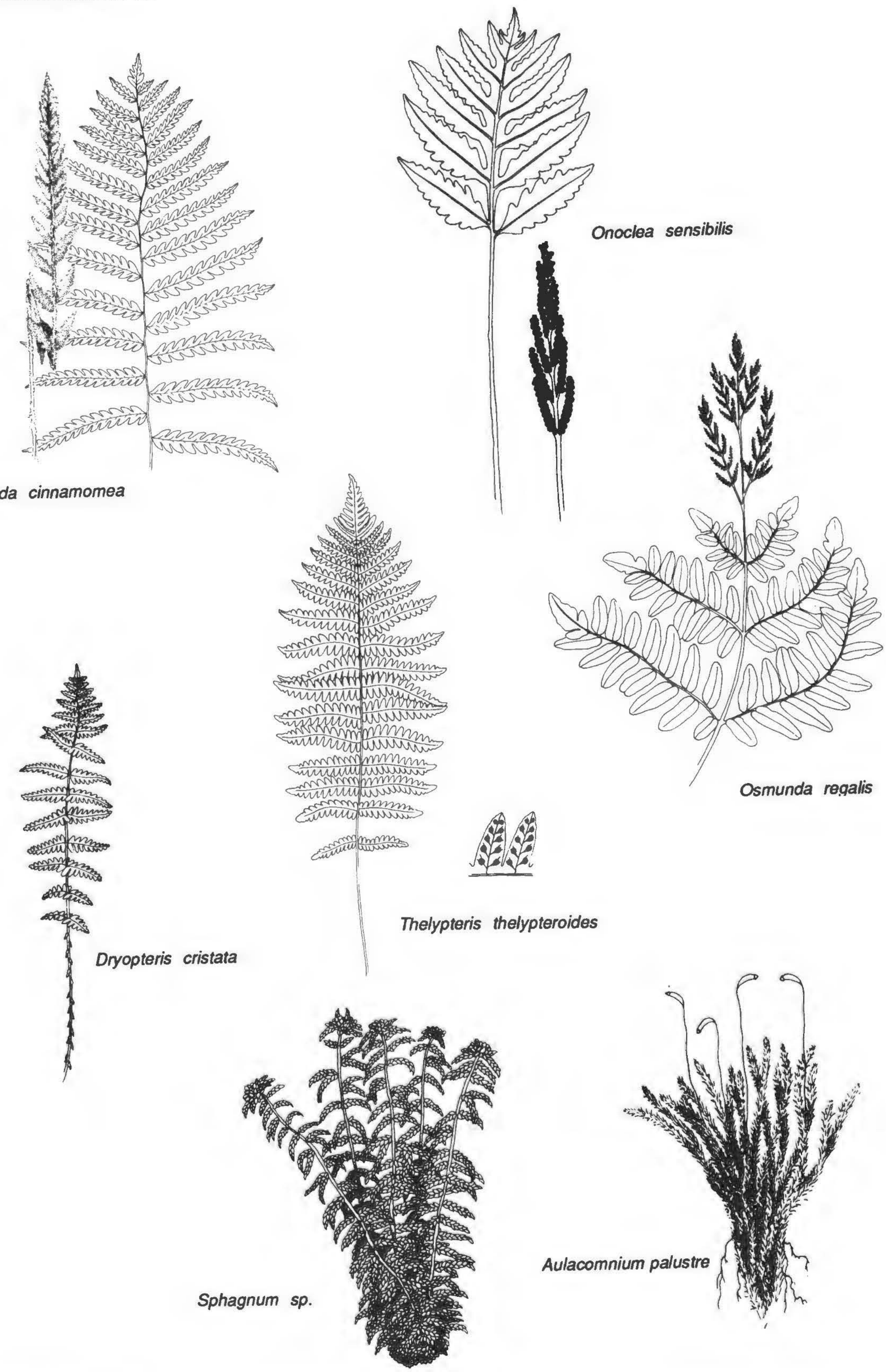

Fig. 3.4. Common ferns and mosses of northeastern red maple swamps. See text and Table 3.3 for the relative importance and occurrence of these and other species in various sections of the glaciated Northeast. *Drawings by A. Rorer.*

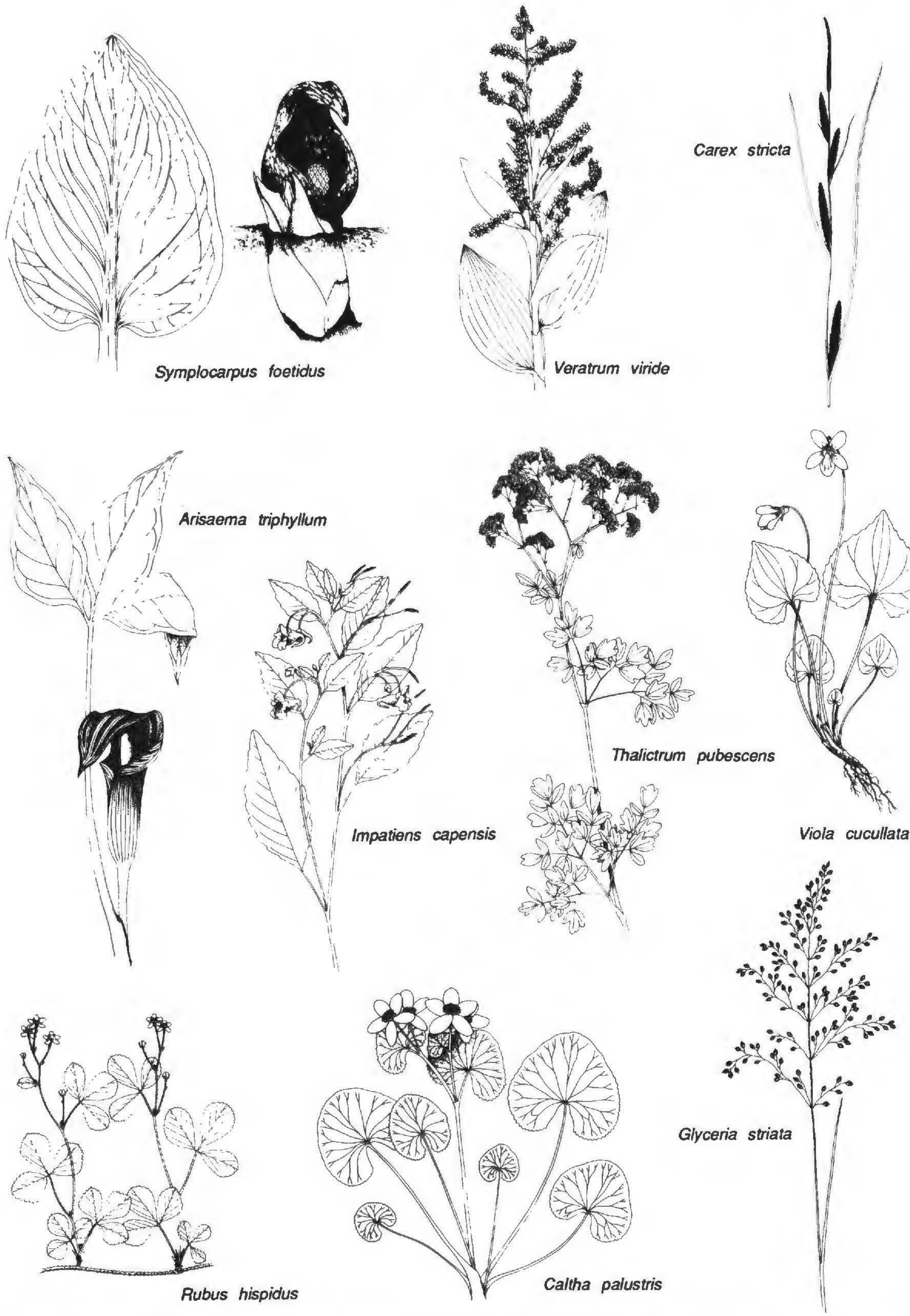

Fig. 3.5. Common forbs and graminoids of northeastern red maple swamps. See text and Table 3.3 for the relative importance and occurrence of these and other species in various sections of the glaciated Northeast. *Drawings by A. Rorer.*

Community Structure

Red maple swamps contain as many as five distinct vegetation life-form layers: trees, saplings, shrubs, herbs, and ground cover (Fig. 3.6). In this report, trees are considered to be woody plants at least 6 m tall (after Cowardin et al. 1979), while saplings are woody plants of tree form that are shorter than 6 m. In mature red maple swamps (i.e., those at least 40–50 years of age), the tree canopy typically forms a layer about 8 to 15 m above the forest floor. Sapling crowns are most evident at a height of 3 to 6 m above the ground; however, at most sites, the sapling layer is the most poorly developed. The shrub layer includes woody plants that are usually less than 3 m tall. Shrub foliage is commonly dense and often extends to within a meter of the ground. The herb layer consists of nonwoody erect plants such as ferns, grasses, sedges, and broad-leaved herbs that are normally less than 1.5 m tall. Bryophytes, clubmosses (*Lycopodiaceae*), trailing shrubs (e.g., *Rubus hispidus*, *Gaultheria procumbens*), and other low-growing plants form the ground cover layer. Vines such as greenbriers (*Smilax* spp.), Virginia creeper (*Parthenocissus quinquefolia*), and poison ivy (*Toxicodendron radicans*) also are a conspicuous component of many red maple swamps. Tree, shrub, and herb strata predominate in most red maple swamps, and we will emphasize these life forms in this report.

The following paragraphs present a description of plant community structure in northeastern red maple swamps. Studies on this topic have been few; most have been conducted in southern New England, New York, or New Jersey. While some of the New Jersey sites lie outside the glaciated Northeast, they are included here because of their obvious similarity, both structurally and floristically, to swamps farther north. Quantitative data from the studies cited in this section often cannot be compared directly because of differing definitions of the life forms sampled. Variations among sites in stand age, origin (sprout vs. seedling), and environmental conditions such as water regime also confound comparisons among studies. Nevertheless, the following data provide a general picture of community structure in several areas of the Northeast.

Tree Layer

Forested wetlands in the United States are generally characterized by high stem density, high basal area, and tree heights in excess of 10 m (Brown et al. 1979). Trees in northern swamps (≥35° N latitude) tend to be shorter and to have lower basal areas than trees in southern swamps. A review of structural data from mature northeastern red maple swamps (Table 3.1) suggests that tree heights are comparable to those from other temperate, nonfloodplain wetland forests (Brown et al. 1979), but tree density and basal area are commonly below average.

Heights of red maple stands 30–100 years of age span a relatively narrow range. Stand heights reported from southern New England and northern

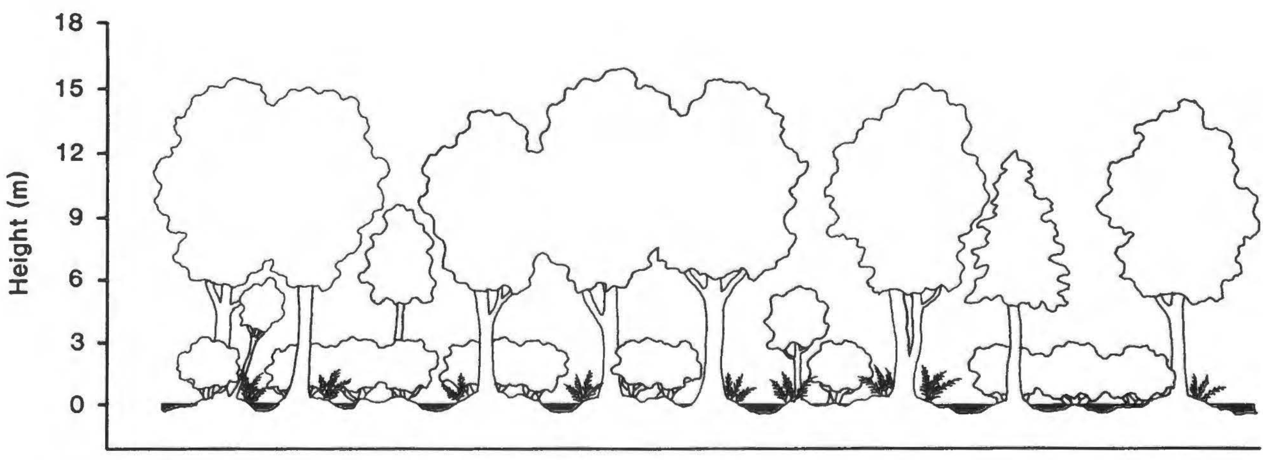

Fig. 3.6. Structural profile of a seasonally flooded red maple swamp. Illustrated are tree (>6 m), sapling (3–6 m), shrub (<3 m), and herb (<1.5 m) layers. Mound-and-pool microrelief also is depicted.

New Jersey averaged 13–15 m (Table 3.1). This narrow range suggests that height growth in red maple is rapid during the first 30–40 years and then slows considerably. Individual red maple trees may attain heights exceeding 25 m (Anderson et al. 1980), but such specimens are not common.

Stand density values reported for red maple swamps vary widely, depending upon the minimum size of stems tallied (Table 3.1). Stems at least 10 cm in diameter or at least 6 m tall number 200–1,000/ha (average usually 450–750/ha). Highest densities generally occur in young, sprout-origin stands (Braiewa 1983). Basal area values for northeastern red maple swamps range from less than 12 m^2/ha to more than 40 m^2/ha. Lowest average values have been reported from Rhode Island, and highest values from New Hampshire and northern New Jersey. Close inspection of Table 3.1

Table 3.1. *Structural characteristics of the tree layer in northeastern red maple swamps.*

Characteristic	No. stands	Mean[a]	Range[b]	Comment	Source	State
Stand height (m)	3	13.2	12.6–13.7		Unpublished data[c]	RI
	3	14.0	12.8–16.4	Stand ages 32–55 years	Braiewa (1983)	RI
	6	14.3	10.4–16.1	Stand ages 55–105 years	Lowry (1984)	RI
	12	15.1	13.5–17.7		Merrow (1990)	RI
	5	12.8	7.9–15.6		Swift et al. (1984)	MA
	1	14.8			Taylor (1984)	NJ
	1	15.2			Meyers et al. (1981)	NJ
Stand density (stems/ha)	6	471	225–758	DBH[d] ≥ 10 cm	Lowry (1984)	RI
	12	511	342–1,002	Height ≥ 6 m	Merrow (1990)	RI
	3	631	528–791	Height ≥ 6 m	Unpublished data[c]	RI
	3	1,958	908–3,067	DBH ≥ 4.1 cm	Braiewa (1983)	RI
	2	876	827–925	DBH ≥ 2.5 cm	Reed (1968)	NY
	1	737		DBH ≥ 10 cm	Taylor (1984)	NJ
	1	1,458		DBH ≥ 7.6 cm	Meyers et al. (1981)	NJ
	5	1,290	910–1,570	DBH ≥ 2.5 cm; stand ages 46–104 years	Ehrenfeld and Gulick (1981)	NJ[e]
	10	1,349		DBH ≥ 2.5 cm; stand ages 50–100 years	Ehrenfeld (1986)	NJ[e]
Basal area (m^2/ha)	6	21.6	11.6–33.1	DBH ≥ 10 cm	Lowry (1984)	RI
	3	22.7	20.1–24.9	Height ≥ 6 m	Unpublished data[c]	RI
	12	23.4	17.1–30.3	Height ≥ 6 m	Merrow (1990)	RI
	1	27.2		Red maple portion of conifer–hardwood swamp	Paratley and Fahey (1986)	NY
	2	37.8	36.5–39.0	DBH > 10 cm	DeGraaf and Rudis (1990)	NH
	1	16.6		DBH ≥ 10 cm	Taylor (1984)	NJ
	1	41.3		DBH ≥ 7.6 cm	Meyers et al. (1981)	NJ
	5	29.3	19.5–37.2	DBH ≥ 2.5 cm	Ehrenfeld and Gulick (1981)	NJ[e]
	10	29.2		DBH ≥ 2.5 cm	Ehrenfeld (1986)	NJ[e]

[a] Average of stand means, except where $n = 1$.
[b] Range of stand means.
[c] Data from Rhode Island transition-zone study (see the section on hydrology in chapter 4).
[d] Diameter at breast height (1.4 m).
[e] Study conducted outside the glaciated Northeast.

suggests a strong correlation between basal area and stand density.

In mature red maple forested wetlands, canopy cover commonly exceeds 80% (Miller and Getz 1977a; Lowry 1984; Merrow 1990). Lower values are most likely in old stands where gaps have been created by tree mortality, in stands that have been logged or subjected to recent hurricanes or other extreme weather events, and at sites too wet to support continuous forest cover.

Shrub Layer

Most red maple swamps in the Northeast are characterized by a dense, well-developed shrub layer (Ehrenfeld and Gulick 1981; Lowry 1984; Ehrenfeld 1986). This stratum is typically dominated by broad-leaved deciduous shrubs 2–3 m tall (Figs. 2.3 and 2.6), but lower shrubs, vines, saplings, and tree seedlings may be present as well. Broad-leaved evergreen shrubs, such as mountain laurel (*Kalmia latifolia*), sheep laurel (*K. angustifolia*), and inkberry (*Ilex glabra*), compose a small percentage of the cover at some sites, and needle-leaved evergreens, including balsam fir and American yew (*Taxus canadensis*), may be an important component of the understory in some red maple swamps in northern New England. A unique, often monotypic, shrub stratum found in some southern New England swamps is formed by great rhododendron (*Rhododendron maximum*), a broad-leaved evergreen that may reach heights of 5–6 m (Fig. 3.7). Where this species predominates, other shrubs and herbs usually are scarce (Lowry 1984). While the shrub layer is well developed in most undisturbed red maple swamps, it may be practically nonexistent in young forests that have developed directly from wet meadows without an intervening shrub stage (Fig. 3.8), or in forests that are grazed by cattle. Shrub abundance may vary widely within a swamp as well.

Total shrub cover exceeds 50% in most red maple swamps, but reported values range from as low as 21% to as high as 99% (Table 3.2). The extent of cover varies not only among swamps, but also among shrub height classes. Nearly all of the dominant shrub species in red maple swamps range from 2 to 4 m in height at maturity; as a result, this height class constitutes the bulk of the cover at most sites. In six mature Rhode Island swamps, for example, cover values for saplings

Fig. 3.7. Red maple swamp with understory dominated by great rhododendron (*Rhododendron maximum*).

Fig. 3.8. Young red maple forested wetland with a poorly developed shrub layer. This swamp was formerly a wet meadow dominated by tussock sedge (*Carex stricta*).

(4–6 m), tall shrubs (1–4 m), and short shrubs (<1 m) averaged 6, 73, and 44%, respectively (Lowry 1984). Total shrub cover generally decreases as the tree canopy becomes more closed; however, values of 50–70% are common even in swamps with canopy cover exceeding 85% (Lowry 1984; Merrow 1990).

Shrub density in red maple swamps is variable, but often exceedingly high (Table 3.2). Densities for shrubs at least 2.0–2.5 cm in stem diameter range nearly 20-fold among nonfloodplain sites, from as low as 470 stems/ha (Ehrenfeld and Gulick 1981) to as high as 8,000 stems/ha (Lowry 1984). Densities for shrubs with smaller diameters (including shrub seedlings) range even more widely, from 4,000 stems/ha (Reed 1968) to more than 130,000 stems/ha (Lowry 1984). Shrub stem diameter and density are both determined to a great degree by the age and growth form of the dominant shrub species. Species such as highbush blueberry (*Vaccinium corymbosum*), speckled alder (*Alnus rugosa*), and spicebush (*Lindera benzoin*) commonly grow in clumps, producing stems that are large in diameter (often exceeding 4 cm) but few in number, especially in old stands. Rhizomatous shrubs such as sweet pepperbush (*Clethra alnifolia*), on the other hand, generally have smaller stems but occur in very dense stands.

The important contribution of the shrub stratum to the overall structure of the red maple swamp community can be seen by comparing the relative basal areas of shrubs and trees. In six Rhode Island swamps, shrubs composed from 32 to 68% of the total basal area of woody stems; values averaged about 7 m^2/ha for stems at least 2.5 cm in diameter, and 8 m^2/ha for smaller stems (Lowry 1984).

Herb Layer

The herb layer in red maple swamps varies markedly in height, density, and percent cover. In swamps where tall herbs such as cinnamon fern (*Osmunda cinnamomea*) predominate, the height of the herb layer may exceed 1.5 m (Fig. 3.9); at other sites, it may be less than 0.5 m. Mean cover values for individual swamps range from zero to nearly 90% (Table 3.2). Because forest structure, hydrology, and other site conditions are unique to each swamp, and the herb layer is particularly sensitive to environmental gradients (Allen et al. 1989), a "typical" herb layer structure cannot be described. Since the abundance of herbs is clearly influenced by light intensity at the forest floor, tree and shrub cover and foliage density are key controlling factors. In swamps where shrubs such as great rhododendron form a nearly complete cover near the ground, herbs are almost nonexistent; where shrub cover is moderate to sparse, herb cover is usually greater (Lowry 1984). In swamps where shrub cover is not a limiting factor, herb abundance may be controlled more by water regime, surface microrelief, or other abiotic factors.

Species Richness

On a regional scale, the flora of red maple swamps is rich, including at least 50 species of trees, more than 90 species of shrubs and vines, and more than 300 species of nonwoody plants

Table 3.2. *Structural characteristics of the shrub and herb layers in northeastern red maple swamps.*

Characteristic	No. stands	Mean[a]	Range[b]	Comments	Source	State
Shrubs						
Cover (%)	6	6	3-16	Height 4-6 m	Lowry (1984)	RI
		73	53-93	Height 1-4 m	Lowry (1984)	RI
		44	28-90	Height <1 m	Lowry (1984)	RI
	12	87	77-99	Height <6 m	Merrow (1990)	RI
	3	34	28-42	All shrub species	Braiewa (1983)	RI
	9[c]	55	21-27	Height ≤2 m	Miller and Getz (1977a)	CT
Density (stems/ha)	6	4,667	2,250-8,000	BD[d] ≥2.5 cm and DBH[e] <10 cm	Lowry (1984)	RI
		86,656	38,188-132,812	BD <2.5 cm	Lowry (1984)	RI
		91,323	14,810-186,440	All stems <10 cm DBH	Lowry (1984)	RI
	3	61,000	49,000-71,000	DBH <4.1 cm	Braiewa (1983)	RI
	2	4,068	3,796-4,340	DBH <2.5 cm	Reed (1968)	NY
	1	18,046		Understory woody plants >0.5 m tall; red maple portion of mixed conifer-hardwood swamp	Paratley and Fahey (1986)	NY
	2	2,630	1,960-3,300	DBH 2.5-10 cm	DeGraaf and Rudis (1990)	NH
		710	490-930	DBH <2.5 cm and height >1.5 m	DeGraaf and Rudis (1990)	NH
		16,000		Height ≤1.5 m	DeGraaf and Rudis (1990)	NH
	1	878		DBH 2.5-7.6 cm	Taylor (1984)	NJ
	5	2,986	470-5,510	BD ≥2.5 cm	Ehrenfeld and Gulick (1981)	NJ[f]
	2	245		BD >2.0 cm; floodplain sites	Ehrenfeld (1986)	NJ[f]
	4	2,457		BD >2.0 cm; dry hardwood swamps	Ehrenfeld (1986)	NJ[f]
	4	4,470		BD >2.0 cm; wet hardwood swamps	Ehrenfeld (1986)	NJ[f]
Basal area (m^2/ha)	6	6.69	3.10-11.58	BD >2.5 cm and DBH <10 cm	Lowry (1984)	RI
		8.19	4.22-13.08	BD <2.5 cm	Lowry (1984)	RI
Herbs						
Cover (%)	6	29	2-70	Nonwoody vascular plants and woody vines	Lowry (1984)	RI
	12	22	0-57	Nonwoody vascular plants only	Merrow (1990)	RI
	3	19	17-22	Nonwoody vascular plants and trailing plants	Braiewa (1983)	RI
	9[c]	43	12-88		Miller and Getz (1977a)	CT

[a] Average of stand means, except where $n = 1$.
[b] Range of stand means.
[c] Number of transects sampled in red maple swamps; number of different stands not stated.
[d] Basal diameter.
[e] Diameter at breast height (1.4 m).
[f] Study conducted outside the glaciated Northeast.

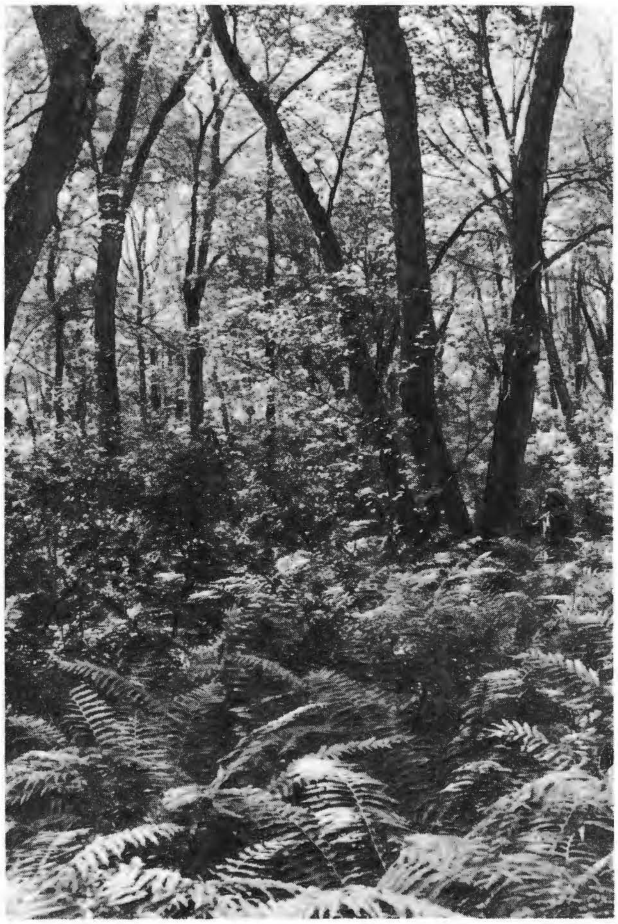

Fig. 3.9. Red maple swamp with an herb layer dominated by cinnamon fern (*Osmunda cinnamomea*). This is the most common species of fern in northeastern swamps.

(Table 3.3). At any single site, however, a few species usually predominate. In the tree layer, the average number of species recorded per swamp (sources in Appendix A) is about four (range 1–9). In southeastern New England swamps, red maple alone may compose as much as 90% of the relative density and relative basal area (Lowry 1984). In other parts of the Northeast, other tree species frequently are better represented.

The shrub stratum in most red maple swamps consists of a small number of common species whose relative importance may vary widely from site to site (Little 1951; Ehrenfeld and Gulick 1981; Braiewa 1983; Lowry 1984). The number of species per site reported in the literature ranges from 1 to 15 (sources in Appendix A). Up to 28 species of shrubs and vines have been found in individual red maple swamps fed by calcareous seepage (The Nature Conservancy, Boston, Mass., unpublished data).

As few as one to three species commonly make up the majority of the shrub stems in an individual swamp. In Rhode Island, for example, the relative density of sweet pepperbush averaged 53% (range 3–91%) at nine sites studied by Braiewa (1983) and Lowry (1984). This species dominates the shrub layer in many New Jersey red maple swamps as well (Ehrenfeld and Gulick 1981; Ehrenfeld 1986). Common winterberry (*Ilex verticillata*) composed nearly 50% of the shrub stems sampled in two red maple swamps in central New York (Reed 1968). At other sites, species such as highbush blueberry,

Table 3.3. *Flora of red maple swamps in the glaciated Northeast. Zone locations are shown in Fig. 3.10. Species listed in the zone columns were reported from acidic swamps or swamps of unknown base status; plants listed in the calcareous column (C) were reported from swamps fed by calcareous seepage. Sources for this list are cited in Appendix A. Data for Zone V are too few to be listed.*

Species[a]	Zone I	Zone II	Zone III	Zone IV	C[b]
Trees					
Abies balsamea (balsam fir)	X	X	X	X	
Acer negundo (boxelder)	X		X		
Acer rubrum (red maple)	X	X	X	X	X
Acer saccharinum (silver maple)	X	X	X		
Acer saccharum (sugar maple)	X	X	X	X	
Amelanchier arborea (downy serviceberry)	X		X		
Amelanchier canadensis (oblong-leaf serviceberry)	X				X
Amelanchier X *intermedia* (swamp shadbush)		X			
Betula alleghaniensis (yellow birch)	X	X	X	X	X
Betula lenta (black birch)	X	X	X		
Betula papyrifera (paper birch)	X	X	X	X	
Betula populifolia (gray birch)	X	X	X	X	X
Carpinus caroliniana (blue beech)	X	X			X
Carya cordiformis (bitternut hickory)	X	X			
Carya laciniosa (big shellbark hickory)		X			
Carya ovata (shagbark hickory)		X			
Carya tomentosa (mockernut hickory)	X				
Chamaecyparis thyoides (Atlantic white cedar)	X				

Table 3.3. *Continued.*

Species[a]	Zone I	Zone II	Zone III	Zone IV	C[b]
Fagus grandifolia (American beech)	X	X	X		
Fraxinus americana (white ash)	X	X	X	X	X
Fraxinus nigra (black ash)	X	X	X		X
Fraxinus pennsylvanica (green ash)	X	X	X	X	
Hamamelis virginiana (American witch-hazel)	X				
Juglans cinerea (butternut)		X			
Juglans nigra (black walnut)		X			
Juniperus virginiana (eastern red cedar)			X		X
Larix laricina (tamarack)	X	X	X	X	X
Liquidambar styraciflua (sweet gum)	X				
Liriodendron tulipifera (yellow-poplar)	X				
Magnolia virginiana (sweetbay)	X				
Nyssa sylvatica (black gum)	X	X	X		
Picea glauca (white spruce)	X				
Picea mariana (black spruce)	X	X	X	X	
Picea rubens (red spruce)	X	X	X	X	
Pinus rigida (pitch pine)	X				
Pinus strobus (white pine)	X	X	X	X	X
Platanus occidentalis (American sycamore)	X	X			
Populus deltoides (eastern cottonwood)		X	X	X	
Populus grandidentata (big-tooth aspen)	X				
Populus tremuloides (quaking aspen)	X	X	X	X	X
Prunus serotina (black cherry)	X	X	X	X	
Quercus alba (white oak)	X	X	X		
Quercus bicolor (swamp white oak)	X	X	X	X	
Quercus coccinea (scarlet oak)	X				
Quercus imbricaria (shingle oak)		X			
Quercus macrocarpa (mossy-cup oak)		X			X
Quercus palustris (pin oak)	X	X			
Quercus rubra (northern red oak)	X	X			
Salix amygdaloides (peach-leaf willow)		X			
Salix nigra (black willow)	X	X	X		
Sassafras albidum (sassafras)	X				
Thuja occidentalis (northern white cedar)	X	X	X	X	
Tilia americana (American basswood)	X	X	X		X
Tsuga canadensis (eastern hemlock)	X	X	X	X	
Ulmus americana (American elm)	X	X	X	X	X
Ulmus rubra (slippery elm)	X	X			
Erect shrubs and woody vines					
Acer pensylvanicum (striped maple)	X		X		
Acer spicatum (mountain maple)				X	
Alnus incana (white alder)		X			
Alnus rugosa (speckled alder)	X	X	X	X	X
Alnus serrulata (brookside alder)	X	X			X
Amelanchier spp. (serviceberries)	X			X	X
Aronia arbutifolia (red chokeberry)	X				
Aronia melanocarpa (black chokeberry)	X	X			X
Aronia prunifolia (purple chokeberry)	X				
Aronia spp. (chokeberries)			X		
Berberis thunbergii (Japanese barberry)	X				
Berberis vulgaris (European barberry)	X				X
Betula pumila (bog birch)	X				X
Carpinus caroliniana (blue-beech)	X	X	X	X	X
Celastrus orbiculata (Asiatic bittersweet)	X				
Celastrus scandens (American bittersweet)	X	X			
Celtis occidentalis (American hackberry)		X		X	
Cephalanthus occidentalis (buttonbush)	X	X	X		
Clethra alnifolia (sweet pepperbush)	X				
Cornus alternifolia (alternate-leaf dogwood)		X			
Cornus amomum (silky dogwood)	X	X	X		X
Cornus foemina (stiff dogwood)		X			X
Cornus stolonifera (red-osier dogwood)	X	X	X		X
Cornus spp. (dogwoods)				X	
Corylus cornuta (beaked hazelnut)	X		X		X
Crataegus flabellata (hawthorn)	X				
Crataegus spp. (hawthorns)		X	X		
Diervilla lonicera (northern bush-honeysuckle)	X				
Gaylussacia baccata (black huckleberry)	X				
Gaylussacia frondosa (dangleberry)	X				
Hamamelis virginiana (American witch-hazel)	X	X			X
Ilex glabra (inkberry)	X				
Ilex laevigata (smooth winterberry)	X				
Ilex verticillata (common winterberry)	X	X	X	X	X
Juniperus communis (common juniper)	X				

Table 3.3. *Continued.*

Species[a]	Zone I	Zone II	Zone III	Zone IV	C[b]
Kalmia angustifolia (sheep laurel)	X		X		X
Kalmia latifolia (mountain laurel)	X				
Ledum groenlandicum (Labrador tea)	X				
Leucothoe racemosa (fetterbush)	X				
Lindera benzoin (spicebush)	X	X			X
Lonicera dioica (mountain honeysuckle)					X
Lonicera tatarica (tartarian honeysuckle)			X		
Lyonia ligustrina (maleberry)	X				X
Menispermum canadense (Canada moonseed)		X			
Myrica gale (sweet gale)	X				
Myrica pensylvanica (northern bayberry)	X				
Nemopanthus mucronata (mountain holly)	X		X		
Ostrya virginiana (eastern hop-hornbeam)	X				
Parthenocissus quinquefolia (Virginia creeper)	X	X			X
Physocarpus opulifolius (eastern ninebark)		X			
Potentilla fruticosa (shrubby cinquefoil)					X
Prunus virginiana (chokecherry)	X				
Rhamnus alnifolia (alder-leaf buckthorn)					X
Rhamnus cathartica (common buckthorn)	X				
Rhamnus frangula (European buckthorn)	X				
Rhamnus sp. (buckthorn)			X		
Rhododendron canadense (rhodora)	X				
Rhododendron maximum (great rhododendron)	X	X			
Rhododendron periclymenoides (pink azalea)	X				
Rhododendron viscosum (swamp azalea)	X	X			X
Ribes americanum (wild black currant)		X			X
Ribes hirtellum (smooth gooseberry)					X
Ribes lacustre (bristly black currant)	X				
Ribes triste (swamp red currant)					X
Ribes spp. (currants)		X	X		
Rosa palustris (swamp rose)	X			X	X
Rosa virginiana (Virginia rose)	X				
Rubus allegheniensis (sow-teat blackberry)	X		X		
Rubus idaeus (red raspberry)					X
Salix discolor (pussy willow)		X		X	
Salix sericea (silky willow)		X			
Salix spp. (willows)	X		X		X
Sambucus canadensis (common elderberry)	X	X	X	X	X
Smilax glauca (cat greenbrier)	X				
Smilax hispida (bristly greenbrier)		X			
Smilax rotundifolia (common greenbrier)	X				
Smilax tamnoides (halberd-leaf greenbrier)		X			
Spiraea latifolia (meadowsweet)	X		X	X	X
Spiraea tomentosa (steeplebush)	X		X		
Staphylea trifolia (American bladdernut)	X				
Taxus canadensis (American yew)	X	X	X		
Toxicodendron radicans (poison ivy)	X	X	X		X
Toxicodendron rydbergii (Rydberg's poison ivy)	X				
Toxicodendron vernix (poison sumac)	X	X			X
Vaccinium corymbosum (highbush blueberry)	X	X	X		X
Vaccinium myrtilloides (velvet-leaf blueberry)	X				
Viburnum acerifolium (maple-leaved viburnum)	X		X		
Viburnum cassinoides (witherod)	X	X	X	X	X
Viburnum dentatum (southern arrow-wood)	X	X			
Viburnum lantanoides (hobble-bush)	X				
Viburnum lentago (nannyberry)	X	X	X	X	
Viburnum opulus (guelder-rose)					X
Viburnum recognitum (northern arrow-wood)	X	X	X		X
Viburnum trilobum (highbush cranberry)			X		
Vitis labrusca (fox grape)	X				
Vitis riparia (riverbank grape)	X				
Vitis vulpina (frost grape)		X			
Vitis spp. (grapes)				X	
Zanthoxylum americanum (northern prickly-ash)		X			
Ferns, clubmosses, and horsetails					
Adiantum pedatum (northern maidenhair fern)	X	X			
Athyrium filix-femina (lady fern)	X	X	X		X
Cystopteris fragilis (brittle fern)	X				
Dennstaedtia punctilobula (hay-scented fern)	X				
Dryopteris cristata (crested fern)	X	X	X		X
Dryopteris spinulosa (spinulose woodfern)	X	X	X	X	X
Dryopteris spp. (woodferns)				X	
Equisetum arvense (field horsetail)		X			X
Equisetum fluviatile (water horsetail)	X		X		X

Table 3.3. *Continued.*

Species[a]	Zone I	II	III	IV	C[b]
Equisetum sylvaticum (woodland horsetail)					X
Lycopodium clavatum (running pine)	X	X			
Lycopodium complanatum (trailing clubmoss)	X	X			
Lycopodium lucidulum (shining clubmoss)	X	X			
Lycopodium obscurum (tree clubmoss)	X		X		
Lygodium palmatum (climbing fern)	X				
Matteuccia struthiopteris (ostrich fern)	X	X	X		
Onoclea sensibilis (sensitive fern)	X	X	X	X	X
Osmunda cinnamomea (cinnamon fern)	X	X	X	X	X
Osmunda claytoniana (interrupted fern)	X	X	X		
Osmunda regalis (royal fern)	X	X	X	X	X
Pteridium aquilinum (bracken fern)	X		X		
Thelypteris noveboracensis (New York fern)	X		X		
Thelypteris simulata (Massachusetts fern)	X				
Thelypteris thelypteroides (marsh fern)	X	X	X		X
Woodwardia areolata (netted chain-fern)	X				
Woodwardia virginica (Virginia chain-fern)	X		X		
Graminoids					
Agropyron repens (quackgrass)	X				
Anthoxanthum odoratum (sweet vernal grass)					X
Bromus ciliatus (fringed brome)					X
Brachyelytrum erectum (grass)	X				
Calamagrostis canadensis (blue-joint grass)	X		X		X
Carex blanda (woodland sedge)	X				
Carex bromoides (brome-like sedge)	X				X
Carex brunnescens (brownish sedge)	X				
Carex canescens (hoary sedge)	X				
Carex comosa (bearded sedge)		X			X
Carex crinita (fringed sedge)	X	X	X		
Carex disperma (soft-leaf sedge)	X				X
Carex flava (yellow sedge)					X
Carex gracillima (graceful sedge)	X	X			
Carex grayi (Gray's sedge)		X	X		
Carex howei (Howe's sedge)	X				
Carex hystericina (porcupine sedge)					X
Carex interior (inland sedge)	X	X			X
Carex intumescens (bladder sedge)	X	X	X		
Carex lacustris (lakebank sedge)	X	X			X
Carex laxiculmis (loose-culmed sedge)	X				
Carex laxiflora (loose-flowered sedge)		X			
Carex leptalea (bristly-stalked sedge)	X				X
Carex lonchocarpa (long-seeded sedge)	X		X		
Carex lupulina (hop sedge)		X			
Carex lurida (sallow sedge)	X	X			
Carex pensylvanica (Pennsylvania sedge)	X				
Carex pseudocyperus (cyperus-like sedge)		X			
Carex rostrata (beaked sedge)	X				
Carex scoparia (pointed broom sedge)					X
Carex seorsa (weak stellate sedge)	X				
Carex stipata (crowded sedge)	X	X			X
Carex stricta (tussock sedge)	X	X	X		X
Carex tenuiflora (sparse-flowered sedge)			X		X
Carex tetanica (rigid sedge)					X
Carex tribuloides (blunt broom sedge)		X			
Carex trisperma (three-seeded sedge)	X	X			
Cinna arundinacea (stout wood reedgrass)	X	X			X
Cinna latifolia (slender wood reedgrass)		X			
Cladium mariscoides (twig-rush)	X				
Eleocharis palustris (creeping spikerush)					X
Elymus virginicus (wild rye)		X			
Glyceria canadensis (rattlesnake manna grass)	X				
Glyceria maxima (reed meadowgrass)					X
Glyceria melicaria (melic manna grass)		X			
Glyceria obtusa (Atlantic manna grass)	X				
Glyceria striata (fowl manna grass)	X	X			X
Glyceria spp. (manna grasses)			X		
Juncus effusus (soft rush)	X		X	X	X
Leersia oryzoides (rice cutgrass)	X		X		X
Muhlenbergia glomerata (marsh muhly)					X
Panicum capillare (witchgrass)	X				
Phalaris arundinacea (reed canary grass)	X		X	X	
Phragmites australis (common reed)	X				X
Poa palustris (fowl bluegrass)	X				

Table 3.3. *Continued.*

Species[a]	Zone I	Zone II	Zone III	Zone IV	C[b]
Scirpus cyperinus (woolly bulrush)			X	X	
Scirpus microcarpus (small-fruited bulrush)					X
Forbs and trailing shrubs					
Actaea rubra (red baneberry)			X		
Acorus calamus (sweet flag)			X		
Ageratina altissima (white snakeroot)		X			
Alisma sp. (water plaintain)	X		X		
Alliaria petiolata (garlic mustard)	X				
Amphicarpaea bracteata (hog-peanut)		X			X
Anemone canadensis (Canada anemone)		X			
Anemone quinquefolia (wood anemone)	X				
Angelica atropurpurea (purple-stemmed angelica)					X
Apios americana (groundnut)	X				X
Aralia hispida (bristly sarsaparilla)			X		
Aralia nudicaulis (wild sarsaparilla)	X	X	X	X	X
Arisaema triphyllum (swamp jack-in-the-pulpit)	X	X			X
Asclepias incarnata (swamp milkweed)			X		X
Aster acuminatus (whorled wood aster)	X		X		
Aster divaricatus (white wood aster)	X	X			
Aster lateriflorus (calico aster)	X				
Aster macrophyllus (large-leaved aster)	X				
Aster novae-angliae (New England aster)		X	X		
Aster novi-belgii (New York aster)	X				
Aster prenanthoides (crooked-stemmed aster)		X			
Aster puniceus (swamp aster)		X			X
Aster umbellatus (flat-topped white aster)	X	X			
Aster vimineus (small white aster)			X		
Aster spp. (asters)		X		X	
Baptisia australis (blue false indigo)	X				
Bartonia virginica (yellow screwstem)			X		
Bidens cernua (nodding beggar-ticks)	X				
Bidens frondosa (stick-tight beggar-ticks)					X
Bidens spp. (beggar-ticks)			X	X	
Boehmeria cylindrica (false nettle)	X	X	X		X
Calla palustris (water arum)			X		
Caltha palustris (marsh marigold)	X	X	X		X
Campanula aparinoides (marsh bellflower)	X				X
Cardamine bulbosa (bulbous bittercress)		X			X
Cardamine pensylvanica (Pennsylvania bittercress)	X	X			X
Cardamine pratensis (meadow bittercress)					X
Chelone glabra (turtlehead)	X	X			X
Chimaphila maculata (spotted wintergreen)	X				
Chrysosplenium americanum (golden saxifrage)	X				X
Cicuta bulbifera (bulb-bearing water hemlock)	X				X
Cicuta maculata (spotted water hemlock)		X			X
Circaea alpina (small enchanter's nightshade)	X	X			
Circaea lutetiana (enchanter's nightshade)	X	X			
Cirsium muticum (swamp thistle)	X				X
Claytonia virginica (spring beauty)	X				
Clematis virginiana (virgin's-bower)	X				X
Clematis sp. (clematis)			X		
Clintonia borealis (blue bead-lily)	X	X	X		
Clintonia umbellulata (white clintonia)		X			
Conioselinum chinense (hemlock parsley)					X
Convolvulus spp. (bindweeds)	X				
Coptis trifolia (goldthread)	X	X	X	X	
Corallorhiza trifida (northern coralroot)			X		
Cornus canadensis (bunchberry)	X		X		
Cuscuta compacta (compact dodder)	X				
Cypripedium acaule (pink lady's slipper)	X	X			
Cypripedium calceolus (yellow lady's slipper)			X		X
Cypripedium reginae (showy lady's slipper)			X		
Decodon verticillatus (swamp loosestrife)	X	X			
Dioscorea villosa (wild yam)	X				
Drosera intermedia (spoon-leaf sundew)					X
Epigaea repens (trailing arbutus)	X				
Epilobium hirsutum (great hairy willow-herb)		X			
Epilobium leptophyllum (linear-leaf willow-herb)					X
Epilobium palustre (marsh willow-herb)	X				
Epilobium sp. (willow-herb)			X		
Erythronium umbilicatum (trout lily)			X	X	

Table 3.3. *Continued.*

Species[a]	Zone I	II	III	IV	C[b]
Eupatoriadelphus dubius (joe-pye weed)	X	X			
Eupatoriadelphus maculatus (spotted joe-pye weed)	X		X		X
Eupatoriadelphus sp. (joe-pye weed)		X			
Eupatorium perfoliatum (common boneset)	X	X	X		X
Fragaria vesca (woodland strawberry)	X				
Fragaria virginiana (common strawberry)	X	X			X
Galium aparine (cleavers)	X				
Galium asprellum (rough bedstraw)	X				
Galium triflorum (fragrant bedstraw)	X	X			
Galium spp. (bedstraws)			X		X
Gaultheria procumbens (teaberry)	X	X			
Gentiana sp. (gentian)					X
Geranium maculatum (wild geranium)	X				X
Geum canadense (white avens)	X	X			X
Geum rivale (water avens)	X	X			X
Geum sp. (avens)			X		
Hydrocotyle americana (water pennywort)	X				X
Hydrophyllum canadense (broad-leaved waterleaf)		X			
Hydrophyllum virginianum (Virginia waterleaf)		X			
Hypericum denticulatum (coppery St. John's-wort)		X			
Impatiens capensis (spotted touch-me-not)	X	X	X	X	X
Impatiens pallida (pale touch-me-not)	X	X			
Iris versicolor (blue flag)	X	X			X
Lactuca canadensis (tall wild lettuce)		X			
Laportea canadensis (wood nettle)	X	X			
Lathyrus palustris (vetchling)		X			
Lilium canadense (Canada lily)					X
Lilium philadelphicum (wood lily)	X				
Lilium superbum (Turk's-cap Lily)	X				
Liparis loeselii (fen orchid)					X
Lobelia cardinalis (cardinal flower)	X	X			
Lobelia siphilitica (great blue lobelia)		X			
Ludwigia palustris (water purslane)	X				
Lycopus americanus (American bugleweed)		X			
Lycopus rubellus (gypsywort)	X				
Lycopus uniflorus (northern bugleweed)	X	X			X
Lycopus virginicus (Virginia bugleweed)	X				X
Lycopus sp. (bugleweed)			X		
Lysimachia ciliata (fringed loosestrife)	X	X			X
Lysimachia nummularia (moneywort)		X			
Lysimachia quadrifolia (whorled loosestrife)	X				
Lysimachia terrestris (swamp candles)	X	X	X		
Lysimachia thyrsiflora (tufted loosestrife)	X	X			X
Lythrum salicaria (purple loosestrife)			X		X
Maianthemum canadense (wild lily-of-the-valley)	X	X	X	X	X
Malaxis monophyllus (white adder's-mouth)					X
Medeola virginiana (Indian cucumber root)	X		X	X	
Mentha arvensis (field mint)	X				
Mentha spicata (spearmint)					X
Mikania scandens (climbing hempweed)	X	X	X		
Mitchella repens (partridgeberry)	X	X	X		
Mitella diphylla (two-leaved miterwort)	X				X
Mitella nuda (naked miterwort)			X		X
Moehringia lateriflora (grove sandwort)	X	X			X
Monarda didyma (bee-balm)		X			
Monotropa uniflora (Indian pipe)	X				
Myosotis scorpioides (true forget-me-not)	X				
Oxalis sp. (wood sorrel)				X	
Panax trifolius (dwarf ginseng)					X
Pedicularis canadensis (early wood lousewort)					X
Pedicularis lanceolata (swamp lousewort)	X				X
Peltandra virginica (arrow arum)		X			X
Penthorum sedoides (ditch stonecrop)					X
Petasites palmatus (sweet coltsfoot)					X
Pilea pumila (clearweed)	X	X			
Platanthera clavellata (small woodland orchid)	X				
Platanthera grandiflora (large purple-fringed orchid)	X				
Platanthera psycodes (small purple-fringed orchid)		X			X
Podophyllum peltatum (May-apple)		X			
Polygonatum biflorum (Solomon's seal)	X				
Polygonatum pubescens (hairy Solomon's seal)	X				

Table 3.3. *Continued.*

Species[a]	Zone I	II	III	IV	C[b]
Polygonum arifolium (halberd-leaved tearthumb)	X				X
Polygonum punctatum (dotted smartweed)	X	X			
Polygonum sagittatum (arrow-leaved tearthumb)	X		X		X
Polygonum virginianum (Virginia knot-weed)		X			
Potentilla canadensis (dwarf cinquefoil)	X				
Potentilla simplex (common cinquefoil)	X				
Prenanthes trifoliata (gall-of-the-earth)	X				
Prenanthes sp. (rattlesnake root)			X		X
Prunella vulgaris (heal-all)					X
Pyrola asarifolia (pink winter-green)					X
Ranunculus abortivus (kidney-leaf buttercup)	X				
Ranunculus acris (common buttercup)		X			
Ranunculus recurvatus (hooked buttercup)	X				
Ranunculus septentrionalis (swamp buttercup)	X		X		X
Rubus flagellaris (prickly dewberry)	X				
Rubus hispidus (bristly dewberry)	X	X	X		X
Rubus pubescens (dwarf blackberry)	X	X			X
Rudbeckia laciniata (green-headed coneflower)		X			
Rumex verticillatus (swamp dock)			X		
Sanguinaria canadensis (bloodroot)			X		
Sarracenia purpurea (northern pitcher plant)					X
Saururus cernuus (lizard's tail)		X			
Saxifraga pensylvanica (swamp saxifrage)	X	X			X
Scutellaria galericulata (hooded skullcap)		X			X
Scutellaria lateriflora (mad-dog skullcap)	X	X			X
Scutellaria sp. (skullcap)			X		
Senecio aureus (golden ragwort)	X	X			X
Sisyrinchium sp. (blue-eyed grass)		X			
Sium suave (water parsnip)		X			
Smilacina racemosa (false Solomon's seal)	X	X	X		X
Smilacina stellata (starry false Solomon's seal)			X		
Smilax herbacea (carrion-flower)	X	X			
Solanum dulcamara (bittersweet nightshade)	X	X	X		X
Solidago altissima (tall goldenrod)		X			
Solidago canadensis (Canada goldenrod)		X			
Solidago gigantea (giant goldenrod)		X			
Solidago patula (rough-leaved goldenrod)		X			X
Solidago rugosa (wrinkled goldenrod)	X	X			
Solidago uliginosa (bog goldenrod)	X				X
Solidago spp. (goldenrods)			X	X	
Sparganium spp. (bur-reeds)	X	X	X		
Sphenopholis pensylvanica (swamp oats)	X				
Streptopus amplexifolius (twisted-stalk)	X				
Streptopus roseus (rosy twisted-stalk)	X				
Symplocarpus foetidus (skunk cabbage)	X	X			X
Thalictrum dioicum (early meadow-rue)		X			X
Thalictrum pubescens (tall meadow-rue)	X	X	X		X
Thalictrum sp. (meadow-rue)				X	
Tiarella cordifolia (foamflower)		X			
Triadenum virginicum (marsh St. John's-wort)	X		X		
Trientalis borealis (starflower)	X	X		X	X
Trillium cernuum (nodding trillium)		X			X
Trillium erectum (purple trillium)	X				
Trillium grandiflorum (large-flowered trillium)			X		
Trillium undulatum (painted trillium)	X				
Trillium spp. (trilliums)				X	
Trollius laxus (globeflower)					X
Typha latifolia (broad-leaved cattail)	X	X	X	X	X
Urtica dioica (stinging nettle)		X	X		
Uvularia sessilifolia (sessile-leaved bellwort)	X				
Vaccinium macrocarpon (large cranberry)	X				
Veratrum viride (false hellebore)	X	X	X		X
Vernonia sp. (ironweed)			X		
Viola blanda (sweet white violet)		X			
Viola brittoniana (Britton's violet)	X				
Viola conspersa (dog violet)	X				
Viola cucullata (marsh blue violet)	X	X			
Viola incognita (large-leaved violet)			X		
Viola pallens (northern white violet)	X	X			
Viola papilionacea (common blue violet)		X			X
Zizia aurea (golden alexanders)	X				X

Table 3.3. *Continued.*

Species[a]	Zone I	II	III	IV	C[b]
Bryophytes and lichens[c]					
Mosses					
Atrichum undulatum					
Aulacomnium palustre					
Bryum pseudotriquetrum					
Calliergon cordifolium					
Calliergon stramineum					
Climacium americanum					
Climacium dendroides					
Dicranum flagellare					
Dicranum fuscescens					
Dicranum scoparium					
Drepanocladus sp.					
Hypnum spp.					
Leucobryum glaucum					
Mnium affine					
Mnium cinclidioides					
Mnium hornum					
Mnium punctatum					
Philonotis fontana					
Pleurozium schreberi					
Polystichum acrostichoides					
Polytrichum sp.					
Sphagnum cuspidatum					
Sphagnum fimbriatum					
Sphagnum fuscum					
Sphagnum inundatum					
Sphagnum palustre					
Sphagnum teres					
Tetraphis pellucida					
Thuidium delicatulum					
Liverworts					
Anthoceros laevis					
Bazzania trilobata					
Cephalozia connivens					
Conocephalum conicum					
Moerckia hibernica					
Pellia epiphylla					
Lichens					
Cladina spp.					

[a] Taxonomy of vascular plants according to the *National List of Scientific Plant Names* (U.S. Soil Conservation Service 1982); taxonomy of mosses according to Crum and Anderson (1981); common names are predominantly from Reed (1988), Petrides (1972), and Little (1979).

[b] Data are primarily from five calcareous red maple swamps: one each in Strafford County, N.H., Berkshire County, Mass., and Litchfield County, Conn., and two in Columbia County, N.Y.

[c] Most bryophytes and lichens were reported from zone I swamps; information from other zones is scarce.

spicebush, or northern arrow-wood (*Viburnum recognitum*) may be the clear dominants.

The variety of habitats provided by pronounced microrelief is one reason for the relatively high herb species richness found in forested wetlands (Huenneke 1982; Paratley and Fahey 1986). The number of species of herbs reported per site may exceed 50 in calcareous red maple swamps but is generally less than 20 at noncalcareous sites (sources in Appendix A).

Floristic Composition

Although a relatively small number of species dominate the flora in red maple swamps of the glaciated Northeast, significant variations in overall community composition are evident, both among different parts of the region and among swamps in the same general locale. Regional variation is best explained by differences in physiography and climate. Just as major forest regions follow general physiographic patterns, so does the variation in red maple swamp communities. Floristic differences among swamps within the same physiographic region are largely due to differences in hydrogeologic setting and, to a lesser extent, land-use history. Even subtle changes in water regime and water chemistry, often strongly influenced by surficial and bedrock geology, may have a major effect on species composition locally.

The glaciated Northeast can be divided into five broad zones that differ in both the relative abundance and floristic composition of red maple swamps (Fig. 3.10). These zones were delineated strictly for the purposes of this profile; they are based on data derived from more than 60 sources (Appendix A). In most cases, the boundaries of these floristic zones correspond closely to the boundaries of either the physiographic regions or the major forest regions described in the introduction. Scale limitations and a scarcity of information on red maple swamps in many areas of the Northeast make it impossible to precisely delineate the boundaries between zones; boundaries shown in Fig. 3.10 should be regarded as highly generalized.

Plant species lists for red maple swamps in the various zones appear in Table 3.3. These lists are not comprehensive; they simply include those species that have been (1) cited in either published or unpublished papers and reports, (2) recorded on National Wetlands Inventory field data sheets (U.S. Fish and Wildlife Service, Newton Corner, Mass.), (3) mentioned to the authors of this report via personal communications, or (4) observed directly by the authors. Species listed in any zone most likely occur in red maple swamps in other zones as well, as long as those zones also lie within

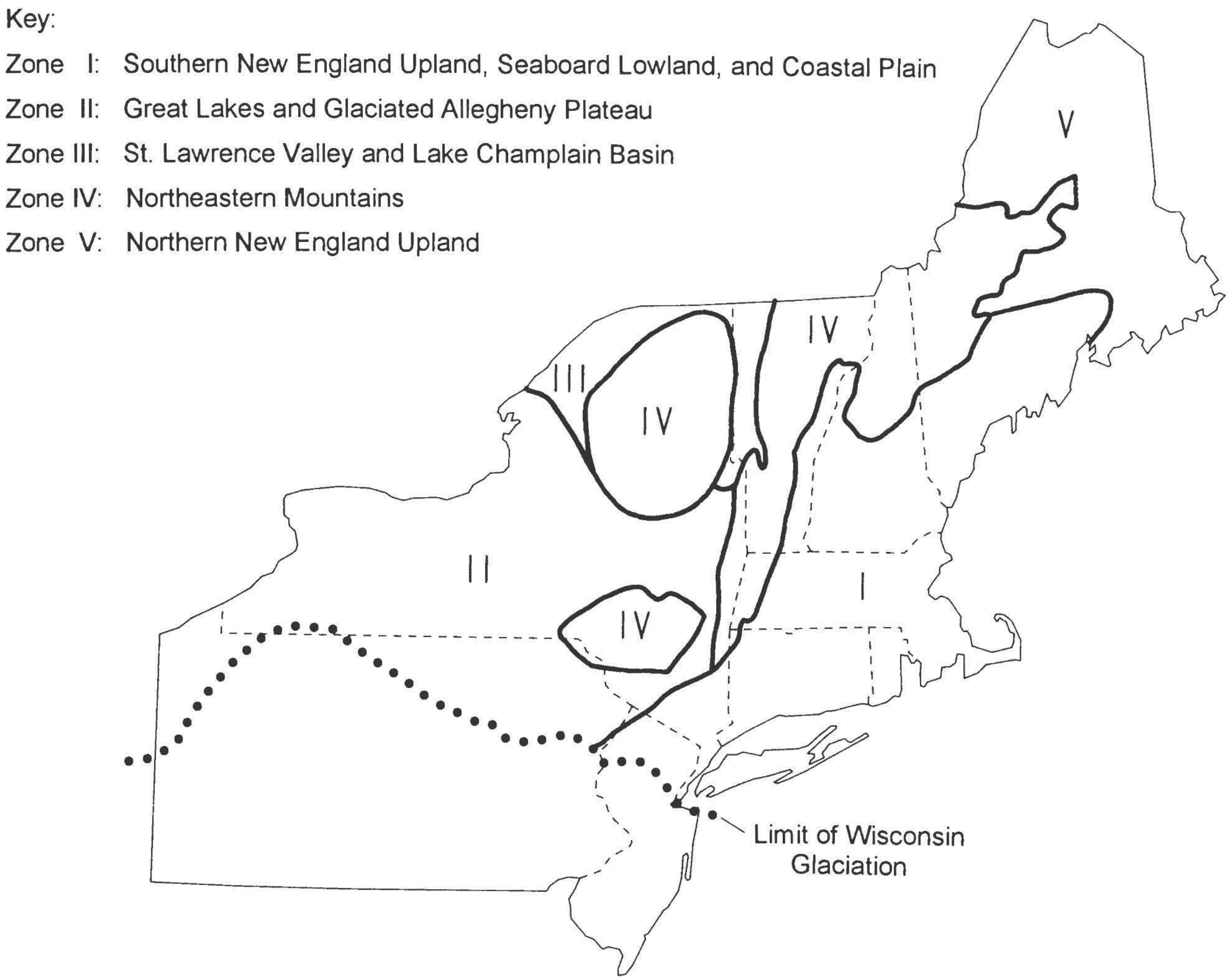

Fig. 3.10. Zones depicting variation in floristic composition and relative abundance of red maple swamps in the glaciated Northeast.

the species' geographic range. Characteristic species for each zone are described below.

Two special types of swamps that may be found in more than one floristic zone are calcareous swamps and transitional swamps. These are briefly described following the descriptions of zones.

Zone I. Southern New England Upland, Seaboard Lowland, and Coastal Plain

Red maple swamps are most abundant in zone I, which includes Rhode Island, Connecticut, all of Massachusetts except for the Berkshire Hills, southern New Hampshire, southeastern Vermont, southern Maine, Long Island and a small part of the southeastern section of New York State, and northern New Jersey (Fig. 3.10). The abundance of these wetlands peaks in southern New England east of the Connecticut River valley and in New Jersey; they are somewhat less abundant to the north and west. Glaciofluvial and glaciolacustrine deposits underlie the most extensive red maple swamps in this zone. Hillside seeps and swamps in isolated kettles and along drainageways in till landscapes are usually smaller than swamps in stratified drift, but they are far more numerous. The white pine–hemlock–hardwood forest predominates in upland habitats throughout zone I, except for southern areas (Fig. 1.3).

Red maple often occurs in nearly pure stands in zone I. Common associates throughout this zone include yellow birch (*Betula alleghaniensis*), black gum, white ash, eastern white pine, American elm, and eastern hemlock (Table 3.3). In southern New England, northern New Jersey, and on Long Island, pin oak, swamp white oak, white oak (*Quercus alba*), and northern red oak (*Q. rubra*) occur locally in red maple swamps. Less common hardwood associates in the southern section of zone I include serviceberry (*Amelanchier* spp.), black cherry (*Prunus serotina*), blue-beech (*Carpinus caroliniana*), yellow-poplar (*Liriodendron tulipifera*), and basswood (*Tilia americana*).

Atlantic white cedar is a common associate of red maple in coastal areas from New Jersey to southern Maine (Laderman 1989). This species typically occurs in pure stands on sites that are slightly wetter than most of those supporting red maple (Reynolds et al. 1982; Lowry 1984). However, cedar logging and water level changes have made mixed stands of red maple and Atlantic white cedar common in zone I. White pine is a common associate of red maple in many zone I swamps; in parts of southeastern New England these species may be codominant (Tiner 1989b). Black spruce is common in the northern portion of zone I, but also associates with red maple in southern areas, typically along the margins of bogs (Damman and French 1987).

Gray birch (*Betula populifolia*), black ash, balsam fir, and northern white cedar commonly occur in red maple swamps in the southern parts of New Hampshire, Vermont, and Maine. The Vermont Natural Heritage Program (Thompson 1988) has described the black gum swamp, composed of black gum, hemlock, and red maple, as a rare association restricted to the southeastern part of that state. This association has also been described in Vermont by Fosberg and Blunt (1970), and in New Hampshire by Baldwin (1961). Oaks are less common in red maple swamps from the northern section of zone I; northern red oak is the most common species in that area.

Fewer than a dozen species dominate the shrub layer of red maple swamps in zone I. Highbush blueberry, common winterberry, sweet pepperbush, spicebush, swamp azalea (*Rhododendron viscosum*), northern arrow-wood, southern arrowwood (*Viburnum dentatum*), speckled alder, nannyberry (*V. lentago*), and poison sumac (*Toxicodendron vernix*) are the most common shrubs; greenbriers also are common, especially in southern New England (Table 3.3). Other common species include fetterbush (*Leucothoe racemosa*), maleberry (*Lyonia ligustrina*), chokeberries (*Aronia* spp.), swamp rose (*Rosa palustris*), mountain holly (*Nemopanthus mucronata*), witherod (*Viburnum cassinoides*), poison ivy, European buckthorn (*Rhamnus frangula*), mountain laurel, sheep laurel, and American witch-hazel (*Hamamelis virginiana*). Sweet pepperbush and swamp azalea are most common east of the Connecticut River, in the southern section of zone I. Great rhododendron occurs locally from southern New England southward. Mountain holly, speckled alder, hobblebush (*Viburnum lantanoides*), American yew, and striped maple (*Acer pensylvanicum*) are more important in red maple swamps in the northern section of zone I.

Species composition in the herb layer is more variable than in the tree or shrub layers of red maple swamps. Some common constituents are listed below, but these species do not necessarily associate with each other, nor do they all occur throughout zone I.

Cinnamon fern is the most common fern in zone I red maple swamps (see Fig. 3.9). Sensitive fern (*Onoclea sensibilis*), royal fern (*Osmunda regalis*), marsh fern (*Thelypteris thelypteroides*), and spinulose woodfern (*Dryopteris spinulosa*) are other species that are commonly found throughout this zone (Table 3.3). Locally common species include Virginia chain-fern (*Woodwardia virginica*), netted chain-fern (*W. areolata*), interrupted fern (*Osmunda claytoniana*), Massachusetts fern (*Thelypteris simulata*), New York fern (*T. noveboracensis*), and ostrich fern (*Matteuccia struthiopteris*).

Graminoid plants from zone I red maple swamps commonly include sedges (e.g., *Carex stricta, C. lacustris, C. lonchocarpa, C. crinita*) and grasses such as bluejoint grass (*Calamagrostis canadensis*) and manna grass (*Glyceria* spp.). Skunk cabbage (*Symplocarpus foetidus*), false hellebore (*Veratrum viride*), marsh marigold (*Caltha palustris*), spotted touch-me-not (*Impatiens capensis*), wild lily-of-the-valley (*Maianthemum canadense*), violets (*Viola* spp.), wild sarsaparilla (*Aralia nudicaulis*), blue flag (*Iris versicolor*), bugleweeds (*Lycopus* spp.), starflower (*Trientalis borealis*), and goldthread (*Coptis trifolia*) are common forbs. Because of their low stature, trailing shrubs are listed with the forbs in Table 3.3; swamp dewberry (*Rubus hispidus*), teaberry (*Gaultheria procumbens*), and partridgeberry (*Mitchella repens*) are three of the most common species in zone I red maple swamps.

Mosses represent an important component of the flora in many red maple swamps. Since few studies describe any but the most common genera and species, however, a comprehensive listing of this taxonomic group by zone is not possible. Table 3.3 lists mosses, as well as liverworts and lichens, that are known to occur in northeastern red maple swamps.

The floristic composition of the great majority of red maple swamps in zone I can be broadly described through various combinations of the plant species listed above. As already indicated, the community composition of a particular swamp is often strongly related to its hydrogeologic setting. Three basic types of red maple swamps, differentiated by landscape position and flora, are outlined below. These types were first recognized in Connecticut by Metzler and Tiner (1992), but they are clearly applicable throughout southern New England and much of the remainder of zone I. Floristic descriptions are based heavily on Metzler and Tiner.

Hillside Seeps and Upland Drainageways

These swamps occur most commonly on slopes or in shallow depressions along intermittent or upper perennial streams where till predominates (see Figs. 2.4 and 2.9). They are fed primarily by groundwater seepage and overland flow. Shallow flooding may occur along watercourses during the early spring and after heavy rains, but surface water seldom persists. Most of these sites have a seasonally saturated water regime (Table 2.3). Mineral soils predominate, and surface microrelief is limited except where the ground is strewn with glacial erratics. Dominant trees include red maple, yellow birch, American elm, swamp white oak, and pin oak; black gum and white ash (*Fraxinus americana*) also are common. A moderately dense understory dominated by spicebush, but with few other important species, is a characteristic feature of this type of swamp (Fig. 3.11). Skunk cabbage, false hellebore, and marsh marigold are dominant herbs. Other common species include cinnamon fern, sensitive fern, spinulose woodfern, swamp jack-in-the-pulpit (*Arisaema triphyllum*), shining clubmoss (*Lycopodium lucidulum*), marsh blue violet (*Viola cucullata*), and northern white violet (*V. pallens*).

Seasonally Flooded Basin Swamps

This type of swamp occurs primarily in undrained basins in either till or stratified drift. Typically, surface water is present throughout the dormant season and for the early part of the growing season in most years. Because of the extended period of soil saturation, organic soils are common and microrelief is pronounced. Trees and shrubs are rooted primarily in mounds, which are elevated slightly above the seasonal high-water level (Fig. 2.6). Red maple, yellow birch, hemlock, black gum, and white pine are the principal tree species in these swamps. The shrub layer, which is often exceedingly dense, is dominated by species such as highbush blueberry, swamp azalea, common winterberry, sweet pepperbush, northern arrowwood, and witherod. Cinnamon fern, sensitive fern, marsh fern, skunk cabbage, manna grass, and sedges (*Carex* spp.) are among the most common herbs. Mosses, including peat moss (*Sphagnum* spp.), broom mosses (*Dicranum* spp.), delicate-

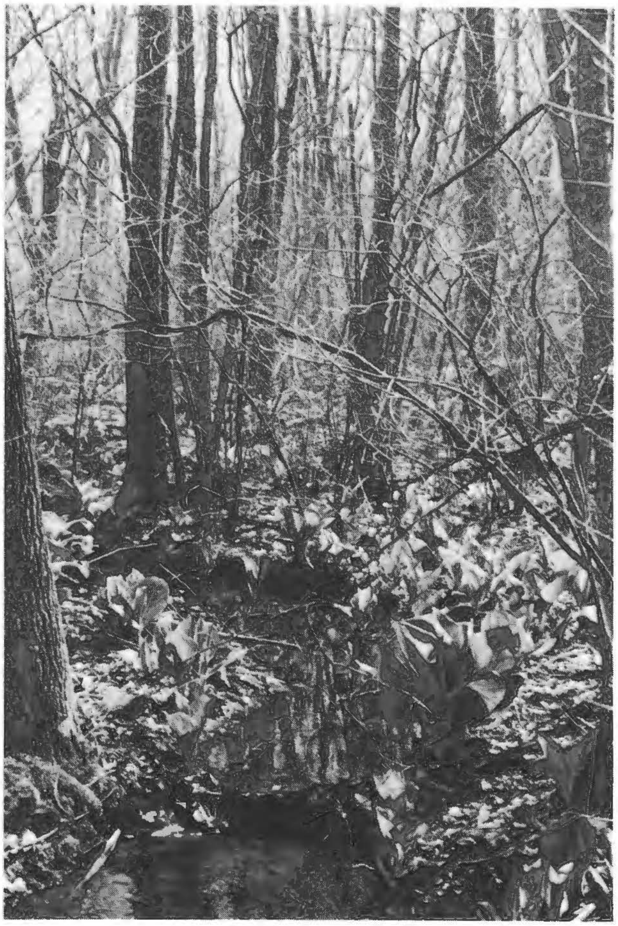

Fig. 3.11. Red maple swamp along an upland drainageway in southern New England. Spicebush (*Lindera benzoin*) and skunk cabbage (*Symplocarpus foetidus*) are the dominant shrub and herb, respectively. Other common species at this site include American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), false hellebore (*Veratrum viride*), marsh marigold (*Caltha palustris*), and northern white violet (*Viola pallens*).

fern moss (*Thuidium delicatulum*), and *Mnium* spp., are abundant in depressions and at the bases of mounds.

Alluvial Swamps

Red maple swamps also occur on river terraces and in oxbows (Nichols 1915; Holland and Burk 1984) or behind natural levees, on the low-lying, inner floodplain of rivers (Buell and Wistendahl 1955; Tiner 1985; Metzler and Tiner 1992). These swamps may be temporarily flooded or seasonally flooded, but most remain wet through the growing season because they receive groundwater inflow and surface runoff as well as overbank flooding (Fig. 3.12). Alluvial swamps are commonly more nutrient-rich than nonfloodplain swamps, and they often support a more diverse plant community. The variety of microhabitats provided by undrained sloughs and ridges, and the proximity to more typical floodplain communities (e.g., silver maple–cottonwood–ash–black willow), also help to explain the greater species richness in these swamps.

While red maple dominates many alluvial swamps, the tree layer is usually more mixed than in the other swamp types. Common associates of red maple in zone I alluvial swamps include white ash, pin oak, swamp white oak, American elm, black willow, sycamore, basswood, and blue-beech. Scarce or absent are most of the coniferous species commonly found in nonfloodplain swamps. Bitternut hickory (*Carya cordiformis*), boxelder (*Acer negundo*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and red oak may be found on temporarily flooded sites. Spicebush, silky dogwood (*Cornus amomum*), speckled alder, common elderberry (*Sambucus canadensis*), nannyberry, Japanese barberry (*Berberis thunbergii*), northern arrow-wood, bladdernut (*Staphylea trifolia*), and hawthorn (*Crataegus* sp.) have been reported in the shrub layer. Vines that are particularly common in alluvial swamps include grapes (*Vitis* sp.), Virginia creeper, bittersweet (*Celastrus* sp.), and poison ivy. Common herbs include sensitive fern, cinnamon fern, royal fern, skunk cabbage, false hellebore, false nettle (*Boehmeria cylin-*

Fig. 3.12. Southern New England alluvial swamp in mid-April. This site, which is dominated by red maple, tussock sedge, and royal fern (*Osmunda regalis*), has a seasonally flooded water regime. The sparse shrub layer is common in alluvial swamps.

drica), bugleweeds, violets, and bedstraws (*Galium* spp.).

Zone II. Great Lakes and Glaciated Allegheny Plateau

Zone II includes the greater part of New York State, as well as northeastern and northwestern Pennsylvania (Fig. 3.10). The white pine–hemlock–hardwood forest dominates upland habitats in those sections where red maple swamps are most abundant. The Lake Erie coastline falls within the oak–yellow-poplar forest region, while the beech–birch–maple forest predominates in eastern New York and northern Pennsylvania (Fig. 1.3).

Red maple swamps in zone II commonly occur over extensive glaciolacustrine and glaciofluvial deposits (Van Dersal 1933; Stewart and Merrell 1937; Goodwin 1942; Shanks 1966; Huenneke 1982; Malecki et al. 1983). Bedrock in most of this zone is shale, sandstone, or limestone (Fenneman 1938). Where limestone occurs, calcareous swamps are common. Often, however, the influence of underlying marl layers on soil pH and nutrient status is diminished by overlying organic deposits; hence, the flora of many swamps in limestone areas do not exhibit an enriched status (Huenneke 1982; Malecki et al. 1983). Swamps that developed over alluvial deposits or former bog soils also are common in this region (Bray 1915; Van Dersal 1933; Goodwin 1942).

Early in this century, Bray (1915) identified two major swamp forest associations in New York: mixed conifer–hardwood swamp and hardwood swamp. These two types, which have been recognized in more recent literature as well, are described briefly below.

Mixed Conifer–Hardwood Swamps

These wetlands are distributed primarily from the eastern Ontario Basin to the Adirondacks, along the drainage divides of north–south valleys of the Allegheny Plateau, and from the Syracuse region east through the Mohawk River valley. Red maple swamps described by Huenneke (1982) in the southern Finger Lakes region and by Paratley and Fahey (1986) in the Oneida Lake region are examples of this community. Tree species that are common in the mixed conifer–hardwood swamps of zone II, namely, hemlock, white pine, yellow birch, red maple, and elms, are also found in zone I swamps. However, red maple assumes a less important role in many of the swamps in zone II; frequently it is codominant with evergreen species (Van Dersal 1933). Although such mixed associations occur in zone I, they are not as common as in zone II. Black and green ash frequently occur in swamps near the Great Lakes. Black spruce, balsam fir, and tamarack are found in mixed conifer–hardwood swamps of New York, both at higher elevations and in cool lowlands. In northwestern Pennsylvania, hemlock is the principal conifer in this wetland type (Brooks and Tiner 1989); red spruce (*Picea rubens*), tamarack, black spruce, and white pine all occur in the mixed conifer–hardwood swamps of northeastern Pennsylvania (Brooks et al. 1987).

Hardwood Swamps

These forested wetlands, referred to as red maple–hardwood swamps by the New York Natural Heritage Program (Reschke 1990), are most abundant in the western portion of the Ontario Basin and in the Hudson River valley of New York (Bray 1915), but they occur throughout zone II. Historically, they were dominated by American elm, but with the decline of this species because of Dutch elm disease, the relative importance of other tree species has increased (Huenneke 1982; Malecki et al. 1983). Some of the most common trees besides red maple are green ash, black ash, swamp white oak, basswood, and butternut (*Juglans cinerea*). White pine and hemlock are rare components, while northern white cedar, tamarack, and balsam fir are absent (Stewart and Merrell 1937; Goodwin 1942; Malecki et al. 1983). Pin oak, shingle oak (*Quercus imbricaria*), red oak, bitternut hickory, and shagbark hickory (*Carya ovata*) are common in hardwood swamps in the Ontario Basin west of Rochester, N.Y. (Stewart and Merrell 1937, Goodwin 1942), and at the glacial limit in western Pennsylvania (Phillips 1971).

Brooks and Tiner (1989) recognized two common hardwood swamp associations in northwestern Pennsylvania. The first includes red maple, American elm, green ash, black ash, and swamp white oak, while the second includes red maple, yellow birch, and black cherry. In the Pocono region of northeastern Pennsylvania, red maple and yellow birch are the dominant broad-leaved deciduous wetland trees (Brooks et al. 1987).

The composition of the shrub stratum does not vary greatly among the various swamp associations in zone II. Highbush blueberry, common winterberry, spicebush, viburnums, black chokeberry (*Aronia melanocarpa*), speckled alder, American witch-hazel, and poison sumac are commonly encountered (Table 3.3). The herb layer in zone II red maple swamps may be quite diverse. Common ferns include cinnamon fern, sensitive fern, royal fern, marsh fern, ostrich fern, interrupted fern, crested fern (*Dryopteris cristata*), and spinulose woodfern. Skunk cabbage, marsh marigold, false hellebore, spotted touch-me-not, wild sarsaparilla, swamp jack-in-the-pulpit, lizard's tail (*Saururus cernuus*), smartweeds (*Polygonum* spp.), sedges (e.g., *Carex crinita*, *C. lurida*, and *C. stricta*), goldthread, blue bead-lily (*Clintonia borealis*), and white clintonia (*C. umbellulata*) are common herbs. Species such as water avens (*Geum rivale*), maidenhair fern (*Adiantum pedatum*), and foamflower (*Tiarella cordifolia*) are indicative of moderate- to high-base status.

Zone III. St. Lawrence Valley and Lake Champlain Basin

Zone III, which coincides with the St. Lawrence Valley physiographic region in New York and Vermont (Fig. 3.10), falls almost entirely within the white pine–hemlock–hardwood forest region (Fig. 1.3). Both upland and wetland forests in the eastern portion of this zone are strongly influenced by the moderating effect of Lake Champlain on local climate (Bray 1915). Little published information on red maple swamp communities is available for this area. Floristic data for the New York portion of this zone are derived primarily from Vosburgh (1979) and National Wetlands Inventory (NWI) field notes (U.S. Fish and Wildlife Service, National Wetlands Inventory, Newton Corner, Mass,). Descriptions of Vermont forested wetlands in zone III are derived mainly from Vosburgh (1979), the Vermont Natural Heritage Program (VNHP), NWI field notes, and personal communications.

Along the shores of Lake Champlain, forested wetlands are found on poorly drained deltas and in drowned river valleys. Red maple swamp associations also occur in poorly drained depressions on the inner floodplain of creeks, behind natural levees (H.W. Vogelmann, University of Vermont, Burlington, personal communication). These swamps are commonly underlain by alluvium that overlies glaciolacustrine and glaciofluvial deposits. Outside of the Lake Champlain basin, red maple swamps are found along upland drainageways and in isolated basins in both till and stratified drift. Zone III supports two distinct red maple swamp communities: lake floodplain swamps, which are commonly found on the eastern shore of Lake Champlain (e.g., Missisquoi River delta and Sandbar Swamp), and red maple–black ash swamps.

Lake Floodplain Swamps

Lake floodplain swamps are characterized by a red maple–silver maple–swamp white oak association, which is distinctly different from floodplain forests found along major rivers in Vermont. River floodplain forests are composed largely of silver maple, eastern cottonwood, sycamore, and butternut (Thompson 1988). Silver maple dominates that part of the lake floodplain forest nearest the edge of Lake Champlain, and red maple predominates toward the landward edge. In the middle, both species are present, and dominance alternates locally. A hybrid maple, known as *Acer* X *freemanii*, has been identified in this intermediate zone; it displays characteristics of both red maple and silver maple (W. Countryman, Northfield, Vt., personal communication). The open shrub layer of the lake floodplain swamps frequently includes mountain holly and buttonbush (*Cephalanthus occidentalis*). A fern-dominated herb layer includes such species as sensitive fern, interrupted fern, and cinnamon fern. About 30 species of trees and shrubs have been documented in these swamps (Vogelmann, personal communication).

Red Maple–Black Ash Swamps

This second major red maple swamp association is found in nonfloodplain areas throughout zone III. Bray (1915) described this community, which is designated by the Society of American Foresters as the black ash–elm–red maple forest cover type (SAF type no. 39; Eyre 1980), as a climax wetland forest ranging from the lower Hudson River valley north to the Champlain valley. It predominates from the northern edge of the Adirondack Mountains to the Canadian border as well. Part of the Cornwall Swamp along Otter Creek in Addison County, Vt., has been considered a classic example of this forest cover type (Goodwin and Niering 1975). The decline of American elm prompted the Vermont Natural Heritage Program to classify these forested wetlands as the red maple–black ash natural community (Thompson 1988). Dominated by red maple, black ash, and, to a lesser extent, American elm, these swamps also support white pine, gray birch, paper birch (*Betula papyrifera*), green ash, yellow birch, hemlock, northern white cedar, quaking aspen (*Populus tremuloides*), tamarack, and balsam fir. Swamp white oak and silver maple occur locally in Vermont swamps (Vogelmann, personal communication).

The shrub layer in the red maple–black ash community is typically dense and includes common winterberry, blue-beech, highbush blueberry, speckled alder, beaked hazelnut (*Corylus cornuta*), nannyberry, mountain holly, red-osier dogwood (*Cornus stolonifera*), meadowsweet (*Spiraea latifolia*), and highbush cranberry (*Viburnum trilobum*) (Goodwin and Niering 1975; Vogelmann, personal communication). The herb stratum, which is well developed and generally characterized by herbs more than a meter tall, includes cinnamon fern, ostrich fern, royal fern, sensitive fern, interrupted fern, tall meadow-rue (*Thalictrum pubescens*), wild sarsaparilla, goldenrods (*Solidago* spp.), spotted touch-me-not, manna grass, swamp dock (*Rumex verticillatus*), and sedges (E. Thompson, VNHP, Burlington, personal communication; Vogelmann, personal communication). Sphagnum moss is also common. The red maple–black ash community is far more diverse floristically than the lake floodplain red maple community.

Deciduous trees dominate most of the forested wetlands in zone III, and although evergreen forested wetlands including northern white cedar swamps and spruce–fir–tamarack swamps occur, they are less common here than at higher elevations or farther north. In the Otter Creek valley (southern Champlain River valley) of Vermont, swamps consisting of mixed stands of hardwoods and northern white cedar cover thousands of acres (Thompson, personal communication). The hardwoods, which dominate these swamps, include red maple, black ash, and silver maple.

Zone IV. Northeastern Mountains

Zone IV, which includes the White Mountains, Green Mountains, Taconic Range, Berkshires, Adirondacks, and Catskills, falls largely within the beech–birch–maple and spruce–fir forest regions (Fig. 1.3). Deciduous forested wetlands dominated by red maple are restricted to streamside locations in narrow valleys and to isolated depressions. Floristic data for these swamps are scarce; the zone IV species list in Table 3.3 is based on a single study conducted in the White Mountains of New Hampshire (DeGraaf and Rudis 1990) and National Wetlands Inventory field notes (U.S. Fish and Wildlife Service, Newton Corner, Mass.) gathered at 11 sites in Maine, New Hampshire, and Vermont.

Tree species that commonly associate with red maple in mountain swamps include balsam fir, gray birch, paper birch, yellow birch, American elm, quaking aspen, and ashes. White pine, black cherry, black spruce, red spruce, northern white-cedar, hemlock, larch, and sugar maple also may be present. The shrub layer frequently includes speckled alder, viburnums (e.g., nannyberry, witherod), common winterberry, willows (*Salix* spp.), balsam fir, and meadowsweet. Cinnamon fern and sensitive fern are the most common ferns. Manna grasses, sedges (*Carex* spp.), asters (*Aster* spp.), goldenrods (*Solidago* spp.), meadow-rue (*Thalictrum* sp.), wild lily-of-the-valley, starflower, and wild sarsaparilla are representative herbs.

Zone V. Northern New England Upland

The northern New England upland includes most of northern and eastern Maine, as well as the nonmountainous parts of western Maine, central New Hampshire, and northeastern Vermont that are too small to delineate in Fig. 3.10. This zone supports primarily beech–birch–maple forest and spruce–fir forest in the uplands (Fig. 1.3). Information on red maple swamps in zone V is generally lacking; hence, zone V floristic data have been omitted from Table 3.3. Red maple and other swamp hardwoods are usually subordinate to softwoods such as hemlock, tamarack, northern white cedar, spruces, and balsam fir. Most of the wet basins contain either bogs or conifer swamps (R.B. Davis, University of Maine, Orono, personal communication; H. Nowell, New Hampshire Fish and Game Department, Concord, personal communication). Wet sites with calcareous groundwater inflow commonly support northern white cedar forests, whereas more acidic sites support various combinations of northern white cedar, tamarack, spruces, white pine, red maple, yellow birch, and black ash. Stream bottoms in zone V often contain balsam fir and alder (*Alnus* spp.) with little or no red maple (Nowell, personal communication). Deciduous forested wetlands most often occur in narrow bands along streams, in complexes with shrub swamps, or in small, isolated depressions. The red maple–black ash community is found in northeastern Vermont, but to a lesser extent than in southern and western regions of that state (Thompson 1988).

Calcareous Seepage Swamps

Bedrock and surficial geologic deposits throughout most of the Northeast are low in base content. As a result, most swamps in this region are acidic and nutrient-poor. The majority of swamps described thus far fall in that category. In several areas of the Northeast, calcareous groundwater or surface water derived from limestone, marble, or lime-rich surficial deposits enters wetlands and has a dramatic effect on the composition and richness of the plant community. In northeastern Vermont, northern New Hampshire, and Maine, calcareous swamps are typically dominated by northern white cedar (Thompson, personal communication; Nowell, personal communication; Davis, personal communication), while in southern New England and New York, hemlock or mixed conifer–hardwood forests often predominate (T.J. Rawinski, The Nature Conservancy, Boston, Mass., personal communication). Calcareous swamps dominated by red maple occur primarily in southern New England, southern New Hampshire, the Lake Champlain basin, and central and eastern New York.

The Eastern Regional Office of The Nature Conservancy has compiled detailed floristic data from at least 15 wetlands that it classifies as southern New England calcareous seepage swamps (Rawinski 1984). The species list labelled "calcareous" in Table 3.3 includes all of the species recorded at five of these swamps where red maple was either dominant or codominant. The locations of these red maple swamps range from southeastern New Hampshire through western Massachusetts to northwestern Connecticut and adjacent New York state.

While some calcareous swamps in the glaciated Northeast occur in seasonally flooded basins, the swamps described by The Nature Conservancy typically occur at the headwaters, or along the valley edges, of small streams where soils are saturated by groundwater seepage for most or all of the year, but where surface flooding is infrequent. The New York Natural Heritage Program recognizes a red maple–tamarack peat swamp, which is floristically similar to the southern New England seepage swamps, but which occurs in poorly drained depressions fed by calcareous groundwater and contains organic soil (Reschke 1990). Calcareous seepage swamps tend to support a much greater diversity of plant species than seasonally flooded swamps lacking groundwater inflow (Rawinski, personal communication). Over 150 species were recorded at the five southern New England sites mentioned above, and individual swamps held as many as 90 species in some cases.

Black ash, which is the most nutrient-demanding and least acid-tolerant ash species (Eyre 1980), is a conspicuous overstory associate of red maple in calcareous seepage swamps. American elm, white pine, tamarack, and swamp white oak are also common. Nearly 30 species of shrubs have been recorded at individual sites; some of the most characteristic include red-osier dogwood, alder-leaf buckthorn (*Rhamnus alnifolia*), shrubby cinquefoil (*Potentilla fruticosa*), stiff dogwood (*Cornus foemina*), and meadowsweet. Ericaceous species are notably scarce, except for highbush blueberry (Metzler and Tiner 1992). Speckled alder, silky dogwood, common winterberry, swamp rose, poison sumac, and poison ivy are other common shrubs.

Nutrient-rich conditions of calcareous seepage swamps are most clearly reflected in the herb layer, which may include 60 or more species at a single site. Among the most frequently encountered are lakebank sedge (*Carex lacustris*), tussock sedge (*Carex stricta*), cinnamon fern, royal fern, and tall meadow-rue. Crested fern, marsh fern, bluejoint grass, linear-leaf willow-herb (*Epilobium leptophyllum*), bedstraws, boneset (*Eupatorium perfoliatum*), water pennywort (*Hydrocotyle americana*), swamp buttercup (*Ranunculus septentrionalis*), and skunk cabbage are other common herbs.

Certain herbs of calcareous seepage swamps may not be seen as frequently as those above, but are strong indicators of either groundwater discharge or calcium-rich soils (Rawinski, personal communication). Groundwater indicator plants include bristly-stalked sedge (*Carex leptalea*), marsh marigold, golden saxifrage (*Chrysosplenium americanum*), purple-stemmed angelica (*Angelica atropurpurea*), soft-leaf sedge (*Carex disperma*), water avens, fen orchid (*Liparis loeselii*), swamp saxifrage (*Saxifraga pensylvanica*), small purple-fringed orchid (*Platanthera psycodes*), woodland horsetail (*Equisetum sylvaticum*), and golden ragwort (*Senecio aureus*). Most of these plants are scarce or absent from swamps lacking groundwater discharge. Calcicoles (plants normally growing in calcareous soils) found in these seepage swamps include fringed brome (*Bromus ciliatus*), inland sedge (*Carex interior*), yellow sedge (*Carex flava*), bulbous bittercress (*Cardamine bulbosa*), hemlock parsley (*Conioselinum chinense*), tufted loosestrife (*Lysimachia thyrsiflora*), swamp thistle (*Cirsium muticum*), and globeflower (*Trollius laxus*). Bog birch (*Betula pumila*), shrubby cinquefoil, mossy-cup oak (*Quercus macrocarpa*), and alder-leaf buckthorn are woody plants that also indicate calcium-rich soils in southern New England seepage swamps.

Transitional Swamps

Where the land slopes abruptly at the edge of wetland basins containing open water, marsh, shrub swamp, fen, or bog communities, red maple forests commonly form a narrow transitional belt between these wetland types and the adjacent upland. While such belts are often less than 30 m wide, they are a conspicuous feature of many northeastern wetlands and have been referred to specifically by several authors. The floristic composition of these transitional communities is often somewhat unique in that plants from both the adjacent upland and wetland communities are represented, along with the more typical swamp species.

In association with Atlantic white cedar, northern white cedar, hemlock, or balsam fir, red maple commonly forms a narrow border around northeastern bogs (Nichols 1913; Goodwin 1942; Montgomery and Fairbrothers 1963; Moizuk and Livingston 1966; Osvald 1970; Ellis 1980; Damman and French 1987). In a study of six peat bogs in southern Maine, R.B. Davis (University of Maine, Orono, personal communication) noted the presence of Labrador tea (*Ledum groenlandicum*) and rhodora (*Rhododendron canadense*), typical bog shrubs, in the bordering red maple swamps. Balsam fir, black spruce, velvet-leaf blueberry (*Vaccinium myrtilloides*), black huckleberry (*Gaylussacia baccata*), mountain holly, and speckled alder were also present in the shrub stratum. Black spruce, tamarack, and white pine were associated with red maple in the overstory of those swamps.

A red maple–cinnamon fern association has also been recognized as a transitional community in southern New England (Egler and Niering 1967; Damman and Kershner 1977; Anderson et al. 1980; Messier 1980; Metzler 1982). This community typically occupies a sloping, poorly drained soil zone, often just upslope from a seasonally flooded swamp community. The lack of surface water and the drier soil conditions during the growing season, which characterize this transitional community, make the site suitable for species that are more frequently found outside of wetlands. White oak and American beech, for example, are commonly observed in this community in Rhode Island. (Not all red maple–cinnamon fern communities occur in this situation. Some have very poorly drained soils and are seasonally flooded.)

In summary, the differences in floristic composition among northeastern red maple swamps are best explained by either physiographic location, which takes into account climatic and elevational influences, or hydrogeologic setting, which determines water regime, water chemistry, and microclimate. Floristic differences are further explained by the complex overlap of the geographic ranges of individual species. Land-use history undoubtedly influences swamp floristics as well, but the details of that relationship have not been described.

Plants of Special Concern

None of the plant species in Table 3.3 is listed as endangered or threatened by the Federal Government (J. Dowhan, U.S. Fish and Wildlife Service, Charlestown, R.I., personal communication), and none of those species is restricted to red maple swamps. However, many of the species that have been observed in red maple swamps also appear in the official rare-plant lists published by the various northeastern states. Appendix B identifies those species and gives their status in each state. Overall, nearly 140 (33%) of the species known to occur in red maple swamps are considered rare, threatened, or endangered in one or more states.

Owing to the broad extent and physiographic diversity of the northeast region, some species are common in the red maple swamps of certain states but rare in others. Sweet pepperbush, spicebush, and swamp azalea for example, are endangered in Maine, but they are among the most common wetland shrubs in southern New England. Conversely, northern white cedar is common in northern New England but rare in Connecticut, Massachusetts, and New Jersey. A few plants are listed by five or more northeastern states; these include climbing fern (*Lygodium palmatum*), bog birch, great rhododendron, showy lady's slipper (*Cypripedium reginae*), small yellow lady's slipper (*C. calceolus* var. *parviflorum*), white adder's-mouth (*Malaxis monophyllus* var. *brachypoda*), Britton's violet (*Viola brittoniana*), and gypsywort (*Lycopus rubellus*). Swamp red currant (*Ribes triste*), hemlock parsley, sweet coltsfoot (*Petasites palmatus*), marsh willow-herb (*Epilobium palustre*), cyperus-like sedge (*Carex pseudocyperus*), and globeflower are listed in four states. The occurrence of bulbous bittercress, globeflower, mossy-cup oak, and several other species is largely determined by the distribution of calcareous soil; thus they are rare or absent in many areas of the Northeast.

Appendix B should be regarded simply as a potential list of species of concern. All of the species listed there have been observed in red maple swamps somewhere in the region, but many have not been documented in that habitat in states where they are considered rare or endangered. Some of the species in the list occur most frequently in upland habitats or in wetlands other than red maple swamps. Finally, we must emphasize that Appendix B lists only those rare species that appear in Table 3.3. Identification of additional rare species will be possible only after more comprehensive floristic surveys of red maple swamps have been conducted.

Chapter 4. Abiotic Influences on the Plant Community

The structure and floristic composition of red maple swamps are determined by the interplay of a wide variety of environmental factors, including climate and microclimate; abiotic factors such as water regime, soil and water chemistry, and the physical properties of soils; microrelief of the forest floor; biotic factors such as plant competition, disease, insect infestations, and the activities of beavers (*Castor canadensis*); anthropogenic influences such as logging, grazing, and water level manipulation; and natural catastrophes such as hurricanes and fire. A thorough examination of the role of each of these environmental factors in the ecology of red maple swamps is not possible, simply because most of these topics have not been investigated. Studies of vegetation and environment in northern swamps have identified two key gradients, one related to the position of the water table and the other related to the availability and means of supply of mineral nutrients (Paratley and Fahey 1986). Of the environmental factors that have been studied in red maple swamps, hydrology and nutrient status appear to be most directly responsible for variations in the structure and species composition of the plant community. Ultimately, both of these factors are dictated by the wetland's hydrogeologic setting: the physical and chemical composition of the geologic substrate, the size and slope of the drainage basin, and the relative magnitude of the wetland's hydrologic inputs and outputs.

Hydrology

Research in forested wetlands throughout the United States has shown that hydrology is the primary force controlling the development of these wetlands and their structural and floristic attributes (Conner and Day 1976; Gosselink and Turner 1978; Brown et al. 1979; Carter et al. 1979; Harms et al. 1980; Dunn and Stearns 1987a). Hydrology also has been linked to the morphological and chemical properties of wetland soils (Heinselman 1970; Conner and Day 1976; Veneman et al. 1976; Pickering and Veneman 1984), and to the degree of development of surface microrelief (Satterlund 1960; Ehrenfeld and Gulick 1981; Lowry 1984). For these reasons, this chapter emphasizes the central role of hydrology in shaping the structure and composition of red maple forested wetlands. The influence of water regime on tree growth is addressed in the following chapter.

Influence on Community Structure

The influence of hydrology on the structure of red maple swamps is poorly documented in the glaciated Northeast. In floodplain environments, the rate of flow of surface water through wetland forests may restrict woody plant establishment and hasten tree and shrub mortality simply through erosion of soils and mechanical damage to the vegetation itself (Brown et al. 1979; Harms et al. 1980; Huenneke 1982; Ehrenfeld 1986). Brown et al. (1979) found tree density in still-water wetlands to be more than twice as high as in floodplain wetlands, and they concluded that water movement was a key factor explaining wetland forest structure in general.

Most red maple swamps in the glaciated Northeast are still-water wetlands. Where the swamps occur in streamside locations, either the streams are small and lack true floodplains, or the maple stands are located on the inner floodplain, at some distance from the channel. For these reasons, one might expect the effect of flowing water on community structure to be minimal. Ehrenfeld (1986) found, however, that red maple floodplain forests in the New Jersey Pine Barrens had fewer woody species and lower tree and shrub density and biomass than nonfloodplain red maple swamps. Floodplain forests also had higher tree mortality and lower densities of tree seedlings and saplings. Like Brown et al. (1979), Ehrenfeld concluded that the physical disturbance caused by flowing water and associated debris in floodplain forests was the most likely reason for differences in community structure between floodplain and nonfloodplain sites.

Whether stand structure in nonfloodplain red maple swamps varies with water regime is unclear. Tree density and basal area have been shown to be both higher (Ehrenfeld and Gulick 1981; Lowry 1984) and lower (Ehrenfeld 1986; Paratley and Fahey 1986) on wetter sites. Comparison of results of different studies is difficult because the range of hydrologic conditions examined and the meanings of "wetter" and "drier" often vary widely. Further, tree density is influenced by both stand age and stand origin (Braiewa 1983). The ability of red maple to dominate sites that range widely in wetness itself suggests that, once established, the trees adapt well to the prevailing hydrologic regime and that unusually low density or basal area can be expected to occur only where site wetness exceeds the species' tolerance level.

Relative abundance and biomass of shrubs have been shown to increase with wetness in nonfloodplain red maple swamps (Ehrenfeld and Gulick 1981; Lowry 1984; Swift et al. 1984; Paratley and Fahey 1986). In Rhode Island, Lowry found that both density and percentage cover of shrubs were greatest at sites with the highest mean water levels, but he noted that these sites also had the lowest tree canopy cover, the most pronounced microrelief, and the highest groundwater pH. A strong relation between water regime and the structure of both the woody understory and the ground vegetation layer was observed by Paratley and Fahey (1986) in a New York mixed conifer–hardwood swamp. In severely flooded and moderately flooded areas of the swamp, woody understory densities were 18,046 and 10,881 stems/ha, respectively, while values for seeps and moderately dry areas were 7,429 and 8,936 stems/ha. The percentage cover of woody seedlings, graminoids, and bryophytes was found to vary significantly among six ground vegetation associations as well. Sedges and mosses were most abundant in those red maple communities with the highest mean water levels during the growing season. Percentage cover of woody seedlings was greatest in a moderately wet red maple community that received large inflow of nutrient-rich surface water from a nearby creek during the spring.

Research in red maple swamps in southern New Jersey (Ehrenfeld and Gulick 1981; Ehrenfeld 1986) reaffirms the conclusions drawn in glaciated areas of the Northeast. In two separate studies, shrub density and biomass were much higher in wet hardwood swamps than in dry hardwood swamps. While the biomass of herbs was small to negligible at these sites, its relative contribution to total biomass was much greater at the wetter sites; herb biomass totaled 195 kg/ha in the wet swamps, but only 53 kg/ha in the dry swamps. If the influence of hydrology on vegetation structure is to be further elucidated, however, detailed measurements of standard hydrologic parameters over several years will be required.

Influence on Floristic Composition

The influence of water regime or soil moisture on species composition and distribution in wetland forests has been most clearly demonstrated in floodplain communities. In the bottomland hardwood forests of the southern United States, which often include a red maple component, plant community composition has been shown to be a function of the timing, frequency, and duration of flooding or of anaerobic soil conditions (Monk 1966; Brown et al. 1979; Huffman and Forsythe 1981; Conner and Day 1982; Parsons and Ware 1982). A strong relation between species distribution and hydrologic regime has been shown on northeastern floodplains as well. In this region, red maple generally occurs in alluvial basins on the inner floodplain (Buell and Wistendahl 1955; Pierce 1981; Tiner 1985) or in oxbows or on floodplain terraces (Pierce 1981; Holland and Burk 1984; Metzler and Damman 1985) where the forest is less frequently flooded by river waters and the soil is less well drained after floods subside than on the outer floodplain. Information on relationships between water regime and the floristics of nonfloodplain red maple swamps in the glaciated Northeast comes primarily from research conducted in southern New England and New York.

Hydrologic Variation Among Swamp Communities

Damman and Kershner (1977) identified soil moisture regime as a key determinant of floristic variation in western Connecticut forests located over till and gneissic bedrock. They described three red maple swamp communities in that region and suggested that the floristic differences among those communities were caused by differences in nutrient levels, which were influenced by topographic position and hydrology.

The most common type of red maple swamp encountered in the Damman and Kershner (1977) study was the *Symplocarpus foetidus–Acer rubrum* community that typically occurs in valley bottoms where soils are very poorly drained and fed by groundwater seepage (Fig. 4.1). These swamps are usually drained by a stream, so that surface water does not persist for long periods. If groundwater inflow is especially abundant and nutrient-rich, a *Symplocarpus–Acer rubrum–Ranunculus septentrionalis* community is often found. Distinguishing species, besides swamp buttercup, in this floristically rich community include swamp saxifrage, bulbous bittercress, and golden ragwort. Upslope from the *Symplocarpus–Acer rubrum* community, in areas where soils are poorly drained but surface water is rarely present, a *Betula alleghaniensis–Acer rubrum–Osmunda cinnamomea* community is commonly found (Fig. 4.1). This transitional community frequently forms only a narrow belt at the bases of slopes; it is slightly drier and poorer in nutrients than the other two types of red maple forests.

In devising a floristic classification for wetlands in the gneissic–schistose bedrock region of northwestern Connecticut, Messier (1980) also underscored the link between water regime and nutrient levels. He observed that, for a given nutrient regime, the type of wetland community was closely related to the elevation and degree of fluctuation of the water table. Figure 4.2 compares the extent of water level fluctuation during a single year among five red maple swamp communities and five other wetland types he encountered. In reviewing the following findings, remember that the extent of water level fluctuation may vary widely among years, even within the same swamp (Fig. 2.7).

The *Osmunda cinnamomea–Acer* swamp occurred on peat soils of the valley floor, unlike the sloping sites described by Damman and Kershner (1977), and had a saturated water regime. The water table remained within 10–15 cm of the surface throughout the growing season, but surface water was present only briefly. The *Rhododendron viscosum–Acer* community occurred both in valley basins, where groundwater inflow was presumed to occur, and in basins farther upslope, which were perched above the local groundwater table. Water

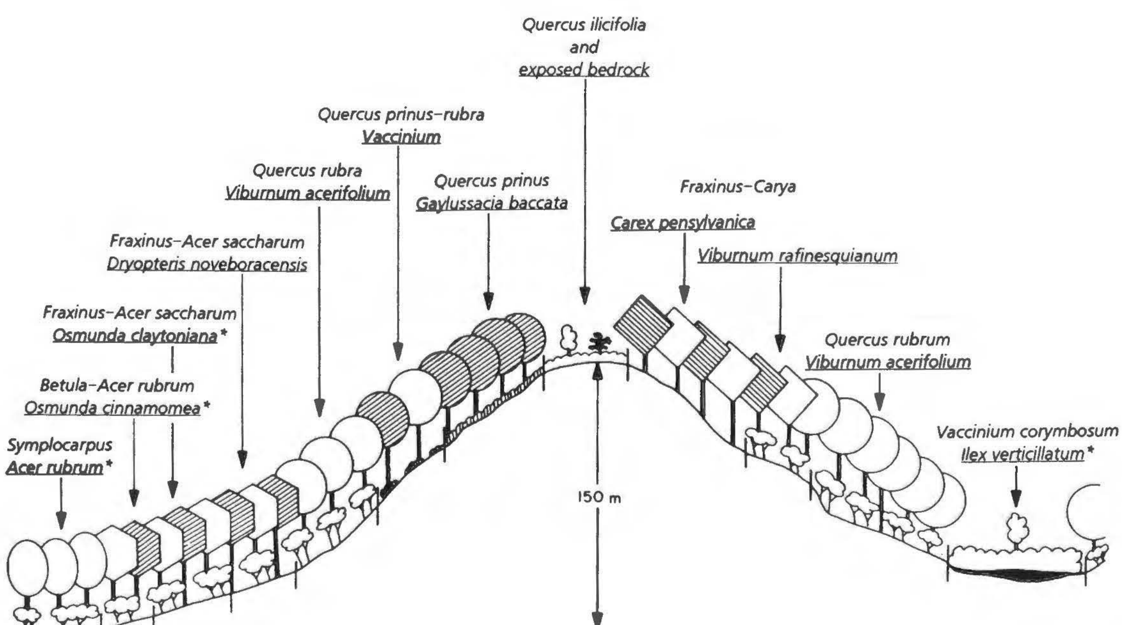

Fig. 4.1. Toposequences of plant communities on a till-covered gneiss hill in western Connecticut (after Damman and Kershner 1977). *Left side* of diagram represents normal toposequence; *right side* is that of certain south-facing slopes. Wetland communities are marked with an *asterisk*. Elevation of summit is between 350 and 400 m above sea level.

level fluctuation during the growing season was comparable in the two locations, but the valley basins held much more water after spring snowmelt. Messier (1980) noted that variants of this community, dominated by different shrub species, could be distinguished by the minimum growing-season water level. Either *Rhododendron viscosum* or *Ilex verticillata* appeared to be dominant where the water table remained within 10 cm of the surface (in 1978), while *Vaccinium corymbosum* was dominant where the water table dropped to at least 20 cm below the surface.

The remaining three red maple swamp communities, *Carex stricta–Acer*, *Carex lacustris–Acer*, and *Symplocarpus–Acer*, were observed both in valley bottoms and in association with springs at the bases of valley slopes. In valley bottoms, water levels for all the communities ranged from about 20 to 30 cm above to 20 to 30 cm below the surface during the growing season; however, during March, surface water was considerably deeper in the sedge communities (Fig. 4.2). At spring sites, both sedge communities had water levels within 5–10 cm of the surface throughout the growing season and were flooded to a depth of only 10–20 cm during the spring. The sedge communities differed chiefly in nutrient status, the *Carex lacustris–Acer* community occurring in slightly richer areas. The *Symplocarpus–Acer* community occurred at spring sites that were only seasonally saturated; by the end of the growing season, the water table was commonly 60 cm or more below the surface.

Paratley and Fahey (1986) identified three major forested wetland communities in a mixed conifer–hardwood swamp in central New York: hemlock swamp; mixed conifer–red maple swamp, larch phase; and mixed conifer–red maple swamp, white pine phase. Using water level data gathered weekly during one growing season, the authors demonstrated that the distribution of woody species was controlled largely by the mean depth to the water table during the growing season and the duration of the summer drawdown. Red maple was the dominant tree in the severely flooded sites, where the water level was highest and the period of drawdown was 8 weeks or less. Hemlock swamp had a lower mean water level, but shorter drawdown period, than the mixed conifer–red maple communities (Table 4.1). Mean depth to the water table was also one of the key factors separating four ground vegetation associations occurring in the mixed conifer–red maple swamps; ash content and bulk density of the organic soils were other important factors (Table 4.1).

Paratley and Fahey (1986) concluded that, in areas of the forested wetland with low mean water levels, the duration of summer drawdown was an important factor influencing both overstory and ground vegetation composition. Where mean

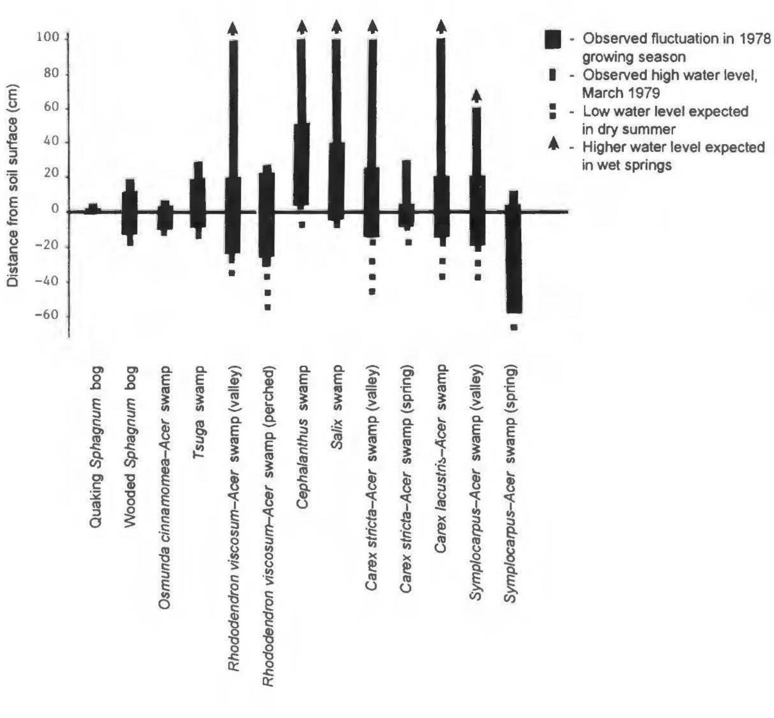

Fig. 4.2. Water level fluctuation in red maple swamps and other wetland communities of northwestern Connecticut (redrafted from Messier 1980).

Table 4.1. *Soil and water table characteristics of three forested wetland communities at Labrador Hollow Swamp in central New York (modified from Paratley and Fahey 1986).*

Association	No. of soil samples	Mean litter pH	Mean soil pH at 12 cm	Mean % nonvolatile matter	Mean bulk density (g/cm^3)	Mean water table depth[a] (cm)	Duration of draw-down[a] (weeks)
Forest							
Hemlock swamp	50	3.92	3.93	14.3	0.086	18.52	4.9
Mixed conifer–red maple (white pine phase)	40	3.95	4.06	12.0	0.068	15.59	10.6
Mixed conifer–red maple (larch phase)	60	3.97	4.54	14.8	0.068	11.15	8.8
Ground vegetation[b]							
BT	35	3.91	3.88	14.8	0.086	18.49	4.6
CL	30	4.18	4.88	12.6	0.078	20.32	11.6
CP	30	4.25	4.83	19.6	0.066	12.72	7.7
IV	40	3.73	3.98	10.4	0.060	10.79	9.6
DV	15	4.11	4.49	11.6	0.083	8.23	9.0

[a] Water table data are based on weekly measurements during one growing season (1984).
[b] Ground vegetation associations were: BT = *Bazzania trilobata, Ptilium crista-castrensis, Carex vulpinoidea, Tetraphis pellucida*; CL = *Cinna latifolia, Clintonia borealis, Galium triflorum, Gaultheria procumbens*; CP = *Caltha palustris, Viola cucullata, Carex laxiflora, Cornus stolonifera*; IV = *Ilex verticillata, Rubus hispidus, Vaccinium myrtilloides, Viburnum cassinoides*; DV = *Decodon verticillatus, Carex trisperma, Lysimachia terrestris, Hypericum denticulatum*. The *B. trilobata* association occurred in the hemlock forest community; the other four ground vegetation associations occurred in mixed conifer–red maple forests.

water levels were high, drawdown duration was less important than historical events (e.g., logging) and the proximity of the site to mineral-rich surface water or groundwater sources. The latter factors were particularly important in explaining the distribution of ground vegetation. Species richness of bryophytes and herbs was relatively low in both the driest and the most flooded portions of the moisture gradient; high vascular plant richness was correlated with high base status of soils and more extended water table drawdown. The highly varied hydrologic conditions in the wetland were considered to be one of the chief reasons for high overall species richness and community heterogeneity.

Species Distribution Along the Moisture Gradient

The influence of hydrology on swamp floristics also is reflected in the distribution of individual plant species along the moisture gradient extending from a swamp into the bordering upland area. Two southern New England studies—one from Connecticut and one from Rhode Island—have examined species distribution in this zone. Anderson et al. (1978, 1980) described vegetation and soils in the transition zones of eight red maple swamps in northeastern Connecticut. Six of the sites were located in till and two were in stratified drift. Soils ranged from very poorly drained organic soils at the wet end to somewhat excessively drained mineral soils at the dry end (see Table 2.4 for drainage class definitions). Table 4.2 presents a list of species recorded in the wetland, transition, and upland zones, along with the frequency of occurrence of each species in each zone. Anderson et al. concluded that species composition and distribution of plants were most closely related to soil water content and elevation; however, quantitative data to verify this conclusion were lacking.

In southern Rhode Island, researchers gathered detailed data on water levels and soil moisture (Allen 1989), chemical and morphologic properties of soils (Sokoloski et al. 1988; Sokoloski 1989), and vegetation (Davis 1988; Allen et al. 1989) along transects extending from red maple swamp into forested upland at three sites, all of which were in stratified drift. In the course of this research, the wetland indicator status assigned by the U.S. Fish and Wildlife Service (Reed 1988) was determined for all species in all vegetation layers in each sample plot. Figure 4.3 shows the distribution of plants, by wetland indicator category, in the various soil drainage classes sampled. Wetland indicator categories are defined in Table 4.3. The following overview of the results of

Table 4.2. *Relative abundance of plant species in wetland (W), transition (T), and upland (U) zones associated with eight red maple swamps in northeastern Connecticut (from Anderson et al. 1978).*[a]

Tree layer	W	T	U
Acer rubrum	V	A	A
Carpinus caroliniana	R	O	F
Quercus alba	F	O	A
Betula alleghaniensis	O	R	F
Quercus rubra	R	R	F
Pinus strobus	R	R	O
Ulmus rubra	O		
Carya cordiformis	R		
Nyssa sylvatica	O	R	
Fraxinus americana	O	R	
Quercus bicolor	R	F	
Sassafras albidum		R	
Acer saccharum		R	
Ulmus americana		R	
Carya ovata		R	F
Betula lenta		O	R
Castanea dentata		R	O
Prunus pensylvanica			R

Shrub layer	W	T	U
Vaccinium corymbosum	A	V	A
Rhododendron viscosum	A	A	A
Lindera benzoin	A	F	F
Clethra alnifolia	F	F	F
Carpinus caroliniana	O	F	F
Ilex verticillata	F	F	F
Lyonia ligustrina	R	F	F
Hamamelis virginiana	O	R	R
Smilax herbacea	R	R	R
Fraxinus americana	R	O	F
Viburnum acerifolium	R	F	F
Nyssa sylvatica	R	O	R
Ribes triste	R		
Carya cordiformis	R		
Pinus strobus	R		
Castanea dentata	R	O	
Viburnum lentago		R	
Ulmus rubra		R	
Gaylussacia baccata		R	A
Quercus alba		F	A
Acer rubrum		F	F
Vaccinium angustifolium		R	F
Acer saccharum		R	F
Carya ovata		R	R
Betula alleghaniensis		R	R
Quercus rubra			F
Prunus serotina			F
Corylus cornuta			F
Amelanchier arborea			O
Sassafras albidum			O
Cornus florida			O
Fagus grandifolia			R
Kalmia angustifolia			R
Betula populifolia			R
Kalmia latifolia			R
Parthenocissus quinquefolia			R
Rosa rugosa			R

Ground cover	W	T	U
Maianthemum canadense	A	V	A
Osmunda cinnamomea	A	V	A
Thelypteris noveboracensis	F	A	A
Mitchella repens	F	A	A
Polygonatum commutatum	F	A	A
Dennstaedtia punctilobula	O	F	A
Trientalis borealis	O	F	A
Rubus hispidus	F	O	O
Coptis trifolia	F	F	F
Medeola virginiana	O	O	F
Lycopodium obscurum	F	A	V
Lycopodium complanatum	F	F	F
Aralia nudicaulis	R	F	A
Sphagnum spp.	A	F	
Symplocarpus foetidus	F		
Onoclea sensibilis	O		
Trillium erectum	R		
Leucobryum glaucum	O		
Monotropa uniflora	R		
Carex stricta	R		
Viola spp.	F	R	
Arisaema triphyllum	F	R	
Thuidium delicatulum	F	O	
Athyrium filix-femina	F	O	
Lycopodium lucidulum	O	R	
Thelypteris thelypteroides	O	R	
Leersia virginica	R	R	
Polystichum acrostichoides		F	
Osmunda regalis		R	
Amphicarpa bracteata		R	
Solidago sp.		R	
Carex pensylvanica		F	A
Rubus spp.		O	F
Actaea pachypoda		R	R
Pyrola rotundifolia			R
Panax trifolius			R

[a] Abundance is based on frequency of occurrence in a particular zone on 31 transects: R = rare (3.2%), O = occasional (6.5%), F = frequent (9.6–25.8%), A = abundant (29.0–51.6%), V = very abundant (≥54.8%).

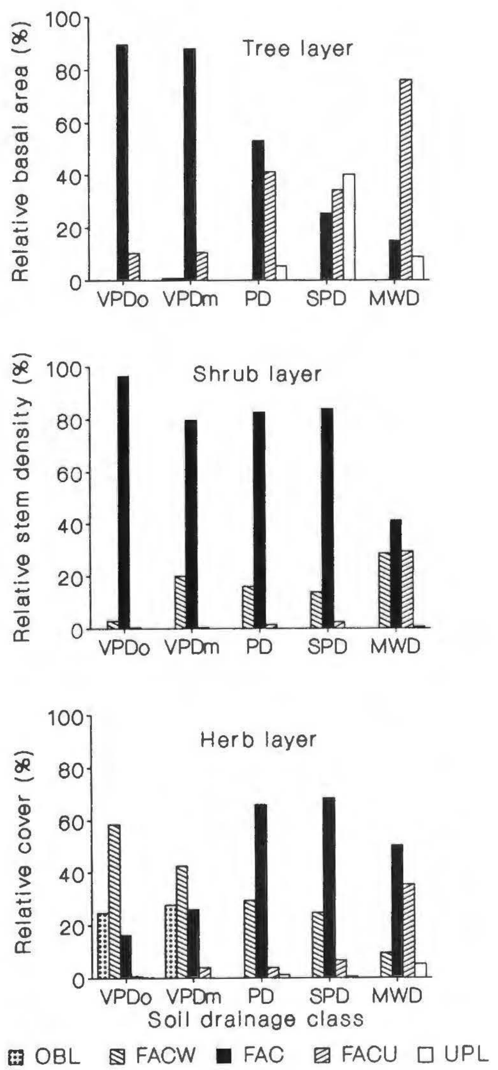

Fig. 4.3. Relative importance of plants from five wetland indicator categories along a soil moisture gradient between red maple swamps and adjacent upland forests in southern Rhode Island. Wetland indicator categories are OBL = obligate wetland, FACW = facultative-wetland, FAC = facultative, FACU = facultative-upland, and UPL = obligate upland. Soil moisture categories are VPDo = very poorly drained organic, VPDm = very poorly drained mineral, PD = poorly drained, SPD = somewhat poorly drained, and MWD = moderately well drained. Data were collected from three sites (F. C. Golet, unpublished data).

this study should provide insight into patterns of species distribution in red maple swamps throughout the Northeast.

The moisture gradient, which was well defined by topographic profiles, groundwater levels, and soil drainage classes at all of the Rhode Island sites (Allen et al. 1989), was most clearly reflected in the changing composition and relative abundance of herb-layer species (Fig. 4.3). As one might expect, facultative-wetland (FACW) herbs declined in abundance while facultative-upland (FACU) herbs increased along the gradient from very poorly drained to moderately well drained soils. Obligate wetland (OBL) herbs occurred only in very poorly drained soils. The relative cover of facultative (FAC) herbs peaked in the poorly drained and somewhat poorly drained soil classes, suggesting that these plants are best adapted to moisture conditions near the middle of the gradient examined.

A moisture-related gradient was evident in the tree layer as well (Fig. 4.3). Red maple (FAC) was dominant in the wetland (VPD–PD) portions of the gradient, and steadily declined in abundance in an upslope direction. White oak (FACU) predominated in moderately well drained soils and generally declined in abundance as soil moisture increased. This species was nearly as abundant as red maple in poorly drained soils, but decreased sharply in very poorly drained soils. In the shrub layer, the great abundance of FAC species along the entire length of most transects (Fig. 4.3) obscured moisture-related trends in vegetation (Allen et al. 1989). Facultative (FAC) shrubs predominated at 48 of the 54 sampling stations. A preponderance of sweet pepperbush throughout the moisture gradient was largely responsible for these results.

The shift in predominant indicator status of herb layer species clearly signaled the change from very poorly drained to poorly drained soils; however, the change from hydric to nonhydric soils, which occurred between poorly drained and somewhat poorly drained stations (Allen et al. 1989), was not accompanied by a distinct change in the wetland indicator composition of any of the vegetation layers (Fig. 4.3). Thus, precise location of the boundary of red maple swamps may be

Table 4.3. *Wetland indicator categories for plant species that occur in wetlands (from Reed 1988).*

Category	Code	Frequency of occurrence in wetlands (%)
Obligate upland	UPL	<1
Facultative-upland	FACU	1–33
Facultative	FAC	34–66
Facultative-wetland	FACW	67–99
Obligate wetland	OBL	>99

difficult to delineate in many instances if only vegetative criteria are used. The shift in relative abundance between red maple (FAC) and white oak (FACU) trees most closely approximated the change from hydric to nonhydric soils.

The great majority of plant species that occur in northeastern red maple swamps can grow under a wide range of soil moisture conditions; that is, most species are FACW, FAC, or FACU. This is not surprising in light of the seasonal and annual water-level fluctuation in these wetlands. Table 4.4 shows the distribution, by soil drainage class, of the major tree, shrub, and herb layer species encountered in the Rhode Island moisture gradient study, along with the wetland indicator status of each.

Obligate wetland (OBL) trees are rare in the glaciated Northeast; Atlantic white cedar is the only relatively common species so classified (Reed 1988). In the Rhode Island study, the few cedars present were restricted to very poorly drained soils. Except for scarlet oak (*Quercus coccinea*), which is an obligate upland (UPL) species, the remaining trees were in one of the facultative categories. The most common of these—*Acer rubrum*, *Quercus alba*, and *Nyssa sylvatica*—occurred in every soil drainage class.

Obligate wetland shrubs also are rare in northeastern red maple swamps. Of the four OBL species recorded in the Rhode Island study—swamp rose, poison sumac, brookside alder (*Alnus serru-*

Table 4.4. *Frequency of occurrence (%) of major tree, shrub, and herb layer species by soil drainage class in the wetland–upland transition zone of three Rhode Island red maple swamps (shrub and herb data from Davis 1988).*

		Soil drainage class[a]				
		VPD				
Species[b]	FWS indicator status[c]	Organic (n = 4/6)[d]	Mineral (n = 9/18)	PD (n = 9/14)	SPD (n = 7)	MWD (n = 9)
Tree layer						
Pinus strobus	FACU					11
Quercus coccinea	UPL			11	57	33
Quercus alba	FACU	50	33	67	71	89
Acer rubrum	FAC	100	100	89	71	56
Nyssa sylvatica	FAC	25	33	44	29	11
Fagus grandifolia	FACU		11	22		
Betula alleghaniensis	FAC	25	22			
Quercus palustris	FACW		11			
Chamaecyparis thyoides	OBL		11			
Shrub layer						
Gaylussacia baccata	FACU				29	100
Kalmia angustifolia	FAC			7		44
Prunus serotina	FACU		11	14	29	56
Viburnum cassinoides	FACW			64	57	67
Lyonia ligustrina	FACW			7	14	56
Smilax glauca	FACU			29	29	22
Amelanchier canadensis	FAC	17	11	7		67
Acer rubrum	FAC	17	11	29	43	78
Vaccinium corymbosum	FACW	17	50	71	71	89
Aronia arbutifolia	FACW		17	29	14	11
Rhododendron viscosum	OBL	67	72	93	100	78
Clethra alnifolia	FAC	100	100	100	100	67
Ilex verticillata	FACW	17	28	7	14	11
Viburnum recognitum	FACW		44			11
Nyssa sylvatica	FAC		17	21	14	22
Leucothoe racemosa	FACW	33	11	21	29	
Smilax rotundifolia	FAC	83	33	50	43	
Lindera benzoin	FACW		28			
Herb layer						
Gaylussacia baccata	FACU				43	100

Table 4.4. *Continued.*

		Soil drainage class[a]				
		VPD				
Species[b]	FWS indicator status[c]	Organic (n = 4/6)[d]	Mineral (n = 9/18)	PD (n = 9/14)	SPD (n = 7)	MWD (n = 9)
Vaccinium vacillans	UPL				29	33
Carex pensylvanica	UPL			36	42	78
Gaultheria procumbens	FACU			57	86	100
Kalmia angustifolia	FAC		11	57	86	89
Aralia nudicaulis	FACU		22	7		44
Lycopodium obscurum	FACU	17	11	14	57	56
Medeola virginiana	na		17	64	71	44
Monotropa uniflora	FACU		17	14	29	22
Mitchella repens	FACU		6	7	43	
Ilex glabra	FACW	33	11	71	71	44
Anemone quinquefolia	FACU		17	36	14	11
Uvularia sessilifolia	FACU	33	50	100	100	44
Maianthemum canadense	FAC	67	89	86	100	89
Trientalis borealis	FAC	100	67	93	100	78
Rubus hispidus	FACW	50	89	14	29	67
Osmunda cinnamomea	FACW	50	56	100	86	
Arisaema triphyllum	FACW		28			
Cuscuta compacta	na		28			
Carex seorsa	FACW		33			
Lycopus uniflorus	OBL		33			
Viola pallens	OBL		39			
Aster novi-belgii	FACW		50			
Carex lonchocarpa	OBL		50			
Toxicodendron radicans	FAC	17	61	7		
Lilium superbum	FACW	50	22	7	14	
Thelypteris simulata	FACW	83	44	36		
Thelypteris thelypteroides	FACW	17	39			
Parthenocissus quinquefolia	FACU	17	22			
Sphagnum spp.	OBL[e]	100	83			
Symplocarpus foetidus	OBL	100	72			

[a] VPD = very poorly drained; PD = poorly drained; SPD = somewhat poorly drained; MWD = moderately well drained. See Table 2.4 for definitions.
[b] Tree layer species include all woody plants at least 6 m in height; shrub layer species include woody plants from 0.5 to 6 m tall; herb layer species include nonwoody vascular plants, woody plants less than 0.5 m tall, and *Sphagnum* mosses.
[c] U.S. Fish and Wildlife Service wetland indicator status for the Northeast region (Reed 1988). See Table 4.3 for definitions; na = indicator status not assigned.
[d] Where n varies, the first number is the sample size for tree layer species; the second is the sample size for shrub and herb layer species. In other cases, the sample size for all layers is the same.
[e] Status for *Sphagnum* assigned by Allen et al. (1989); mosses not included in Reed (1988).

lata), and swamp azalea—only swamp azalea occurred at more than 10% of the sampling stations. This species was very common in both wetland and nonwetland soils at all sites. Anderson et al. (1978) indicated that swamp azalea was common in upland areas adjacent to red maple swamps in Connecticut as well (Table 4.2). These findings and our field observations elsewhere in southern New England suggest that swamp azalea would be more appropriately classified FACW, at least in this part of the Northeast. For additional discussion on this topic, see Davis (1988) and Allen et al. (1989).

The most common shrubs or vines found in the Rhode Island swamps, namely sweet pepperbush, swamp azalea, highbush blueberry, common greenbrier (*Smilax rotundifolia*), and fetterbush, were common on somewhat poorly drained and moderately well drained soils as well (Table 4.4). Varying and seemingly contradictory statements in the literature about the moisture status of particular shrub species can be explained simply by the facultative nature of these species. For reasons other than water regime (e.g., land-use history or soil nutrient status), a particular facultative species may be abundant in very wet swamps and in relatively dry swamps.

Because the root zone for most herb layer species is quite shallow, this vegetation layer is more responsive than the shrub or tree layers to differences in soil moisture at or near the surface of the ground (Davis 1988; Allen et al. 1989). As a result, the herb layer of red maple swamps frequently contains a greater diversity of species in terms of wetland indicator status. In the Rhode Island moisture gradient study, the frequency of occurrence of many herb layer species across the various soil drainage classes closely matched the wetland indicator status assigned to those species by the U.S. Fish and Wildlife Service (Table 4.4). For example, FACU species such as black huckleberry, teaberry, tree clubmoss (*Lycopodium obscurum*), and partridgeberry clearly were more common in upland soils than in wetland soils. Obligate wetland (OBL) species were found only in very poorly drained soils, and FACW species, such as marsh fern, Massachusetts fern, cinnamon fern, and Turk's-cap lily (*Lilium superbum*) were more common in wetland soils than in upland soils. Facultative (FAC) species such as sheep laurel, wild lily-of-the-valley, and starflower were found on every soil drainage class sampled. The high frequencies of these and other FAC species in the very poorly drained soil zone can be explained by their occurrence on mounds that are elevated above the seasonal high water table.

Just as the composition of the herb layer varies along the moisture gradient at the edge of a swamp, it may vary markedly from swamp to swamp depending on the prevailing hydrologic regime. In the three sites examined in the Rhode Island moisture gradient study, the proportion of herb-layer species that were in the OBL and FACW categories ranged from 59% to 37% (Allen et al. 1989). The site with the highest proportion of OBL and FACW herbs also had the highest, most stable water level during the growing season.

Flood Tolerance of Swamp Species

The ability of plant species to tolerate prolonged flooding of their root systems is another characteristic that has been commonly used to array swamp species along a moisture gradient (Hall and Smith 1955; Gill 1970; Bell 1974; Teskey and Hinckley 1977; Theriot 1988). Flood-tolerance data may be used to (1) explain the distribution of species in natural wetlands, (2) forecast the impacts of increased water levels on plant growth and survival, and (3) predict changes in the structure of the plant community. A few wetland tree species are able to survive 3 years of continuous inundation (Green 1947), but most are unable to survive even 2 years (Broadfoot and Williston 1973). Of 39 deciduous tree species studied by Hall and Smith (1955) in Tennessee, none was able to survive if the root system was covered with water for more than 54% of the growing season during an 8-year period.

Flood-tolerance levels for tree species found in northeastern red maple swamps are presented in Table 4.5. Except for green ash (*Fraxinus pennsylvanica*), trees that are classified very tolerant (i.e., capable of surviving continuous flooding for two or more growing seasons) are not important species in red maple swamps. Trees most commonly found in seasonally flooded swamps are typically classified tolerant or intermediately tolerant. Intolerant species, such as American beech, black cherry, white oak, and sassafras (*Sassafras albidum*), most often occur in seasonally saturated swamps. More detailed information on the flood tolerance of individual northeastern tree species can be found in Teskey and Hinckley (1978a, 1978b).

In the only study of its kind in the Northeast, the influence of prolonged seasonal flooding on a red maple swamp community was examined at the Montezuma National Wildlife Refuge in central New York State, where two 120-ha green-timber impoundments were managed for waterfowl production (Malecki et al. 1983). Surface water averaging 27–30 cm in depth was maintained in each swamp from mid-March until late June or early July over a 12-year period. Except for the decline of American elm, which was attributed to Dutch elm disease, the frequency of occurrence of the major tree species did not change during the study period. The density of red maple and green ash trees increased, however, while elm, bluebeech, and swamp white oak trees declined in number. Certain shrubs, including spicebush and common winterberry, also showed a significant decline, along with all species of ferns. Arrow arum (*Peltandra virginica*), swamp loosestrife (*Decodon verticillatus*), and beggar-ticks (*Bidens* spp.) were favored by the lengthened hydroperiod;

Table 4.5. *Flood tolerance of trees and large shrubs that occur in northeastern red maple swamps (from Teskey and Hinckley 1978a, b).*

Very tolerant species: trees that can withstand flooding for periods of two or more growing seasons; these species exhibit good adventitious or secondary root growth during this period

Fraxinus pennsylvanica	*Populus grandidentata*
Picea mariana	*Salix nigra*
Populus deltoides	

Tolerant species: trees that can withstand flooding for most of one growing season; some new root development is expected during this period

Abies balsamea	*Nyssa sylvatica*
Acer negundo	*Platanus occidentalis*
Acer rubrum	*Quercus bicolor*
Acer saccharinum	*Quercus macrocarpa*
Celtis occidentalis	*Tilia americana*
Chamaecyparis thyoides	*Ulmus americana*
Liquidambar styraciflua	

Intermediately tolerant species: species that are able to survive flooding for periods between 1 and 3 months during the growing season; the root systems of these plants produce few new roots or are dormant during the flooded period

Acer saccharum	*Picea glauca*
Alnus incana	*Picea rubens*
Betula alleghaniensis	*Pinus strobus*
Carpinus caroliniana	*Populus tremuloides*
Carya cordiformis	*Quercus palustris*
Crataegus spp.	

Intolerant species: species that cannot withstand flooding for short periods (1 month or less) during the growing season; the root systems die during this period

Alnus rugosa	*Prunus serotina*
Betula papyrifera	*Quercus alba*
Betula populifolia	*Quercus imbricaria*
Fagus grandifolia	*Quercus rubra*
Juniperus virginiana	*Sassafras albidum*
Liriodendron tulipifera	*Tsuga canadensis*
Ostrya virginiana	

as a result, aboveground biomass of herbs increased as much as sevenfold in certain areas. The prolonged flooding greatly curtailed reproduction by green ash, elm, and blue-beech, but favored red maple, which reproduces mainly by stump sprouts and root suckers.

Several authors (e.g., Lowry 1984; Paratley and Fahey 1986) have noted difficulty in attempts to explain differences in community composition of red maple swamps on the basis of water regime alone. This difficulty may arise for at least three reasons: (1) the segment of the moisture continuum examined in such studies may be too narrow to detect moisture-related trends in species distribution; (2) significant local variations in soil moisture, due to surface microrelief, may not have been considered; and (3) other environmental factors, such as nutrient status or land-use history, may be relatively more important than water regime in explaining species distributions in some cases, especially where the range of moisture conditions examined is narrow.

Microrelief

Origin and Relationship to Water Regime

Microrelief, also referred to as mound-and-pool topography, hummock-and-hollow microtopography, and pit-and-mound microtopography, is a characteristic feature of nonfloodplain forested wetlands in the Northeast (Little 1950; Thompson et al. 1968; Grace 1972; Vogelmann 1976; Messier 1980; Swift 1980; Ehrenfeld and Gulick 1981; Huenneke 1982; Malecki et al. 1983; Lowry 1984; Paratley and Fahey 1986). Some floodplain swamps also exhibit pronounced microrelief (Buell and Wistendahl 1955; Hardin and Wistendahl 1983; Menges and Waller 1983). The development of microrelief has been attributed to a variety of causes, including frost action (Satterlund 1960), windthrown trees (Satterlund 1960; Lyford and MacLean 1966; Malecki et al. 1983; Beatty 1984; Lowry 1984; Paratley and Fahey 1986), concentration of tree roots above high water tables (Bray 1915; Lowry 1984; Paratley and Fahey 1986), and rhizomatous growth in shrubs (Ehrenfeld and Gulick 1981; Lowry 1984).

Since trees growing in swamps generally are more shallowly rooted than trees on upland sites, they are particularly susceptible to windthrow (Fig. 4.4), which appears to be the most common cause of mound formation. Red maple has a shallow, horizontal root system in swamps, but often produces a long tap root in upland habitats where water tables are deeper (Toumey 1926). Rooting depth and the frequency of windthrow have been shown to vary as a function of water table depth even among forested wetlands. In mixed conifer–hardwood swamps in northern Michigan, Satterlund (1960) found that the depth of maximum root penetration for red maple ranged from as little as 51 cm in swamps with persistently high water levels to as much as 147 cm in drier swamps. The frequency of wind-damaged trees was 28% on sites where the water table was periodically or permanently high, but only 18% in drier swamps.

Mound heights in red maple swamps range from about 15 cm for small shrub mounds to as much as 1 m for large tree mounds (Van Dersal 1933; Thompson et al. 1968; Messier 1980; Lowry 1984). Microrelief is usually most pronounced in the wettest swamps. In southern New Jersey red maple swamps that are flooded throughout most

Fig. 4.4. Red maple tree toppled by wind. Windthrow is common in swamps, where trees are shallowly rooted, and is believed to be primarily responsible for the development of mound-and-pool microrelief.

of the year, the forest floor commonly consists of deep hollows and convex mounds; in swamps that lack surface water entirely or that are flooded only temporarily, microrelief is not as well developed (Ehrenfeld and Gulick 1981). Lowry (1984) took spot elevations at over 700 points in each of six red maple swamps and six Atlantic white cedar swamps in southern Rhode Island and determined that microrelief was more highly developed in the cedar swamps, which had significantly higher mean water levels as well. He also confirmed that the extent of microrelief in the red maple swamps was related to water level. Considering all points more than 20 cm above the average level of the depressions to be mounded, he calculated that nearly 75% of the variation in the amount of mounded ground among the six swamps could be explained by differences in the 7-year mean water levels among the sites. Figure 4.5 illustrates pronounced microrelief in a seasonally flooded red maple swamp.

How active a role vegetation plays in the development of microrelief is unclear. Initially, the distribution of trees and shrubs in a swamp is determined by the relative wetness of various possible germination sites on the forest floor. Once they are established, those trees that have the ability to develop a compact, elevated root system clearly stand a greater chance of surviving the effects of prolonged high water levels. Root system development thus may increase mound size. Significantly, radial growth of red maple trees in any given year appears to be directly related to the deviation of that year's average water level from the long-term average. Lowry (1984) demonstrated that, in Rhode Island swamps, growth was greatest in years when water levels were closest to the 7-year mean. This finding suggests that in each swamp there may be an optimal distance, depending upon water regime and soil characteristics, between the elevation of the average water level and the depth of tree roots. Whether the role of vegetation in microrelief development is active or passive, variation in surface elevation within a swamp maximizes the opportunity for any tree to achieve that optimum position and to maximize its growth.

Fig. 4.5. Mound-and-pool microrelief in a seasonally flooded red maple swamp. Swamps with particularly high water levels, such as this one, generally have high mounds and little vegetation growing in the pools. The measuring stick is graduated in 10-cm increments; the water averages 15–25 cm in depth. The photograph was taken in mid-April.

Influence on Swamp Vegetation

Floristic Composition

Through its influence on soil aeration (Huenneke 1982; Paratley and Fahey 1986), nutrient availability (Ehrenfeld and Gulick 1981; Paratley and Fahey 1986), and relative litter accumulation (Little 1950; Malecki et al. 1983; Paratley and Fahey 1986), microrelief creates a variety of microhabitats and thus has a major effect on species composition and distribution of swamp flora. Beatty's (1984) research in a sugar maple-American beech upland forest in eastern New York showed that microrelief may cause local variations in soil acidity and soil temperature as well. Pronounced microrelief allows species with widely differing soil moisture requirements or tolerances to coexist in a limited area in red maple swamps (Bergman 1920; Sampson 1930; Thompson et al. 1968; Huenneke 1982; Paratley and Fahey 1986). While mosses, liverworts, and hydrophilic herbs thrive in seasonally flooded or saturated depressions and at the bases of mounds, species unable to tolerate prolonged saturation grow higher up on the mounds (Niering 1953; Thompson et al. 1968; Paratley and Fahey 1986). Figure 4.6 shows the influence of microrelief on plant distribution in a Rhode Island swamp. Paratley and Fahey (1986) found plant species richness to be positively correlated with microrelief; in fact, they cited high microsite heterogeneity as one of the factors most responsible for the unusually high species richness observed in their central New York study area.

Under a given water regime, certain species of plants tend to occur either primarily on mounds or primarily in depressions. However, the microsite preferences of some species may change depending on mound height or on the relative wetness of the depressions. In a detailed analysis of the relation between species distribution and microrelief in a New York swamp with organic soils, Paratley and Fahey (1986) found that five ground-layer plants—including spotted touch-me-not, marsh marigold, mosses of the genus *Mnium*, sensitive fern, and northern bugleweed—

Fig. 4.6. Influence of microrelief on plant distribution in a red maple swamp. At this site, trees, shrubs and herbs are largely restricted to mounds. Sphagnum moss and marsh fern (*Thelypteris thelypteroides*) grow along the lower edges of the mounds, while swamp jack-in-the-pulpit (*Arisaema triphyllum*) grows in the seasonally flooded depressions.

showed a strong preference for depressions in all four drainage classes sampled: moderately dry, seepage, moderately flooded, and severely flooded. Black ash, rough-leaved goldenrod (*Solidago patula*), marsh blue violet, and marsh fern also were most common in depressions. Dwarf blackberry (*Rubus pubescens*), northern white violet, and swamp jack-in-the-pulpit occurred with high frequency in depressions in the moderately dry drainage class only; in other drainage classes, these three species either were infrequent or showed no obvious microsite preferences. Poison ivy was most common in depressions overall, but occurred most frequently on mounds in the severely flooded class.

Six ground-layer species were largely restricted to mounds; they were partridgeberry, white pine, blue bead-lily, goldthread, American yew, and starflower; eastern hemlock, red maple, wild lily-of-the-valley, teaberry, and knight's plume moss (*Ptilium crista-castrensis*) also showed a preference for mounds. Only starflower was relatively common in drainage classes with high mean water levels as well as low mean levels. In the moderately dry class, several of these mound species showed less fidelity to mounds. Wild lily-of-the-valley, teaberry, and blue bead-lily in particular were more common in depressions in the moderately dry class, but more common on mounds in the wetter drainage classes. Figure 4.7 shows the distribution of five common species by microsite and drainage class.

Microsite preferences for the ground-layer species highlighted in Paratley and Fahey's (1986)

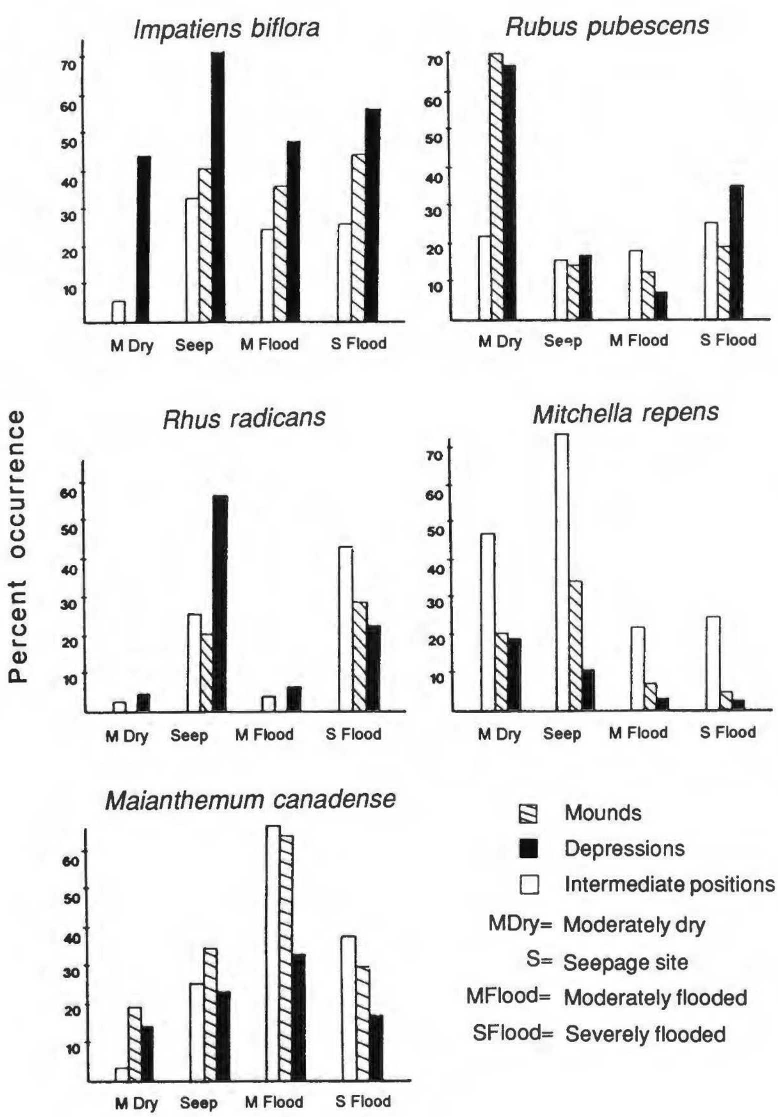

Fig. 4.7. Frequency distributions of five plant species according to microsite and water regime in a central New York swamp (after Paratley and Fahey 1986). *Impatiens biflora* is grouped under *I. capensis* in Table 3.3.

Fig. 4.8. Red maple seedlings in sphagnum moss on the floor of a red maple swamp. Such massive concentrations are common, but few, if any, of these plants survive seasonal flooding.

study are consistent with the U.S. Fish and Wildlife Service wetland indicator status assigned to those species in the northeast region (Reed 1988). All 11 of the classified species that most commonly occurred in depressions were either OBL or FACW species. By contrast, 9 of the 10 classified species with a close affinity for mounds were either FAC or FACU species. Species found both on mounds and in depressions, depending on drainage class, were FAC or FACU.

Vegetation Structure

The relation between microrelief and vegetation structure has not been widely addressed, but it has been acknowledged by several authors (Satterlund 1960; Bucholz 1981; Ehrenfeld and Gulick 1981; Beatty 1984; Lowry 1984). Satterlund (1960), for example, concluded that microrelief had a major influence on both the density and basal area of trees in northern Michigan wetland forests. In swamps where the soil was saturated to the surface most of the year, all crown classes of trees were most abundant on mounds (relative basal area = 73%), less abundant on flats (27%), and scarce in depressions (1%). In swamps where the water table was lower, tree densities were comparable on mounds and flats, but still low in depressions because of seasonal ponding of water there.

Shrub density was positively related to water level and microrelief in six Rhode Island red maple swamps studied by Lowry (1984); the correlation was strongest at the three wettest sites. He noted that, in swamps with hydroperiods exceeding 35% of the growing season, woody plants were virtually restricted to mounds (see Fig. 4.5). Ehrenfeld and Gulick (1981) also suggested that the high shrub densities recorded in red maple swamps may be attributed to pronounced microrelief.

Golet (1969) observed that reproduction of the major tree species in red maple swamps at the Montezuma National Wildlife Refuge in central New York appeared to be influenced by microrelief and related soil moisture levels. Green ash seedlings were found both on mounds and in depressions, but they were noticeably more abundant in the moist depressions. American elm seedlings were almost entirely restricted to the drier mounds. In late summer, red maple seeds sprouted in great numbers in the moist, but dewatered, depressions (Fig. 4.8); rising water levels killed virtually all of these seedlings by the following spring. Successful red maple reproduction occurred primarily from stump sprouts or root suckers.

Chemical and Physical Properties of Soils

The chemical and physical properties of soils have been correlated with floristic variation of forested wetlands in a number of studies (e.g., Monk 1966; Heinselman 1970; Messier 1980; Conner et al. 1981; Huenneke 1982; Parsons and Ware 1982; Reynolds et al. 1982; Paratley and Fahey 1986; Dunn and Stearns 1987b). Among the soil characteristics that have been related to swamp floristics are nutrient status, pH, organic matter content, and texture. Quantitative investigations of the influence of such soil features on the flora of red maple swamps are almost entirely lacking. For this reason, the following discussion is based primarily on qualitative information.

Nutrient status, which refers to the relative abundance and availability of essential plant nutrients, may be one of the most important soil properties influencing the species composition of red maple swamps. Nutrient status is closely tied to hydrology, which in turn is shaped by the topographic position or geomorphic setting of the wetland. The swamp's setting determines the volumes of groundwater and surface water it receives. The chemistry of the water feeding the wetland is influenced by the mineral composition of the local bedrock and surficial deposits, the sources of water entering the wetland, the slope of the surrounding land, and the size of the wetland in relation to the size of its watershed.

Nutrient availability within a wetland may be affected by water regime and by the organic matter content of the soil, which is largely a function of water regime. In wetlands where soils are saturated for much of the growing season, decomposition of organic matter is slowed, and nutrients such as nitrogen and phosphorus may be tied up in undecomposed plant material. The retarded growth of red maple on fibric (bog) soils has been attributed to a shortage of such nutrients in a continuously anaerobic soil environment (Moizuk and Livingston 1966). Seasonal fluctuation of water levels allows aerobic decomposition of organic matter to proceed, releasing nutrients for plant growth. As noted previously, thick deposits of acid, nutrient-poor organic material may effectively isolate plant roots from mineral-rich soil layers beneath. Nutrient levels near the soil surface also may be influenced by *Sphagnum* moss, which has the ability to extract bases from already dilute soil water, lowering its pH (Moore and Bellamy 1974).

Damman and Kershner (1977) placed soil fertility high on a list of factors (including disturbance history and moisture regime) affecting species composition of upland and wetland forests in western Connecticut. Floristically rich red maple swamps were encountered primarily where nutrient-rich groundwater inflow was evident. They noted that their study area contained a much greater variety of plant communities than eastern Connecticut landscapes with similar gneissic bedrock. They conjectured that the possible incorporation of calcareous material into the glacial till deposited in their study area may have been responsible for the greater floristic variation. Groundwater flowing downslope along the upper surface of bedrock or dense till layers could carry calcium and other bases leached from upland soils to lower slopes and valleys where it would be deposited in wetlands.

Messier (1980) provided the most detailed discussion to date on the influence of soil chemistry on the floristics of red maple swamps. He gathered data on floristic composition, water regimes, soil fertility, and pH in 10 wetland communities in northwestern Connecticut, including five types of red maple swamps. Fertility was equated with nitrogen availability and expressed as a carbon-to-nitrogen (C/N) ratio in his study. Assuming that only organic matter with a C/N ratio of 20 or less could provide direct mineral nitrogen to the soil through decomposition, Messier calculated C/N ratios for all communities and classified their nutrient status as nutrient-poor (C/N > 40), nutrient-medium (C/N 20–40), or nutrient-rich (C/N < 20). He noted that soil pH generally increased as the C/N ratio declined, so pH also could be used as a rough index of soil fertility.

Of the 10 wetland communities examined, only wooded bogs were classified as nutrient-poor; the nutrient status of red maple swamps ranged from medium to rich. The medium-fertility *Osmunda cinnamomea–Acer* and *Rhododendron viscosum–Acer* swamps had C/N ratios of about 20 at the soil surface and 26–30 at a depth of 1 m. Messier noted that the communities within this fertility range were separated primarily by moisture regime. Soil pH values for these two communities ranged from about 4.3 to 5.3. *Carex stricta–Acer* swamps, *Symplocarpus foetidus–Acer* swamps, and *Carex lacustris–Acer* swamps all were considered nutrient-rich, the latter two being the richest. Carbon-to-nitrogen ratios generally ranged from 13 to 16 near the surface, while pH ranged from approximately 5.3 to 6.5.

Messier also related the distribution of individual species to moisture and nutrient regimes. He noted, for example, that black ash generally increased in importance with an increase in soil pH. Mountain holly was most common in acidic, nutrient-poor swamps, while swamp azalea was typically found in wet, open swamps with low to medium nutrient levels. Highbush blueberry was most common in drier, medium-rich, densely wooded swamps, and common winterberry was most often found as dense thickets in wet, open, medium-rich swamps.

Messier concluded that a swamp's nutrient status was regulated primarily by (1) its landscape position, which determined the amount of slope runoff, and (2) the degree of water table fluctuation, which influenced the decomposition rate of organic matter. The richest swamps occurred in valleys fed by an abundance of surface runoff and groundwater originating in upslope areas. Figure 4.9 shows the relative distribution of the 10 wetland communities according to both soil pH and moisture regime.

Proximity to mineral-rich groundwater and surface-water sources was believed to be primarily responsible for the variation in the composition

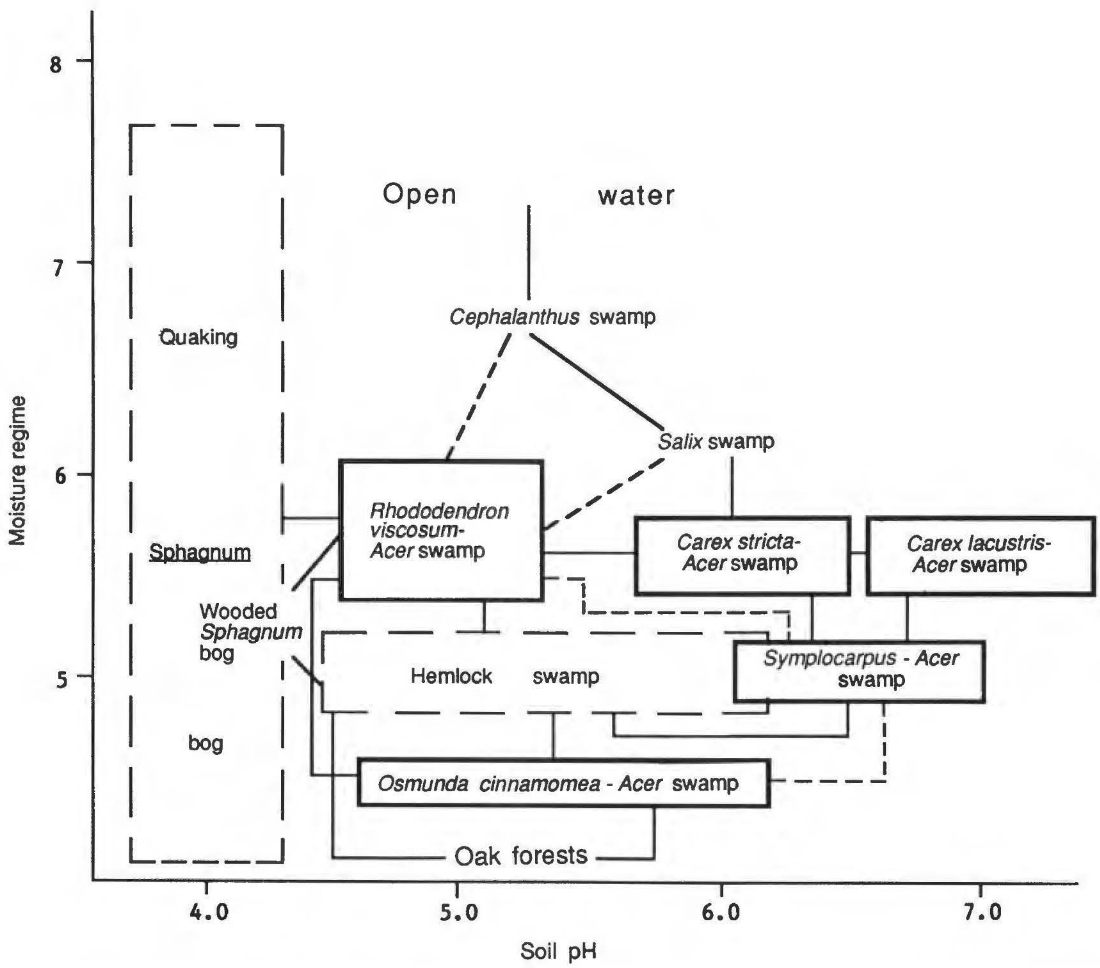

Fig. 4.9. Ecological position of red maple swamps and other wetland types of northwestern Connecticut with respect to moisture regime and pH near the soil surface (after Messier 1980). *Solid boxes* indicate red maple swamps; *broken boxes* indicate broad conditions for certain other community types. *Solid lines* connect communities that are commonly adjacent in the field; *broken lines* link rarely adjacent types. The moisture regime scale is from Damman (1964): 5—maximum water level at or close to the soil surface, 6—water level at surface for most of growing season, 7—water level above surface for most of growing season, 8—permanently inundated.

of ground vegetation within a mixed conifer-red maple forested wetland studied by Paratley and Fahey (1986) in central New York. Although the concentrations of individual elements were not determined, the authors found significant differences in the ash content of the organic soil among the various ground vegetation associations (Table 4.1); they interpreted the differences to mean that base status was a key factor promoting the floristic variation. Generally, ash content of the soil was higher in associations characterized as swamp (CL and CP in Table 4.1) than in those characterized as bog (IV and DV). The swamp communities supported more species as well.

As noted earlier, plant species richness in red maple swamps underlain by calcareous bedrock or calcareous surficial deposits often far exceeds that in acidic swamps. In preparing species lists for southern New England calcareous seepage swamps, Rawinski (1984) noted that the herb layer is the most sensitive indicator of nutrient status. Individual calcareous swamps may support more than 50 species of herbs, more than twice the number usually found in acidic swamps. Key indicator species for calcareous seepage swamps were identified in the previous chapter.

The role of pH in the distribution of red maple swamp flora has not been clearly defined. Published values for pH in northeastern red maple swamps range from below four in some organic soils or areas of acidic bedrock (Anderson et al. 1980; Lowry 1984; Paratley and Fahey 1986) to nearly seven (Messier 1980; Huenneke 1982) in areas with calcareous bedrock or surficial deposits. Studies by Messier (1980), Huenneke (1982), and Dunn and Stearns (1987a,b) demonstrated a relation between pH and swamp floristics in areas where pH values range widely; the strength of this relation within areas of low base status has not been established (Anderson et al. 1978, 1980; Lowry 1984; Paratley and Fahey 1986).

The influence of soil on swamp flora is likely to be mainly hydrologic or chemical, but properties such as organic matter content and soil texture have also been shown to be important in some cases (Frye and Quinn 1979; Huenneke 1982; Dunn and Stearns 1987a,b). Both of these properties vary widely in red maple swamps of the glaciated Northeast. Anderson et al. (1980) and Grace (1972) noted no differences between red maple swamp communities on organic soils and those on mineral soils, but their conclusions were based on general observations rather than quantitative analyses. Because of the scant research and the close relationships between the physical and chemical properties of soils and wetland water regimes, the direct influence of organic matter content and soil texture on the species composition of northeastern red maple swamps remains largely unknown.

Chapter 5. Ecosystem Processes

An ecosystem is a functional unit of the earth's surface that includes both biotic communities and the abiotic environment. The individual components of an ecosystem (i.e., plants, animals, soil, water, nutrients) interact to create the structure and functions of the whole (Odum 1971). The fundamental processes of an ecosystem include organic matter production, decomposition, nutrient cycling, and coupling with adjacent systems. In wetlands, ecosystem processes have a major influence on vegetation dynamics, the quality of wildlife habitat, water quality improvement functions, the productivity of downstream aquatic resources, and other wetland functions and values.

There has been little research on ecosystem processes in red maple swamps or related wetland types. For that reason, the following treatment of this topic is often generalized and incomplete. Primary emphasis is placed on data from the glaciated Northeast, but findings from other regions also are presented where relevant.

Productivity

Productivity of swamps appears to be controlled primarily by hydrology and nutrient availability. Brinson et al. (1981a) reviewed primary productivity data for forested wetlands from Florida to Canada. Lowest productivity rates were recorded on infertile, shallow soils where rainfall was the main source of water and nutrients, while highest rates were found in floodplain forests where nutrient-rich flowing water provided an energy subsidy. Generally, net biomass production in the overstory layer diminished with decreasing water flow; it was highest in flowing-water swamps, less in swamps with sluggish flow, and least in still-water swamps. Gosselink and Turner (1978) also underscored the key role of hydrology, noting that it directly affects other abiotic factors such as soil oxygen levels, nutrient availability, and pH, which, in turn, influence productivity.

Annual Radial Tree Growth

Growth rates of red maple trees in northeastern wetlands have been measured in a number of studies (Golet 1969; Reynolds et al. 1978; Vosburgh 1979; Braiewa 1983; Malecki et al. 1983; Lowry 1984; Ehrenfeld 1986). Several of these studies related radial growth to water regime or other environmental variables. Annual radial growth increments vary widely with tree age; however, before they can be used as a productivity index, stem diameter and tree height also must be considered. Unfortunately, few studies take these other factors into account. For this reason, the following discussion focuses on trends in radial growth rather than on comparisons of absolute growth values among wetlands.

In northeastern swamps, 75% to 90% of the annual radial growth of red maple trees is accomplished by the end of July (Golet 1969; Lowry 1984). Root growth, on the other hand, may continue into late October (Lyford and Wilson 1966). Thus, wetland water levels during early summer may have a direct, immediate influence on annual growth, but soil oxygen availability—even during fall—may affect root development and stem growth the following year. Researchers have also found that water levels during one growing season may influence tree growth the next year. Lowry (1984), for example, found significant relationships between annual radial growth and the previous year's water regime at four of six Rhode Island red maple swamps, and concluded that both current-year and antecedent water levels were important. Phipps (1979) also emphasized the importance of water-level lag effects on tree growth.

Average radial growth rates reported for red maples in northeastern forested wetlands range from less than 1.0 to more than 4.0 mm/year (Vosburgh 1979; Lowry 1984). As illustrated in Fig. 5.1, growth rates in mature swamp forests in Rhode Island (average age 55–105 years) varied considerably among sites and among years, but the pattern of year-to-year variation in growth frequently was similar. In Lake Champlain swamps, annual vari-

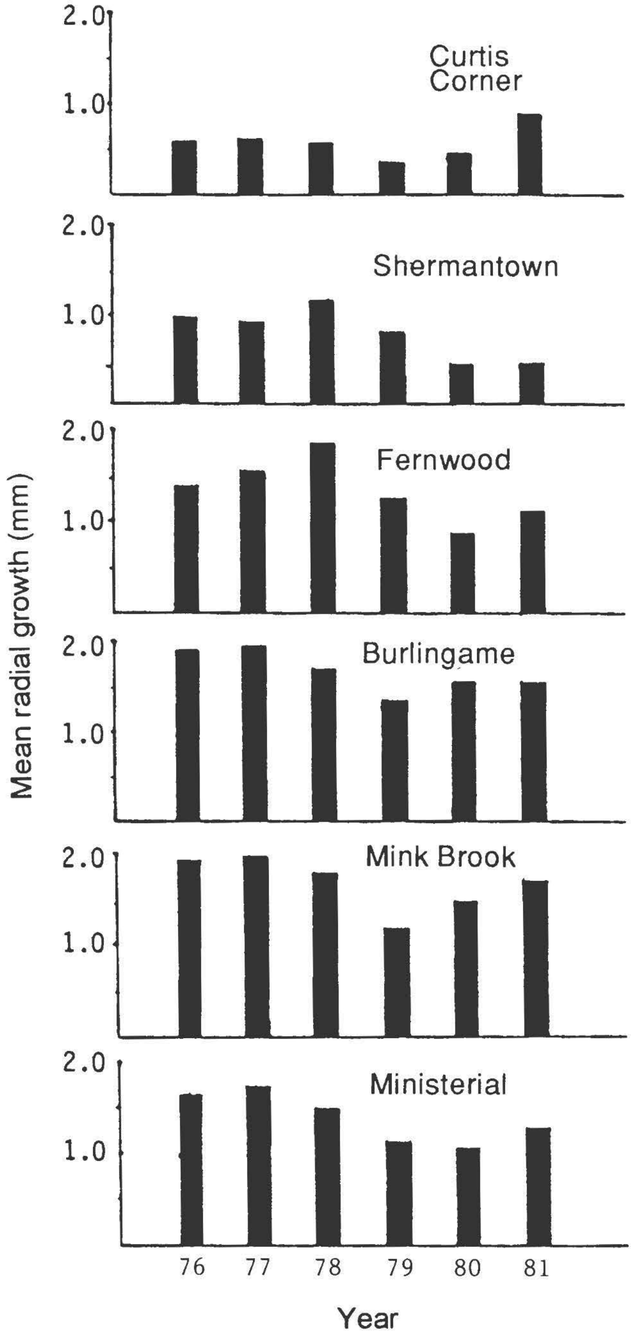

Fig. 5.1. Annual radial growth of red maple in six Rhode Island swamps from 1976 through 1981 (after Lowry 1984). Data are based on 30 trees per site, two increment cores per tree.

ations in growth were also pronounced (Vosburgh 1979). Generally, variation was least on the lowest and wettest sites; trees on slightly more elevated sites with shorter hydroperiods showed more growth response to annual hydrologic variations.

Research at Lake Champlain and in Rhode Island suggests that tree growth is greatest in those years when mean water levels approach the long-term site average. Water levels in Lake Champlain were considered to be normal from 1957 to 1968, but abnormally high from 1969 to 1976 (Vosburgh 1979). Tree growth was greater during the period of normal water levels (Table 5.1), and variations in growth over that time interval were most strongly correlated with tree or stand characteristics. During years of abnormally high water levels, tree growth was most strongly influenced by hydrology. At five of the six Rhode Island swamps studied by Lowry (1984), greatest growth occurred during years when the average annual (April–December) water level was closest to the 6-year mean (Fig. 5.2). Evidently, the trees were well adapted to the average water level conditions at the individual sites, and departures from those average conditions, either markedly wetter or drier, resulted in diminished growth. Site-specific adaptation by trees also may explain why the between-year growth trends shown in Fig. 5.1 were similar at the various sites, even though average water levels differed significantly among sites in most years.

In a study of artificial permanent flooding in Tennessee, Hall and Smith (1955) found that red maples remained healthy if the root crowns were flooded for less than 37% of the growing season; flooding for more than 41% of the growing season resulted in the death of all trees within a few years. Studies in the glaciated Northeast generally support these findings. Red maple growth in Lake Champlain swamps declined when root crowns were submerged for more than 50% of the growing season, on the average (Vosburgh 1979).

Table 5.1. *Annual radial growth of red maple trees in relation to surface-water hydroperiod in 10 Lake Champlain wetlands between 1957 and 1976. Values in parentheses are ranges of annual means (from Vosburgh 1979).*

	Mean annual growth (mm)	Mean seasonal duration of flooding, May–September (days)	Percentage of growing season flooded
1957–68[a]	3.73	32	21
	(3.13–4.19)	(1–52)	(1–34)
1969–76[b]	2.68	80	52
	(1.65–3.36)	(40–121)	(26–79)

[a] Period of normal water levels.
[b] Period of abnormally high water levels.

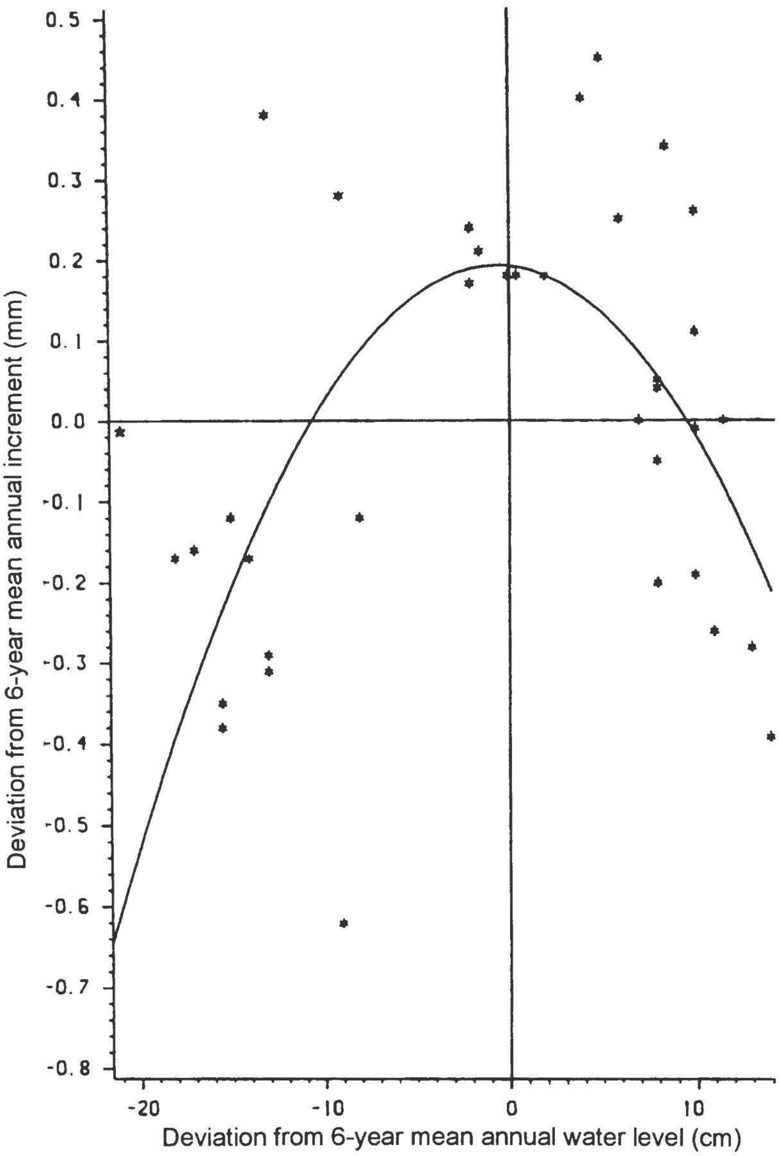

Fig. 5.2. Relationship between annual radial growth of red maple and mean annual water level in six Rhode Island red maple swamps from 1976 through 1981 (after Lowry 1984). Each point represents one year's data from one swamp.

In Rhode Island, even though crowns of tree roots were never completely submerged, radial growth was significantly greater in swamps with surface water persisting for less than 40% of the growing season than in swamps with longer hydroperiods (Lowry 1984). Malecki et al. (1983) found a reduction in radial growth of red maple in New York green-timber impoundments that held 25–30 cm of surface water until early July (roughly 50% of the growing season) over a 12-year period. Although a marked increase in growth occurred during the first 3 years of flooding, a sharp decline was observed by the fourth year (Golet 1969). These results again suggest that tree growth in any particular year may be influenced by water level conditions in preceding years.

Tree, stand, and site characteristics other than water regime may also account for a large proportion of the variability in tree radial growth. Over a 20-year period, red maple growth in Lake Champlain swamps was most highly correlated with tree age (Vosburgh 1979). In Rhode Island, stand density, crown cover, and groundwater pH all appeared to be important (Lowry 1984). Radial growth of red maple trees is also affected by stand origin (Leffelman and Hawley 1925; Braiewa 1983). Braiewa demonstrated that radial growth of red maples from sprout-origin stands exceeded that of trees from seedling-origin stands for about 25 years, but then fell behind as the stands matured. Established root systems permit initially rapid growth in sprout-origin stands, but competition between

Table 5.2. *Mean aboveground biomass values (kg/ha) for northeastern red maple swamps.*

Characteristic	Rhode Island: Braiewa (1983)	New Jersey (nonglaciated): Reynolds et al. (1978)	Ehrenfeld and Gulick (1981)	Ehrenfeld (1986)		
No. of sites	3	1	5	4[a]	4[b]	2[c]
Tree ages (year)	32–55	87–148	46–104			
Total tree biomass	133,116	316,104	150,500	137,943	146,534	130,322
(% red maple)	(100)	(93.5)	(79.8)	(68.0)	(58.6)	(78.6)
Red maple biomass	133,116	295,235	120,060	93,776	85,832	102,380
Trunks	68,925[d]	253,283				
Branches	42,430	40,268				
Foliage	18,221[e]	1,444				
Other tree biomass						
Nyssa sylvatica		13,387	18,560	26,465	25,100	16,656
Magnolia virginiana		7,182	5,860	15,033	2,265	
Chamaecyparis thyoides				2,644	17,739	2,947
Sassafras albidum			260	21	2,888	
Pinus rigida			3,400		6,418	8,242
Shrub biomass			5,838	8,089	3,478	1,897
Herb biomass			146	195	53	353

[a] Wet hardwood swamps (surface water during summer).
[b] Dry hardwood swamps (no surface water during summer).
[c] Floodplain swamps.
[d] Stemwood >10.1 cm in diameter.
[e] Includes branches <2.5 cm in diameter.

sprouts emerging from the same root system and greater susceptibility to decay (Berry 1977) cause reduced growth in later years.

Biomass and Net Primary Productivity

Studies examining biomass or productivity in northeastern red maple forested wetlands are limited to one in Rhode Island (Braiewa 1983; Braiewa et al. 1985) and three in the New Jersey Pine Barrens (Reynolds et al. 1978; Ehrenfeld and Gulick 1981; Ehrenfeld 1986). Table 5.2 consolidates the biomass data from these studies. Overall, average values for the forest overstory ranged from 133,116 to 316,104 kg/ha. The exceptionally high mean value (316,104 kg/ha) reported by Reynolds et al. (1978) was probably due to the advanced age of the trees (87–148 years); this figure is near the upper end of the range reported for forested wetlands in the United States (Brown et al. 1979). Overstory biomass values obtained by Ehrenfeld (1986) and Braiewa (1983) are near the low end of the reported range for forested wetlands, but are comparable to values from other temperate forests (Ovington 1965).

Estimates of belowground tree biomass have not been made for red maple swamps in the Northeast. Brown et al. (1979) indicated that belowground biomass may range from as little as 3% to as much as 51% of aboveground biomass in forested wetlands. In a red maple–black gum stand located in the Virginia section of the Great Dismal Swamp, belowground biomass was estimated to be 12,216 kg/ha, or 6% of the aboveground biomass (Dabel and Day 1977) . The upper 30 cm of soil contained the great bulk (80%) of the belowground biomass, a finding visually confirmed by Lowry (1984) while inspecting red maple root systems in Rhode Island swamps.

Southern New Jersey studies by Ehrenfeld and Gulick (1981) and Ehrenfeld (1986) provide the only estimates of shrub and herb biomass in northeastern red maple swamps. These strata, even when dense, compose a relatively small fraction (2,000–13,000 kg/ha) of the total forest biomass at individual sites. In comparison to figures for upland forests (Whittaker et al. 1974), however, shrub and herb biomass values for red maple swamps may be relatively high.

Annual rates of biomass production for red maple in most northeastern swamps range from about 3,000 to 4,200 kg ha^{-1} $year^{-1}$ (Reynolds et al. 1978; Braiewa 1983; Ehrenfeld 1986). Total overstory production in 10 red maple swamps in New Jersey studied by

Ehrenfeld (1986) was consistent, ranging only from 4,031 to 4,562 kg ha^{-1} $year^{-1}$. Trees accounted for 61–80% of the overall net primary production (NPP), while the shrub layer contributed 13 to 36% and the herb layer 1 to 6%. Annual tissues accounted for 52–62% of the NPP, and the biomass/NPP ratio ranged from 22 to 26. Belowground production was not estimated. Total biomass (trees, shrubs, and herbs) production values calculated for red maple swamps by Ehrenfeld (5,434–6,643 kg ha^{-1} $year^{-1}$) lie toward the low end of the range for forested wetlands in the United States (4,830–17,880 kg ha^{-1} $year^{-1}$; Brinson et al. 1981a). In contrast to results reported by others (e.g., Brown et al. 1979; Brinson et al. 1981a), Ehrenfeld found that floodplain swamps had lower NPP than nonfloodplain swamps.

Organic Matter Decomposition and Nutrient Cycling

Factors Affecting Decomposition Rates

There has been no research on organic matter decomposition and nutrient cycling in northeastern forested wetlands. The most comprehensive data on these processes come from the Virginia section of the Great Dismal Swamp (Day 1982, 1983; Gomez and Day 1982). Whereas the longer growing season and warmer climate in Virginia may increase decomposition rates above those of the Northeast (Bray and Gorham 1964; Brown et al. 1979; Brinson et al. 1981a), similarities in hydrologic regime and soil pH between the Dismal Swamp and many northeastern red maple swamps (Brinson 1977; Day 1982) suggest that the Virginia findings may be applicable to at least the southern portion of the glaciated Northeast.

There is general agreement that the rate of organic matter decomposition is determined principally by the quality of the litter, in combination with climate (Meentemeyer 1978; Brinson et al. 1981a; Day 1982). Relative proportions of refractory (resistant) and labile (unstable) material in the litter layer normally determine the initial decay rate, other factors being equal (Godshalk and Wetzel 1978). Decay is generally retarded by high tannin or tannic acid content, high lignin content, and a high C/N ratio (Day 1982). Limited data (Meentemeyer 1978; Day 1982) indicate that red maple

Fig. 5.3. Red maple leaf litter on the floor of a seasonally flooded alluvial swamp in early spring. Decomposition is retarded by high tannin and lignin content, as well as low temperature and low pH.

litter (Fig. 5.3) is relatively high in value for all of these features.

In the seasonally flooded Great Dismal Swamp, red maple leaf litter decayed about 37% after 1 year and 46% after 2 years (Day 1982). Maple wood decomposed only 16% the first year and 27% in 2 years. Decomposition rates of red maple litter placed in litter bags in maple–gum stands were not significantly different from decomposition rates for red maple litter placed in Atlantic white cedar swamps, mixed hardwood (*Quercus* spp.) forests, or baldcypress (*Taxodium distichum*) swamps, suggesting that litter composition was the primary factor controlling decay rate (Day 1982).

Temperature, water regime, and pH are other important factors influencing decomposition rates. Brinson et al. (1981a) suggested that temperature is probably the single most important variable when moisture and oxygen availability are not limiting. Although a clear relation between decomposition rates and hydrologic regime is difficult to demonstrate, the usual assumption is that rates are lowest under continuously anaerobic conditions. Decay rates tend to increase when aerobic and anaerobic conditions alternate, and they are probably greatest when, along with some degree of wetting and drying, aerobic conditions prevail (Brown et al. 1979; Brinson et al. 1981a; Gomez and Day 1982). Gomez and Day (1982) suggested that alternating periods of exposure and inundation promote pulses of decay and nutrient release.

In contrast to the above, Day (1982) found the decomposition rate of red maple litter to increase with the duration of flooding. He noted that soil pH and nutrient concentrations were higher at flooded sites than at dewatered sites and hypothesized that the higher decay rates stemmed from the more favorable substrate conditions for microbial decomposers. These contradictory findings underscore the need for additional research on the complex relationships among the various factors influencing decomposition rates of red maple litter (i.e., litter composition, water regime, temperature, and other physicochemical conditions).

Oxygen levels in northeastern swamp soils vary seasonally. Decomposition rates in most swamps are probably greatest during mid to late summer, when temperatures are highest and both soils and litter are most likely to be aerobic. The rate of decomposition may also vary among years, along with variations in swamp water levels.

Nutrient Cycling

Biogeochemical cycles in wetlands are complex, at least partly because of the varied influence of groundwater and surface-water hydrology, continuous changes in soil and water oxygen levels, seasonal metabolic changes, and anthropogenic influences. Obtaining even a simplified understanding of cycling for key nutrients (e.g., N, P, Ca, K) requires information on nutrient sources and transport into the ecosystem, potential sinks within the wetland, and transfer rates of nutrients between the major compartments (soil, plants, water) of the system. An understanding of the controlling factors for each of these processes also is required (Richardson et al. 1978). Constructing a nutrient budget that accurately portrays the cycling in any wetland system is difficult; no such research has been conducted for northeastern red maple swamps. General discussion of nutrient cycling in natural wetlands can be found in Richardson et al. (1978), van der Valk et al. (1979), Nixon and Lee (1986), and Bowden (1987), among others. We recommend these publications for an overview of key pathways.

Many of the processes observed in nonforested wetlands or in forested wetlands outside the Northeast clearly occur in northeastern red maple swamps as well (see Fig. 5.4), but the relative magnitude of the various components in these cycles is unknown. Important sources of both N and P include surface-water and groundwater inflow and atmospheric deposition. Nitrogen fixation also may contribute significant loadings of N in some wetlands (summarized in Nixon and Lee 1986), but the significance of this process in red maple swamps is unknown. Potential nutrient removal processes (i.e., sinks) within swamps include sedimentation (burial of particulate and adsorbed fractions), denitrification (the biochemical reduction of nitrate to nitrogen gas), and chemical complexing of phosphorus with ions such as iron to form insoluble compounds (van der Valk et al. 1979; Nixon and Lee 1986). The seasonal uptake of nutrients by higher plants and microbes temporarily detains these elements, and may result in transformations from inorganic to organic forms.

Nutrients taken up by vegetation may be returned to the water or soil through leaching, litter fall, or root excretions. Many studies in wetlands have demonstrated significant losses of certain soluble minerals from plant tissues within a few days or weeks after senescence (Willoughby 1974, cited in Day 1983; Boyd 1970; Mason and Bryant

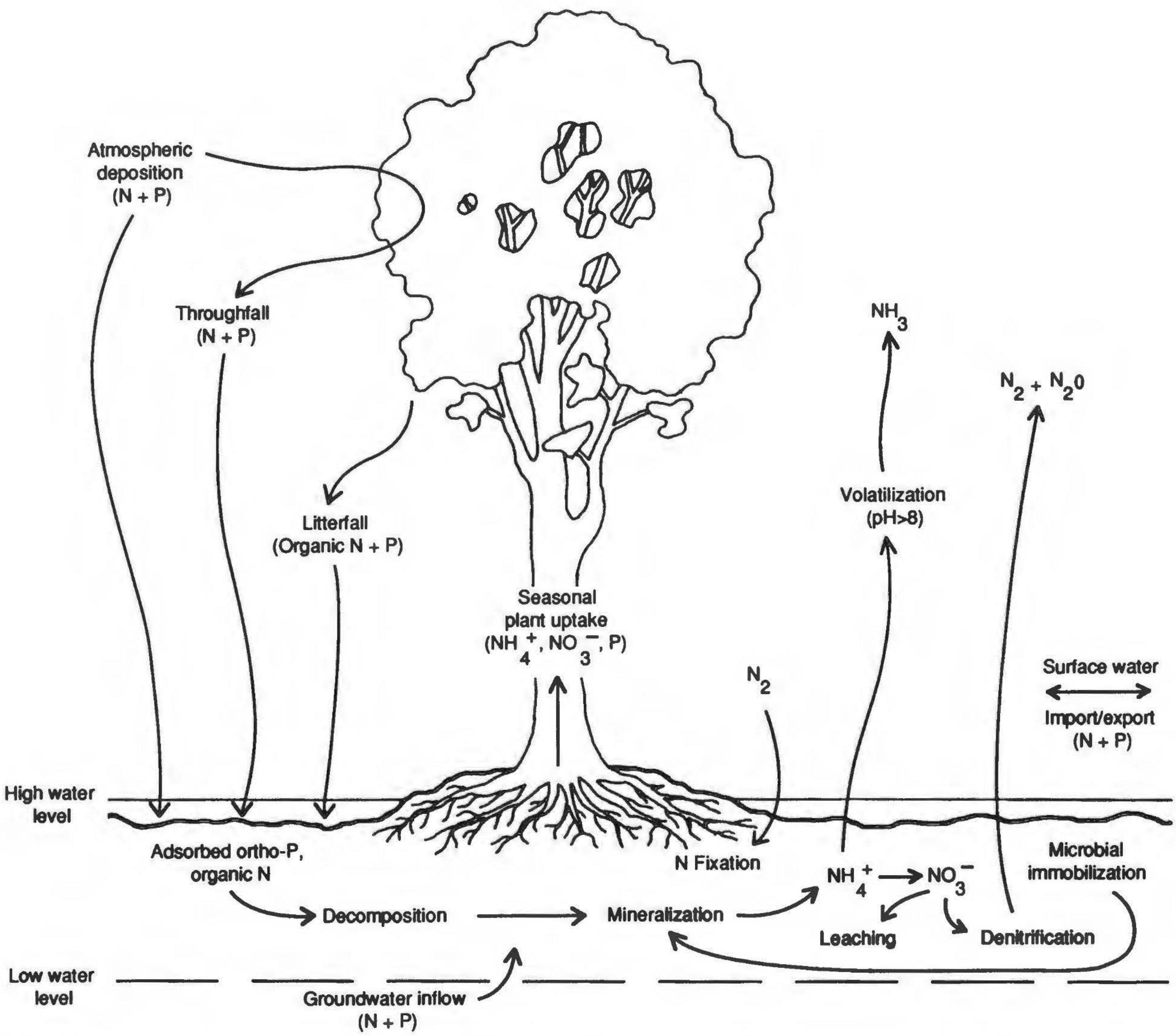

Fig. 5.4. Nutrient-cycling processes and pathways in a red maple forested wetland (modified from Brinson et al. 1981c).

1975; Davis and van der Valk 1978; Brinson et al. 1981b). Such losses are generally attributed to passive leaching; however, rapid mineralization of labile material also contributes to the losses (Brinson et al. 1981b). No data on nutrient cycling in northeastern wetland forests are available; at present, nutrient data are limited to concentrations in various plant tissues or organic soil material.

Nitrogen concentrations of red maple leaf and new twig tissues (1.70 ± 0.12% of dry weight) and

Table 5.3. *Nutrient concentrations (μg/g) in the tissues of red maple trees from New Jersey swamps (from Reynolds et al. 1978).*

Tissue	N	K	Ca	Mg	P	Na	Mn	Fe	Zn
Stem	1,680	978	2,470	199	220	41	21	19	4
Branch	7,400	2,355	3,961	314	580	27	20	8	3
Leaf	18,340	6,575	2,605	795	1,050	41	3	9	7

Table 5.4. *Nutrient concentrations (μg/g) in litter and surface peat from a Connecticut red maple swamp (from Damman 1979 and Laundre 1980).*

Sample	K	Na	Fe	Mn	Pb	Zn	Cu	Ni
Leaf litter	2,687	168	77	845	12	125	7	2
Surface peat	373	147	1,822	25	30	28	8	10

stems (0.54 ± 0.12%) reported by Ehrenfeld (1986) for southern New Jersey red maple swamps fall within the general range reported for other swamps and floodplain forests. Additional data on the nutrient content of red maple stem, branch, and leaf tissues from New Jersey swamps are provided in Table 5.3.

Damman (1979) and Laundre (1980) found higher concentrations of K, Mn, and Zn in red maple leaf litter of a Connecticut swamp than in the upper 40 cm of organic soil beneath, but found higher levels of Fe, Pb, and Ni in the soil; levels of Na and Cu were similar in the two compartments (Table 5.4). These data suggest that K, Mn, and Zn are readily taken up by the vegetation and rapidly cycled, enriching the surface of the swamp annually.

The initial leaching of ions from litter often reverses with time, as concentrations of many minerals subsequently increase there (van der Valk et al. 1979). Immobilization of nutrients by microbes associated with decomposing plant material has been demonstrated or inferred in many wetland studies (Mason and Bryant 1975; Brinson 1977; Day 1982). In the Great Dismal Swamp, litter concentrations of N and P remained unchanged or increased over a 1-year period, while K levels decreased initially and then increased (Day 1982). These data suggest there was active immobilization of nutrients from external sources and net mineralization of Ca and Mg. Laboratory studies also have shown that, without accrual of nutrients from external sources, N and P levels in decomposing red maple leaf litter continue to decline (Day 1983). In studying a North Carolina water tupelo (*Nyssa aquatica*) swamp, Brinson (1977) concluded that element accumulation through immobilization appeared to be an important mechanism for trapping nutrients that might otherwise exist in dissolved form and be exported. He found that immobilization generally lasted beyond spring months, making the nutrients available for plant uptake during the growing season.

There has been so little research on nutrient cycling in northeastern forested wetlands that it is possible to develop only a very simplified scenario of some of the seasonal processes that occur in these swamps (Fig. 5.4). As with most wetlands, the extent to which red maple swamps retain and cycle nutrients is strongly influenced by hydrology, which has pronounced seasonal variability. Both leaching and immobilization of nutrients from external sources may occur from fall into spring. Hydrologic events clearly can influence the magnitude and timing of these processes; flushing events, which remove detritus, or backwater flooding, which brings enriched waters into the wetlands, are examples. Streams carrying suspended sediments and dissolved nutrients overflow into many swamps during flood periods. As water velocities decrease in the wetlands, suspended particles and adsorbed constituents (e.g., phosphorus and heavy metals) settle to the soil surface, and dissolved nutrients in the water may diffuse within the soil and detrital layers. Surface water runoff from surrounding upland areas also may contribute significant loadings to wetlands (van der Valk et al. 1979). The following are conservative estimates for annual nutrient and metal removal via sediment deposition in 1 m^2 of northeastern wetland soils: N, 1.5 g; P, 375 mg; Cu, Pb, and Zn, 25 mg; Cd, 0.2 mg; and Hg, 0.2–2.5 mg (Nixon and Lee 1986). Soil adsorption, immobilization by microbial decomposers, algal uptake, denitrification, and chemical complexing (e.g., as ferric phosphate) may all influence nutrient pathways during the dormant season (Richardson et al. 1978; Brinson et al. 1981a,b).

With the onset of the growing season and warmer conditions in a red maple swamp, increased decomposition of organic matter speeds the release of nutrients at the same time that plant uptake increases. Heightened evapotranspiration gradually lowers the water table, typically to a point within, or just below, the root zone. As a result, soil oxygen levels increase, and soil chemical and biochemical processes are affected. Brinson et al. (1981b), for example, noted that, during dry periods in swamps, ammonium (NH_4+) can be converted to nitrate (NO_3-), thus permitting denitrification during subsequent wet periods. Most forested wetlands in the Northeast appear to have suitable conditions for denitrification (i.e., periodically or continuously anaerobic substrate with high organic carbon content), but the process has received little study (Nixon and Lee 1986; Groffman et al. 1991).

Research is needed on all aspects of nutrient cycling in red maple swamps. Prime topics for study include the following:

- principal sources of nutrients for plant growth (i.e., cycling within the swamp vs. external sources)
- influence of geomorphic setting on nutrient inputs and export
- rates of nutrient uptake and translocation by plants
- extent to which N or P limit productivity
- relative importance of N fixation and denitrification
- role of root processes in nutrient cycling
- role of animals in nutrient cycling

Detritus Export and Food Chain Support

Organic detritus that is not fully decomposed and nutrients that are not immobilized in forested wetlands are available for export to adjacent surface waters. Brinson et al. (1981b) have shown that rivers that drain watersheds with extensive areas of bordering wetlands contain more organic material (dissolved and total organic carbon) than rivers in watersheds without such wetlands. Dissolved materials are believed to originate through leaching of litter and organic soil materials during wetland inundation. Organic carbon exported from swamps in both particulate and dissolved forms may serve as an energy source for consumers in adjacent riverine or lacustrine ecosystems, but studies documenting detrital export and trophic pathways are lacking for red maple swamps.

Many red maple swamps in the glaciated Northeast are hydrologically linked to streams, lakes, or estuaries. The linkage may take the form of overland flow through the wetland during storms or after snowmelt; groundwater discharge and subsequent flow through the swamp; or inundation,

Fig. 5.5. Red maple swamp along a perennial stream. Such alluvial swamps may receive sediment and nutrients from the stream during annual floods and export both nutrients and organic detritus to the stream as floodwaters subside.

followed by recession, of floodwaters from an adjacent stream or lake (Fig. 5.5). No studies have addressed either the export of detritus or nutrients from red maple swamps to adjacent water bodies or the influence of such export on aquatic food chains.

The likelihood of significant export depends on the strength of the hydrologic coupling between the swamp and adjacent aquatic systems; key factors include the frequency, duration, depth, and velocity of floodwaters, as well as the volume and duration of the surface-water discharge from the swamp. However, since cumulative inputs from numerous wetlands in many subwatersheds determine the characteristics and functions of lower perennial riverine systems, even relatively small wetlands with only intermittent surface-water discharge may play a significant role in nutrient export and food chain support.

Chapter 6. Wetland Dynamics

Most northeastern freshwater wetlands originated during the Wisconsin glacial stage more than 12,000 years ago. Since then, changes in climate, together with the accumulation of mineral sediments and peat, have brought about gradual changes in wetland water regimes, soil properties, microrelief, vegetation structure, and plant and animal community composition. Sudden changes in wetlands have also resulted from fire, windstorms, beaver pond construction, and human activities such as vegetation clearing and water level manipulation. Because changes in the biotic and abiotic features of wetlands may effect changes in wetland functions and values, an understanding of wetland dynamics is essential to effective management of this resource. This chapter gives an overview of freshwater wetland dynamics in the glaciated Northeast and describes the dynamics of red maple swamps in that broader context.

Basic Concepts and Processes

Succession, Climax, and Wetland Dynamics

Under the monoclimax theory of plant succession introduced by Frederick Clements (1916), plant communities were believed to succeed each other in an orderly, progressive fashion until a self-perpetuating climax stage was reached. Wetlands were viewed merely as steps in a "hydrarch" successional sequence that would eventually culminate in a terrestrial (nonwetland) climax community. Ecologists such as Whittaker (1953) took issue with this theory, suggesting instead that there might be several stable terrestrial vegetation types (multiple climaxes) in a particular region, depending on edaphic conditions. More recently, Niering (1987) emphasized that, because of natural and human-induced disturbances, changes in plant communities are not undirectional, in contrast to what Clements (1916) suggested. Niering observed that vegetation change can lead to either a relatively stable system or a constantly changing system, depending on the frequency and scope of disturbance. He recommended abandoning the term "succession" because of its Clementsian connotations, and substituting terms such as "vegetation dynamics" or "vegetational development." Some scientists (e.g., van der Valk 1981) continue to use the term "succession," but define it more broadly to avoid confusion with Clements' use.

The concept of climax has been abandoned by most ecologists, and, along with it, the notion that wetlands eventually become terrestrial or nonwetland communities (Moizuk and Livingston 1966; Daubenmire 1968; Huenneke 1982; Niering 1988). There is no scientific evidence to show that wetland changes to nonwetland under natural conditions, except in the case of landslides, shifting sand dunes (Larson et al. 1980), or other rare events. In the glaciated Northeast, forested wetland is the most advanced stage of vegetation development on freshwater sites. Forested wetland soils are unsuitable for the growth of most upland tree sp cies because of their high moisture content, high organic content, low nutrient availability, and other limiting properties (Daubenmire 1968; Niering 1988). For these reasons, forested wetlands can be expected to persist indefinitely, as long as they are not filled, drained, or otherwise altered. The presence of several meters of woody peat in some northeastern wetland forests indicates not only that these sites have been swamps for thousands of years, but also that the groundwater table in these wetlands has gradually risen along with the accumulation of this organic material.

Changes in wetlands may be viewed broadly, from an ecosystem perspective, or more narrowly, from a plant community perspective. In this report, the term "wetland dynamics" is used to describe changes at the ecosystem level—generally changes from one class of wetland (sensu Golet and Larson 1974 or Cowardin et al. 1979) to another. Wetland dynamics entail changes in water regime, dominant life form of vegetation, and often soils. The term "vegetation dynamics" is restricted here to changes in plant community structure and floristics.

Directions of Wetland Change

Most changes in northeastern wetland ecosystems may be categorized as either progressive or retrogressive. Progressive change usually involves an increase in the structural complexity of the dominant vegetation, together with a decrease in site wetness. Common examples include changes from aquatic beds to emergent wetlands, from emergent wetlands to shrub wetlands, and from shrub wetlands to forested wetlands. In some cases, such as in the change from shrub swamp to forested swamp, a decline in wetness may not be readily apparent; in other cases (e.g., change from marsh to wet meadow), there may be an obvious change in water regime, but only a minor change in dominant vegetation life form. In both of these examples, however, the change can be characterized as progressive.

Sedimentation and peat accumulation in wetland basins are primary natural agents of progressive change; artificial lowering of water levels generally accelerates the progression. The rate of change is determined partly by the initial wetland type and its hydrologic regime, partly by factors such as sedimentation rate and nutrient levels, and partly by the frequency and duration of disturbance. In the absence of major disturbance, freshwater wetland changes in the glaciated Northeast are predominantly progressive (Larson et al. 1980; Golet and Parkhurst 1981; Organ 1983).

Retrogressive changes represent a reversal of the progressive pattern. They usually involve a decrease in the structural complexity of the dominant vegetation. Examples include changes from forested wetland to shrub wetland; from forested or shrub wetland to emergent wetland; and from forested, shrub, or emergent wetland to aquatic bed. Retrogressive change is invariably brought about by some form of disturbance, such as impoundment of water by humans or beavers, fires, windstorms, or logging; as a result, the change is often abrupt. A rise in the average wetland water level is frequently associated with retrogressive change. Such a rise may be the cause of the change, as in impoundment, or the result, as in reduced evapotranspiration caused by clearcutting a swamp forest. Examples of retrogressive changes are common throughout the Northeast.

In many cases, it is not possible, by simply viewing a plant community, to determine which direction change is taking, or if it is occurring at all (Egler 1947). In other cases, short-term progressive changes may alternate with short-term retrogressive changes so that the overall pattern appears to be cyclic. Long-term patterns of wetland change may be impossible to determine, given the randomness of many natural phenomena and changing patterns of human land use. For these reasons, the terms "progressive" and "retrogressive" are most appropriately applied to short-term changes from one wetland type to another, where the direction of change is clearly evident.

Short-term changes among wetland classes are often predictable if certain information is available, namely: (1) the species composition and structure of the current plant community; (2) the ecological tolerances of current species; (3) current environmental conditions such as water regime, soil type, substrate stability, and water chemistry; and (4) the degree and duration of the change in environmental conditions that is expected to occur. Changes in species composition within a wetland community occasioned by subtle changes in environmental conditions may be more difficult to predict. Van der Valk (1981) developed a model for forecasting such species changes in wetlands; it is based primarily on a knowledge of the factors listed above, as well as a knowledge of the composition of the wetland seed bank and the life history traits of both current and seed-bank species.

Wetland Dynamics in Southern New England: An Overview

Although there has been considerable debate over the details and predictability of wetland dynamics (Niering 1987), few research results are available to document the nature of these changes. Time-lapse studies of aerial photographs from Massachusetts and Rhode Island provide the clearest picture of short-term wetland change (20–33 years) in the glaciated northeastern United States. Mueller (1974) examined changes in the nonforested freshwater wetlands of Bristol County, Mass., between 1951 and 1971. Parkhurst (1977) detailed the changes in freshwater wetlands in South Kingstown, Rhode Island, between 1939 and 1972. These studies have been summarized by Larson et al. (1980), Golet and Parkhurst (1981), and Larson and Golet (1982). Organ (1983) described the dynamics of freshwater wetlands between 1951 and 1975–77 for 15 cities and towns scattered across the State of Massachusetts. In the

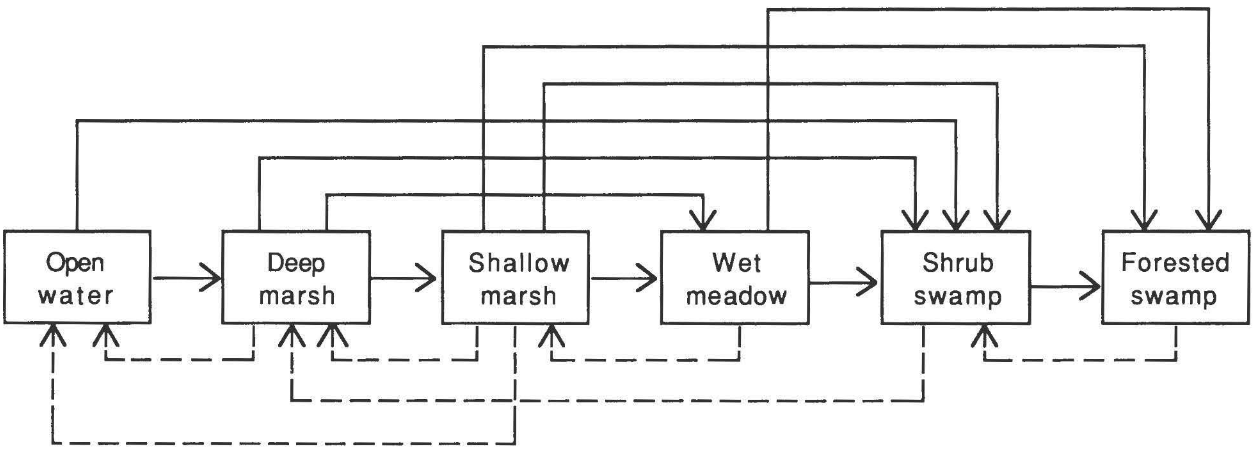

Fig. 6.1. Major changes in southern New England freshwater wetlands over a 20- to 33-year period (based on Larson and Golet 1982 and Organ 1983). Progressive changes are indicated by *solid lines*, retrogressive changes by *dashed lines* (classification according to Golet and Larson 1974).

following paragraphs, we review the major findings of these three studies. We describe only changes from one type of wetland to another; information on wetland losses (i.e., conversion to upland) is provided in a subsequent chapter.

Despite the relatively short periods examined in these studies, the extent of wetland change was dramatic. Overall, nearly 20% of the original wetland area changed classification (Golet and Parkhurst 1981; Organ 1983). In both Rhode Island and Massachusetts, more than 70% of the change was progressive. Retrogressive changes were most often caused by beavers or humans, chiefly through the raising of water levels.

The model in Figure 6.1 summarizes the major changes observed in these time-lapse studies. In all cases, there was a predominantly progressive flow from open water and emergent wetland toward shrub and forested wetland. Certain classes, such as forested swamp, open water, and deep marsh, exhibited relatively little change (Table 6.1). About 95% of the forested wetland that was present at the beginning of the study periods was unchanged at the end. This is not surprising,

Table 6.1. *Degree of change of southern New England freshwater wetland types during the recent past. Values are the percentage of the original area of each type that changed to another type during the study period. Changes from wetland to upland (i.e., wetland losses) are not included here.*

Wetland type[a]	Bristol County, Massachusetts (1951–71)[b]	S. Kingstown, Rhode Island (1939–72)[c]	15 towns, Massachusetts (1951–77)[d]
Open water		18	7
Aquatic bed			34
Deep marsh	17	11	
Shallow marsh	53	82	
Wet meadow	32	59	
Emergent wetland			76
Seasonally flooded flats	32		
Shrub wetland			66
Shrub swamp	60	37	
Forested wetland		5	4

[a] Wetland types are described by either Golet and Larson (1974) or Cowardin et al. (1979).
[b] Study by Larson et al. (1980); forested wetlands were not inventoried.
[c] Study by Golet and Parkhurst (1981).
[d] Study by Organ (1983).

since forested wetland is the endpoint of freshwater wetland development in the Northeast. Open water and deep marsh are also relatively stable classes, at least over short periods, simply because of their considerable water depth.

Shallow marsh, wet meadow, and shrub swamp were highly dynamic. From 30 to 80% of the original acreage of these intermediate wetland types changed classification during the 20- to 33-year study periods (Table 6.1). The dynamic nature of these wetlands can be explained, at least partially, by their similar water regimes; typically, they are seasonally flooded or seasonally saturated, as in the case of forested wetlands. As a result, changes among these classes (and from these classes to forested wetland) may occur relatively quickly, especially if factors retarding change, such as mowing or grazing, are discontinued.

Not only is there a high rate of change in the intermediate wetland classes, but these classes are also declining in abundance regionally (Larson et al. 1980; Golet and Parkhurst 1981; Organ 1983). Conversely, the more stable wetland types, particularly open water and forested swamp, have increased in abundance in most cases. Two major factors responsible for the change in abundance of the various wetland types are the decline of agriculture in the Northeast and the construction of impoundments for water supply, recreation, or irrigation. Abandonment of agriculture has caused formerly cleared wetlands to advance to shrub swamp and forested swamp. That pattern of change, which began in the mid-1800's, is still significant more than 100 years later. The increase in open water resulting from human activities is a nationwide phenomenon (Frayer et al. 1983; Tiner 1984) that is augmented in some parts of the Northeast by the increasing abundance of beaver ponds (Organ 1983).

Dynamics of Red Maple Swamps

In southern New England, significant areas of emergent wetland and shrub wetland have developed into forested wetland since 1940. Golet and Parkhurst (1981) calculated a 7% increase in red maple swamp over a period of 33 years in Rhode Island. Organ (1983) estimated the increase in all forested wetland types in Massachusetts to be 11% over 20 years. By comparison, retrogressive changes in forested wetlands have been relatively minor. Beaver pond construction (Organ 1983), the creation of ponds for irrigating cranberries (Tiner and Zinni 1988), and impoundments for waterfowl (Golet and Parkhurst 1981) have converted some forested wetlands to open water, marsh, or shrub swamp. Retrogression from forested swamp to shrub swamp has also occurred as a result of the cutting of trees for fuelwood and utility rights-of-way.

Even though data documenting forested wetland dynamics in other parts of the Northeast are not available, there is reason to believe the changes found in southern New England hold elsewhere. Based on U.S. Forest Service forest inventory data, Abernethy and Turner (1987) estimated that there was a 6% increase in forested wetland in New York between 1940 and 1980. They attributed the increase to abandonment of pastures. Increases in forested wetland were noted for all other northeastern states as well, except for Maine, New Jersey, and Pennsylvania.

Accurate assessment of the effects of land use on red maple swamps requires a thorough understanding of both the processes of swamp development and the conditions that cause these wetlands to change to other wetland types. In the remainder of this chapter, we describe the progressive and retrogressive changes affecting red maple swamps and the successional relationships between red maple and other wetland forest trees.

Swamp Origins and Development

Some red maple swamps occupy deep, peat-filled basins that were lakes during their early history (Beetham and Niering 1961). Before red maple trees could dominate such sites, a series of other wetland types, including aquatic beds, emergent wetlands, and shrub wetlands, would have developed there. Because of the major change in water regime required, the progression from deep, open water to forested swamp would take thousands of years under natural conditions. Other red maple swamps are in shallow basins that originally may have been only seasonally flooded, or on hillsides that probably had a seasonally saturated water regime throughout their postglacial history. In these cases, the vegetated wetlands that first occupied these sites were most likely emergent wetlands (e.g., wet meadows) dominated by grasses, rushes, or sedges. The transition to shrub and forested wetland in these locations could have been rapid, as long as the climate was conducive and seed sources for woody wetland plants were available.

By definition, wetlands must pass through a shrub stage (<6 m tall) before achieving forested status (≥6 m tall). Commonly, this stage is dominated by tall (2–3 m) shrubs such as highbush blueberry, alders, northern arrow-wood, common winterberry, sweet pepperbush, or similar species. In seasonally flooded shrub swamps, red maples typically colonize mounds supporting shrubs, become dominant during the sapling stage, and eventually develop into the overstory of a forested wetland. Red maples may also directly invade wet meadows no longer maintained by mowing, grazing, or burning. They characteristically colonize tussocks formed by sedges such as *Carex stricta* and, soon afterward, develop into a dense sapling swamp with few other shrub species present (Fig. 6.2). Forested swamps developing in this manner may have a poorly developed shrub layer for many years.

The progression from emergent wetland or shrub wetland to red maple forested wetland may be retarded by land use, as noted above, or by water regime. In many areas of the Northeast, red maple saplings can be found in shrub swamps that appear to be relatively stable. Dominated by many of the tall shrubs mentioned above, as well as by swamp azalea, swamp rose, maleberry, fetterbush, and poison sumac, these shrub swamps are so wet throughout the growing season that red maple cannot advance beyond the sapling stage. This wetland type is easily recognized by the predominance of tall shrubs and the presence of scattered maples 2–3 m tall with dead upper branches (Fig. 6.3). These shrub swamps typically occur in groundwater depression wetlands where water levels are high throughout the year; many are associated with

Fig. 6.2. Former wet meadow invaded by red maple. Each stem originates from an individual sedge tussock.

Fig. 6.3. Stunted red maple saplings in a shrub swamp with continuously saturated soil. Constant saturation within the root zone retards the development of forested wetlands.

kettle bogs, lakes, or large rivers. Similarly, development of forested swamps from wet meadows is likely to be slow where the meadows have prolonged surface water hydroperiods or where surface microrelief is poorly developed.

Retrogressive Changes

The conversion of red maple swamp to nonforested wetland is generally precipitated either by a rise in the local water level or by the cutting of vegetation (Fig. 6.4). A permanent rise in the water level that inundates the root crowns of the trees kills virtually all plants in the swamp and converts the wetland to an open water body or deep marsh. Beaver ponds constructed in former red maple swamps typically contain aquatic beds dominated by plants such as white water lily (*Nymphaea odorata*) and bladderworts (*Utricularia* spp.) in the deepest areas; marsh plants such as bur-reeds (*Sparganium* spp.) where the average water depth is 0.5 m or less; and a variety of rushes (e.g., *Juncus effusus*), sedges (e.g., *Carex stricta*), and grasses (e.g., *Glyceria* spp.) in seasonally flooded areas along the margins of the pond (Fig. 6.5). Once a pond is abandoned and the dam breaks, the former flowage is usually first colonized by graminoids (Fig. 6.6), then soon after by shrubs, such as alders and willows, and finally by trees, such as red maple.

When the increase in the swamp water level is gradual, or more limited in extent, trees may die over a period of years. If microrelief in the swamp is well developed, shrubs and herbs, which are more shallowly rooted than the trees, may survive and eventually dominate the site (Fig. 6.4). Such a retrogressive change has been observed where road culverts draining swamps have become clogged with sediment (Golet and Parkhurst 1981). If shallow surface water persists throughout the growing season, floating mats of *Sphagnum* moss may develop locally, providing a base for colonization of the site by bog plants such as leatherleaf (*Chamaedaphne calyculata*) and cranberries (*Vaccinium macrocarpon*).

Clear-cutting of trees causes a red maple swamp to revert to shrub swamp or, less commonly, to emergent wetland (Fig. 6.4). Shallow marshes or wet meadows dominated by ferns and various graminoids are often produced when trees are removed from maple swamps that contain a poorly developed shrub layer or when all woody vegetation is removed. Due to a reduction in transpiration losses at the site after cutting, a local rise in the summer water table may occur. Such an increase in wetness is most likely to occur in

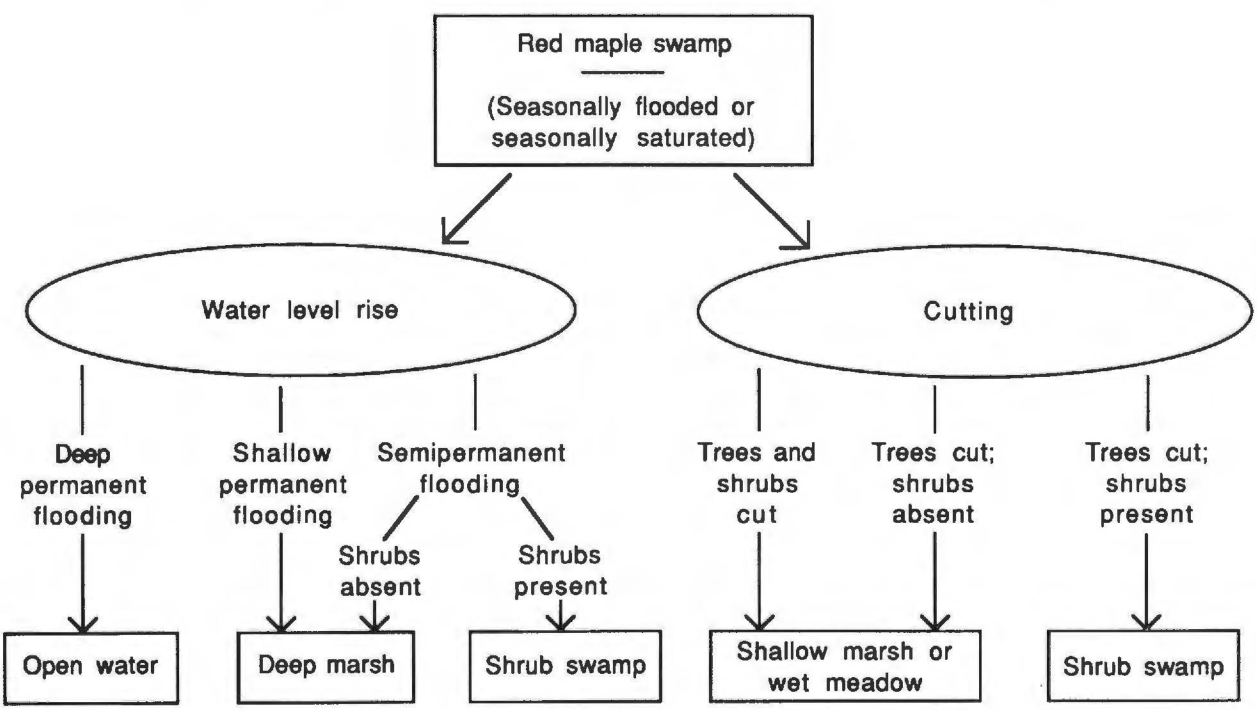

Fig. 6.4. Retrogressive changes in northeastern red maple swamps due to water level rise or cutting.

Fig. 6.5. Active beaver pond constructed in a former red maple swamp. The dominant plant is white water lily (*Nymphaea odorata*).

Fig. 6.6. Recently abandoned beaver flowage dominated by graminoids.

groundwater depression wetlands. Because red maple sprouts prolifically after cutting, cutover swamps usually support a dense cover of maple saplings within a few years, and the progression toward forested wetland resumes. Dense shrub cover may temporarily retard the resurgence of red maple after cutting.

Fire and hurricanes may also be agents of retrogressive change in forested wetlands, but both are relatively unimportant in northeastern red maple swamps. The potential impact of fire is limited by site wetness and by fire protection programs, while hurricane damage tends to be infrequent and highly localized.

Successional Relationships Among Wetland Forest Trees

Grace (1972) argued that red maple lacks the ability to replace itself unless cut, and that in northeastern Connecticut it will eventually lose dominance to eastern hemlock, white pine, or wet-site hardwoods such as yellow birch. Grace also noted that the canopy of red maple stands opens with age and suggested that, if there were no advanced regeneration of other tree species to fill the gaps, even understory shrubs such as sweet pepperbush might assume dominance.

The validity of these assertions is open to debate. The great predominance of red maple swamps throughout major sections of the glaciated Northeast suggests that this wetland type is the normal endpoint of wetland development in these areas. Sprouting frequently occurs in windthrown trees and in trees with decayed stems, as well as in trees that have been cut. In addition, openings in the forest canopy created by tree mortality allow sunlight to reach mounds on the forest floor where red maple seedlings may develop. While species such as hemlock may outcompete red maple on seasonally saturated, poorly drained soils in certain areas of the Northeast, evidence for large-scale future replacement of red maple as the dominant species in northeastern wetland forests is lacking.

The successional relationship between red maple and Atlantic white cedar also is a subject of great interest, especially because of the continuing decline of cedar (Laderman 1987). In his 1950 monograph on Atlantic white cedar, Little stated that, in the New Jersey Pine Barrens, cedar stands are subclimax to a swamp hardwoods association dominated by red maple, black gum, and sweetbay magnolia (*Magnolia virginiana*). He observed that, unless cedar is clearcut in large tracts, it will eventually be replaced by hardwoods because (1) cedar needs open germination sites to achieve the initial growth rate necessary to compete with hardwoods; (2) unlike hardwood stands, cedar stands are typically even-aged, and the trees do not replace themselves under a forest canopy; and (3) rapid growth of hardwood sprouts gives them an advantage over cedar seedlings in forests that are selectively cut.

Research suggests that water regime may be an important factor influencing the rate of conversion from Atlantic white cedar to red maple. In Rhode Island, average surface water hydroperiods are longer, and mean water levels slightly higher, in cedar swamps than in maple swamps (Lowry 1984). Little (1950) also found in greenhouse studies that cedar seedlings were best able to compete with hardwoods where water levels were highest. However, even on unusually wet sites, red maple colonization of mounds is highly likely when canopy openings occur in cedar forests due to tree death, windthrow, or selective cutting. Once red maple is established in an Atlantic white cedar forest, conversion to a maple-dominated swamp appears to be inevitable (Little 1950).

Chapter 7. Vertebrate Fauna

Although red maple swamp is the most abundant freshwater wetland type in much of the glaciated Northeast, relatively little research has been conducted on its fauna and their habitat requirements. This is especially noteworthy because several states (Connecticut, New Jersey, New York, Massachusetts, and Rhode Island) include wildlife habitat as a recognized value of wetlands within regulatory acts.

The vertebrate faunal community of northeastern red maple swamps is large and varied (Appendix C). For the most part, this community is composed of species that select swamps as habitat either on the basis of vegetation structure or on the basis of water regime. Vegetation structure has been shown to be a primary factor in wildlife habitat selection, especially in forested areas (MacArthur and MacArthur 1961; Anderson and Shugart 1974; Miller and Getz 1977a; James and Warner 1982). Water regime is critical for those species that require shallow surface water during part of the year.

No studies have been published on the invertebrate fauna of nonfloodplain forested wetlands of the Northeast. This lack of information merits attention because invertebrates are important as prey of forested wetland wildlife (Getz 1961a; McGilvrey 1968; Clark 1979; Craig 1984). Many aquatic invertebrates found in streams, vernal pools (Kenk 1949; Wiggins et al. 1980), bottomland hardwood forests (Batema et al. 1985; White 1985), and green-timber impoundments (Krull 1969) may occur in red maple swamps as well, but documentation is lacking. Therefore, this profile of the fauna of red maple swamps focuses on vertebrate taxa.

Wetland Dependence of Wildlife

For community analysis and habitat evaluation purposes, it is useful to consider the degree to which various animal species or groups are dependent upon wetlands (Golet 1973). Vertebrate wildlife that inhabit red maple swamps and other types of wetlands can be broadly categorized as either wetland-dependent species or facultative species.

Wetland-dependent Species

Under natural conditions, wetland-dependent species cannot exist without wetlands. Included are two groups that vary in the extent to which they use wetland habitats.

Wetland Species

Species for which wetlands are primary habitat may be considered wetland species. This group lives principally, or exclusively, in wetlands and depends upon wetlands for most or all of its habitat requirements (i.e., food, water, cover, breeding sites). Examples of wetland species that occur in red maple swamps include the wood duck (*Aix sponsa*), American black duck (*Anas rubripes*), northern waterthrush (*Seiurus noveboracensis*), beaver, river otter (*Lutra canadensis*), and mink (*Mustela vison*).

Wetland-dependent Upland Species

These are species such as the spring peeper (*Pseudacris crucifer*), American toad (*Bufo americanus*), wood frog (*Rana sylvatica*), and spotted salamander (*Ambystoma maculatum*), which live primarily in upland habitats but lay their eggs and develop through larval stages in the shallow water of wetlands. Wetlands are as critical to the survival of this group as they are to the wetland species. Red maple swamps provide breeding habitat for many wetland-dependent upland species.

Facultative Species

For the remaining species, the wetness of wetlands is neither a requirement nor a limiting factor. Taxa in this group are generally considered upland wildlife, but they also inhabit wetlands, sometimes in large numbers. Facultative species span a wide range in the extent of wetland use. Many passerine species, such as the gray catbird (*Dumetella carolinensis*), black-capped chickadee (*Parus atricapillus*), common yellowthroat (*Geothlypis trichas*), and black-and-white warbler

(*Mniotilta varia*), regularly breed in both upland habitats and red maple swamps. Others, including several species of warblers, make extensive use of forested wetlands during migration, but breed in uplands. Some facultative species clearly prefer wetlands during winter. In Rhode Island, wild turkeys (*Meleagris gallopavo*) feed in late winter on the sporophylls of sensitive fern in red maple swamps (C. Baker, Department of Natural Resources Science, University of Rhode Island, Kingston, personal communication). Red maple itself is a preferred winter browse of the eastern cottontail (*Sylvilagus floridanus*) (Cronan and Brooks 1968). Additional examples of facultative species that regularly inhabit red maple swamps include the American crow (*Corvus brachyrhynchos*), American robin (*Turdus migratorius*), blue jay (*Cyanocitta cristata*), great crested flycatcher (*Myiarchus crinitus*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), and white-footed mouse (*Peromyscus leucopus*).

Reptiles and Amphibians

Reptiles and amphibians constitute a significant proportion of some northeastern forest animal communities. For instance, in the northern hardwood (American beech-yellow birch-sugar maple) forests of Hubbard Brook, New Hampshire, Burton and Likens (1975) found that the biomass of salamanders was approximately twice that of the breeding bird community, and was roughly equal to the biomass of small mammals. Studies of amphibians and reptiles in northeastern forested wetlands are rare, even though these habitats appear to be of major importance to forest-dwelling species.

DeGraaf and Rudis (1986) identified 45 New England species of amphibians and reptiles that use forest cover at some time during the year. Of the 11 forest cover types reviewed, red maple was the most frequently preferred (by 12 species); it was used, but not preferred, by an additional 30 species (Table 7.1). Because the majority of amphibians require standing water for breeding, vegetation structure may be less important to them than water regime (McCoy 1989). The seasonal flooding of many red maple swamps provides suitable breeding areas for several species and is clearly a prime reason for selection of this habitat type by amphibians and reptiles.

More recently, DeGraaf and Rudis (1990) compared the herpetofauna of three forest cover types in New Hampshire: northern hardwoods, balsam fir, and red maple. All three forest types supported the same number of species of reptiles and amphibians (11); however, relative abundance was significantly higher in red maple and northern hardwood stands

Table 7.1. *Use of red maple swamps by amphibians and reptiles in New England. Habitat suitability for each species is noted either as P = preferred habitat or U = utilized habitat (data from DeGraaf and Rudis 1986).*

Species	Breeding season	Non-breeding season
Amphibians		
Marbled salamander	P	U
Jefferson salamander	P	U
Spotted salamander	P	U
Mountain dusky salamander	P	U
Redback salamander	P	U
Northern slimy salamander	P	U
Four-toed salamander	P	U
Spring salamander	P	U
Northern two-lined salamander	P	U
Pickerel frog	U	U
Northern leopard frog	U	
Silvery salamander		U
Blue-spotted salamander		U
Tremblay's salamander		U
Eastern newt		U
Dusky salamander		U
American toad		U
Fowler's toad		U
Spring peeper		U
Gray treefrog		U
Bullfrog		U
Green frog		U
Mink frog		U
Wood frog		U
Reptiles		
Five-lined skink	P	U
Eastern ribbon snake	P	U
Ringneck snake	P	U
Wood turtle	U	U
Eastern box turtle	U	U
Northern water snake	U	U
Brown snake	U	U
Redbelly snake	U	U
Common garter snake	U	U
Racer	U	U
Rat snake	U	U
Milk snake	U	U
Copperhead	U	U
Timber rattlesnake	U	U
Smooth green snake	U	U
Painted turtle	U	
Snapping turtle		U
Bog turtle		U

Table 7.2. *Relative abundance (%) of reptiles and amphibians captured within or immediately adjacent to red maple swamps in New Hampshire (DeGraaf and Rudis 1990) and Rhode Island (Husband and Eddleman 1990).*

	New Hampshire		
Species	With stream course	Without stream course	Rhode Island
Wood frog	54.5	48.2	20.7
Redback salamander	18.5	39.0	36.4
American toad	18.0	8.0	24.5
Spotted salamander	2.6	0.8	3.1
Eastern newt	1.8	1.6	1.4
Spring peeper	1.8	2.0	0.2
Green frog	0.9		5.8
Northern two-lined salamander	0.7		
Common garter snake	0.6	0.4	0.1
Spring salamander	0.4		<0.1
Dusky salamander	0.2		
Northern leopard frog			2.9
Four-toed salamander			2.6
Pickerel frog			1.6
Marbled salamander			0.3
Gray treefrog			0.2
Fowler's toad			0.1
Painted turtle			<0.1
Snapping turtle			<0.1
Number of sites	1	1	4
Total number of individuals	545	251	2,035
Total species richness	11	7	17

than in balsam fir. Red maple forests containing streams supported a higher number of species and more than twice as many individuals as red maple forests lacking streams.

The species captured by DeGraaf and Rudis (1990) in red maple stands are listed in Table 7.2. Three amphibian species—wood frog, redback salamander (*Plethodon cinereus*), and American toad—accounted for over 90% of the total captures in each stand; these species were present in comparable numbers in northern hardwood stands. Redback salamanders are entirely terrestrial and lay eggs in moist areas under logs, rocks, and other debris (Heatwole 1962). American toads can be found in a large variety of habitats, but require shallow water in which to lay eggs (Conant 1975). Wood frogs (Fig. 7.1) breed in small ponds and shallow surface water in wooded areas during spring, but are often found far from water in a variety of forest types during the remainder of the year (Heatwole 1961).

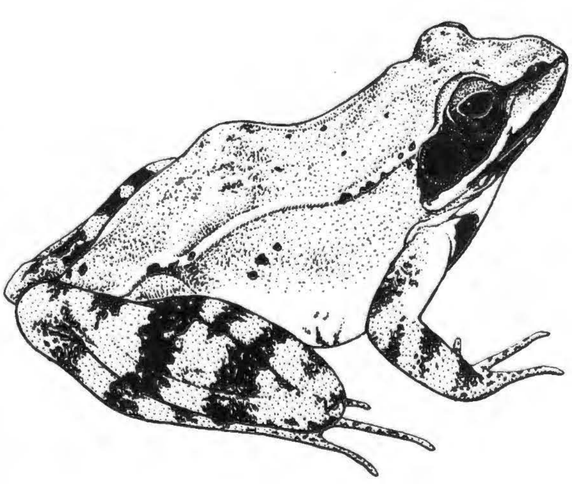

Fig. 7.1. Wood frog (*Rana sylvatica*), one of the most abundant amphibians breeding in red maple swamps. *Drawing by A. Rorer.*

Husband and Eddleman (1990) quantified herpetofaunal use of upland forests immediately surrounding four red maple swamps in Rhode Island. As DeGraaf and Rudis (1990) found in New Hampshire, wood frogs, American toads, and redback salamanders were the most numerous species captured; they constituted about 81% of the total captures (Table 7.2). The highest monthly captures occurred in July and August and consisted primarily of juvenile American toads and green frogs (*Rana clamitans*) leaving the forested swamps.

While data are scarce, the above studies demonstrate that red maple swamps constitute significant habitat for amphibians in widely differing forest regions of the glaciated Northeast. The specific uses (e.g., breeding and feeding) that the various species of amphibians and reptiles make of these swamps and the relative importance of different swamp microhabitats to individual species need additional study.

Birds

Species Composition

Of all the vertebrate classes inhabiting northeastern red maple swamps, birds are the best documented. Avian species composition and density have been determined through standard Breeding Bird Censuses conducted in New Jersey (Black and Seeley 1953; Seeley 1954, 1955, 1956, 1957, 1966; Meyers et al. 1981; Taylor 1984) and western New York (Slack et al. 1975). Anderson and Maxfield (1962) listed birds that were mist-netted during the breeding season in a mixed red maple–Atlantic white cedar swamp in Massachusetts. Two more recent studies have focused specifically on factors determining the composition and structure of the breeding bird communities of red maple swamps in Massachusetts (Swift 1980; Swift et al. 1984) and Rhode Island (Merrow 1990).

Table 7.3 lists the bird species breeding in northeastern red maple swamps, according to published

Table 7.3. *Relative abundance of breeding birds in red maple swamps of the glaciated Northeast. Values are the percentages of all individuals censused in each study.*

	Study[a]							
	1	2	3	4	5	6	7	
Species	N.Y.	N.J.	N.J.	N.J.	Mass.	Mass.	R.I.	Mean
Veery	12.9		14.1	20.8	13.2	13.6	10.2	12.1
Common yellowthroat			22.5	12.5	1.1	17.9	5.2	8.5
Ovenbird	13.6	10.4	7.0		6.3	8.3	0.1	6.5
Black-capped chickadee	1.5		2.8		20.1	3.5	16.6	6.4
Wood thrush	5.3	16.6	2.8	4.2	9.8	1.2	0.7	5.8
Gray catbird	3.0	5.1	5.6	8.3	2.3	6.8	9.0	5.7
American robin	1.5	1.1		8.3	19.5	0.1	3.5	4.9
Blue jay		4.5		16.7	3.4	0.2	4.4	4.2
American redstart	20.5	0.8	5.6			0.2	1.4	4.1
Canada warbler					4.0	12.3	12.1	4.1
Red-eyed vireo	12.1	11.5				3.0	1.5	4.0
Northern waterthrush				4.2	7.5	6.9	4.6	3.3
Rufous-sided towhee		10.7	5.6			0.7	3.1	2.9
Black-and-white warbler		2.3			2.3	5.9	6.7	2.5
Blue-winged warbler			8.5	8.3		0.1	0.5	2.5
Tufted titmouse		4.2		4.2		0.9	6.1	2.2
Northern oriole	1.5			8.3		0.4	1.4	1.7
Great crested flycatcher	1.5	2.5	2.8			0.4	2.4	1.4
House wren	3.8		5.6			0.2	0.4	1.4
Downy woodpecker	1.5	2.3	2.8		2.3		0.5	1.3
Scarlet tanager	1.5	5.6				1.2	0.4	1.2
Northern cardinal	3.0	2.4	2.8			0.1	0.1	1.2
Eastern wood-pewee	6.1	2.4				0.1		1.2
Common grackle					6.3	0.2	0.4	1.0
Rose-breasted grosbeak	1.5		2.8			1.5	0.7	0.9
White-eyed vireo			5.6				0.4	0.9

Table 7.3. *Continued.*

	Study[a]							
Species	1 N.Y.	2 N.J.	3 N.J.	4 N.J.	5 Mass.	6 Mass.	7 R.I.	Mean
Hooded warbler		5.3						0.8
Northern flicker	0.8	3.1				0.1	0.8	0.7
Brown creeper						4.0	1.0	0.7
Yellow-throated warbler				4.2				0.6
Swamp sparrow						4.0		0.6
White-breasted nuthatch		1.7				1.0	1.1	0.5
Indigo bunting	3.8							0.5
Brown-headed cowbird	1.5	0.1				0.5	0.7	0.4
Hairy woodpecker		1.1			1.1	<0.1	0.8	0.4
Carolina chickadee		2.5						0.4
Red-bellied woodpecker			2.8					0.4
Carolina wren		1.7					0.4	0.3
Yellow warbler						2.3		0.3
Acadian flycatcher	1.5					0.1		0.2
Warbling vireo	1.5					<0.1		0.2
Chestnut-sided warbler						0.7	0.4	0.2
Black-throated green warbler					0.6		0.3	0.1
Song sparrow						0.1	0.8	0.1
Blue-gray gnatcatcher						<0.1	0.7	0.1
American crow		0.6						0.1
Red-winged blackbird						0.9		0.1
Ruffed grouse					<0.1	<0.1	0.1	<0.1
Broad-winged hawk		0.3				<0.1		<0.1
Yellow-billed cuckoo		0.3				<0.1		<0.1
Ruby-throated hummingbird		0.3						<0.1
Northern bobwhite		0.3						<0.1
Whip-poor-will		0.1						<0.1
Great horned owl		0.1						<0.1
Solitary vireo						0.1		<0.1
Louisiana waterthrush						0.1		<0.1
Nashville warbler						0.1		<0.1
Eastern phoebe							0.1	<0.1
Yellow-throated vireo							0.1	<0.1
Prairie warbler							0.1	<0.1
Black-billed cuckoo						<0.1		<0.1
Mourning warbler						<0.1		<0.1
White-throated sparrow						<0.1		<0.1
Number of sites	1	1	1	1	1	8	12	
Forested wetland area per site (ha)	9.9	6.5	5.0	5.6	266	30–45	0.5–19.3	
Species richness[b]	21	19.7 (17–24)	16	11	16	22.0 (18–26)	13.6 (7–24)	
Density (males/ha)[b]	6.8	9.1 (6.3–11.0)	7.1	4.3				

[a] Study locations, citations, and census methods were:
1. Chatauqua County, N.Y.; Slack et al. (1975); spot-mapping, Breeding Bird Census (BBC).
2. Monmouth County, N.J.; Black and Seeley (1953), Seeley (1954, 1955, 1956, 1957, 1966); spot-mapping, BBC.
3. Morris County, N.J.; Meyers et al. (1981); spot-mapping, BBC.
4. Morris County, N.J.; Taylor (1984); spot-mapping, BBC.
5. Bristol County, Mass.; Anderson and Maxfield (1962); mist-netting in a mixed red maple–Atlantic white cedar swamp.
6. Hampden and Hampshire Counties, Mass.; Swift (1980), Swift et al. (1984); fixed-plot census during 2 years.
7. Washington and Kent Counties, R.I.; Merrow (1990); fixed-plot census, all bird songs, calls, and visual observations.

[b] Means are given, where appropriate, with ranges in parentheses.

census results. Twenty-five (40%) of the 63 species were encountered in four or more of the seven studies. The avian community is composed principally of facultative species that commonly occur in upland forests as well. Examples of facultative species found throughout the region include black-capped chickadee, gray catbird, ovenbird (*Seiurus aurocapillus*), wood thrush (*Hylocichla mustelina*), American robin, and blue jay. Several other breeding species seem to be attracted to swamps because of the presence of surface water. Species that are most strongly associated with northeastern wetland forests include northern waterthrush (Fig. 7.2), Canada warbler (*Wilsonia canadensis*) (Fig. 7.3), and veery (*Catharus fuscescens*). Of these, only the northern waterthrush does not breed in upland habitats. Canada warblers and veeries are abundant in forested wetlands in southern New England, but they also may be found in streamside or mesic upland forests, particularly in other areas of the Northeast (Bent 1953; Bertin 1977; American Ornithologists' Union [AOU] 1983). Prothonotary warblers (*Protonotaria citrea*) and cerulean warblers (*Dendroica cerulea*) breed in deciduous forested wetlands, but their ranges encompass only the western and southern boundaries of the glaciated Northeast (Bent 1948, 1953; AOU 1983; DeGraaf and Rudis 1986).

Raptors are generally secretive, rapid-moving, and wide-ranging during the breeding season; therefore, they are seldom recorded in censuses using spot-mapping or singing male counts (Fuller and Mosher 1981). Of all northeastern raptors, red-shouldered hawks (*Buteo lineatus*) exhibit the strongest affinity for forested wetlands, both for nest sites and for hunting areas (Henny et al. 1973; Portnoy and Dodge 1979; Rymon 1989). In southeastern New York and northern New Jersey, northern goshawks (*Accipiter gentilis*) have also been found to select nest sites closer to red maple swamps than would be expected by chance alone (Speiser and Bosakowski 1987). The authors noted that the swamps were relatively undisturbed by humans and appeared to support a greater density and diversity of prey species than surrounding xeric oak forests. Other birds of prey that frequently inhabit northeastern red maple swamps include broad-winged hawks (*Buteo platypterus*), barred owls (*Strix varia*), eastern screech-owls (*Otus asio*), and northern saw-whet owls (*Aegolius acadicus*) (AOU 1983; DeGraaf and Rudis 1986; Rymon 1989).

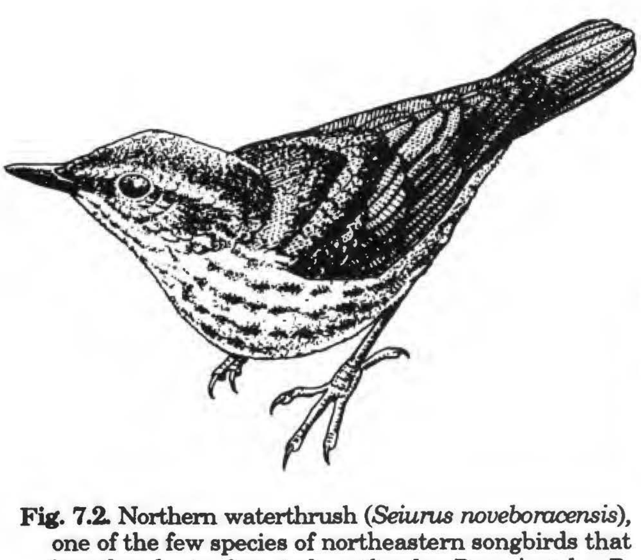

Fig. 7.2. Northern waterthrush (*Seiurus noveboracensis*), one of the few species of northeastern songbirds that breed only in forested wetlands. *Drawing by R. Deegan.*

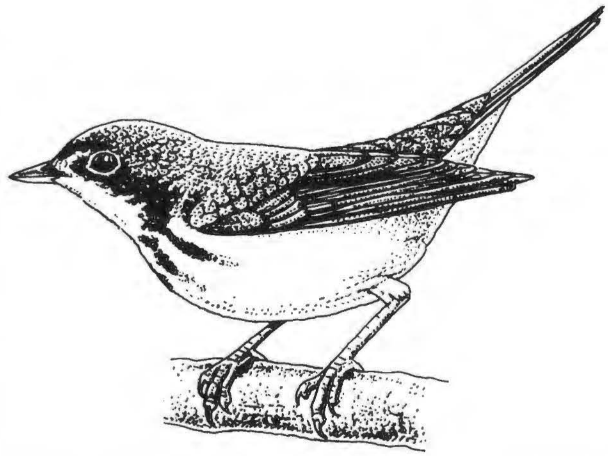

Fig. 7.3. Canada warbler (*Wilsonia canadensis*), one of the most abundant breeding birds in southern New England red maple swamps. *Drawing by R. Deegan.*

Factors Affecting Avian Richness and Abundance

Swift et al. (1984) were the first to identify factors influencing breeding bird communities in northeastern red maple swamps. They censused singing males within eight swamps ranging in area from 30 to 45 ha and measured both vegetation and hydrologic characteristics within bird census plots. Using methods adapted from Swift et al. (1984), Merrow (1990) censused breeding birds in 12 Rhode Island red maple swamps ranging in area from 0.5 to 19.3 ha. Merrow compiled two observational data sets: singing bird observations (i.e., songs of territorial species) and all bird registrations (i.e., songs, calls, and visual observations). Among the most significant factors influencing the avian community in these studies were wetland size, vegetation structure, and water regime.

Wetland Size

Breeding bird species richness is correlated with the size of red maple swamps (Merrow 1990). In Merrow's study, species richness ranged from 3 to 15 species per site for singing birds, and from 7 to 24 species per site for all bird registrations. Sites 4 ha or smaller had significantly lower species richness than sites ranging from 6 to 19 ha. In larger (30–45 ha) swamps in Massachusetts, Swift (1980) found richness to range from 18 to 26 species. By combining data from Swift, Merrow (1990), and pertinent breeding bird censuses, a more comprehensive picture of the species–area relationship can be developed (Fig. 7.4). Although factors other than wetland size also affect avian species richness, size clearly is a key determinant.

Whether swamp size has any effect on breeding bird density or relative abundance is unclear. Breeding bird censuses have shown that avian density may vary widely, from as few as 4.3 to as many as 11.0 males per ha (Table 7.3), even among areas of swamp that are comparable in size (5–10 ha). In Rhode Island red maple swamps less than 20 ha in size, avian relative abundance ranged from 0.6 to 2.0 singing males per census per 0.28-ha plot, and there was no significant relation between relative abundance and wetland size (Merrow 1990). Relative abundance values were higher (mean 2.8 singing males per census per plot; range 0.8–4.5) in the larger swamps censused by Swift et al. (1984). Unfortunately, direct comparisons among studies may be misleading because of differences in census methods. Additional research is needed to clarify the relation between swamp size and avian abundance.

Vegetation Structure

The influence of vegetation structure on breeding bird communities has been well documented (Beecher 1942; MacArthur 1964; Tramer 1969; Anderson and Shugart 1974; James and Wamer 1982). Tramer, for example, showed that species richness and diversity of breeding birds are higher in forest habitats that contain several vegetation layers than in simpler communities dominated by herbs or shrubs. Avian richness and diversity in northeastern red maple swamps are comparable to those of upland deciduous and upland coniferous forests, but lower than in floodplain forests (Fig. 7.5).

The study areas selected by Swift et al. (1984) represented a wide range of vegetation structure; they included five mature red maple forested swamps, as well as three wetlands containing areas of both forested swamp and shrub swamp. Avian abundance was significantly higher in the structurally diverse forested–shrub wetlands (mean 3.7 males per plot per census) than in the mature forests (mean 2.2 males per plot per census), based on our calculations from data in Swift (1980). Species richness, however, was similar for the two types. Species present only in forested-shrub wetlands included the yellow warbler (*Dendroica petechia*), warbling vireo (*Vireo gilvus*), swamp sparrow

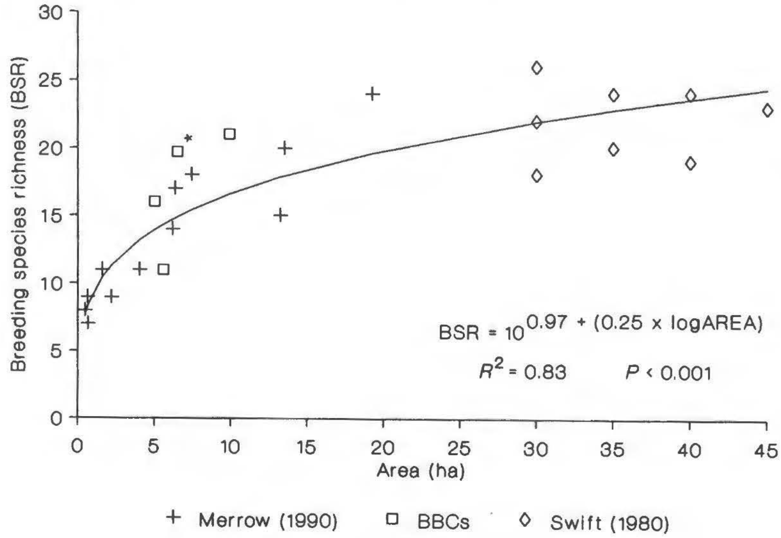

Fig. 7.4. Avian breeding species richness as a function of wetland size in northeastern red maple swamps. Breeding Bird Census (BBC) data are from Slack et al. (1975), Meyers et al. (1981), Taylor (1984), Black and Seeley (1953), and Seeley (1954, 1955, 1956, 1957, 1966). Results of the latter six censuses are plotted as a 6-year mean (identified by *asterisk*).

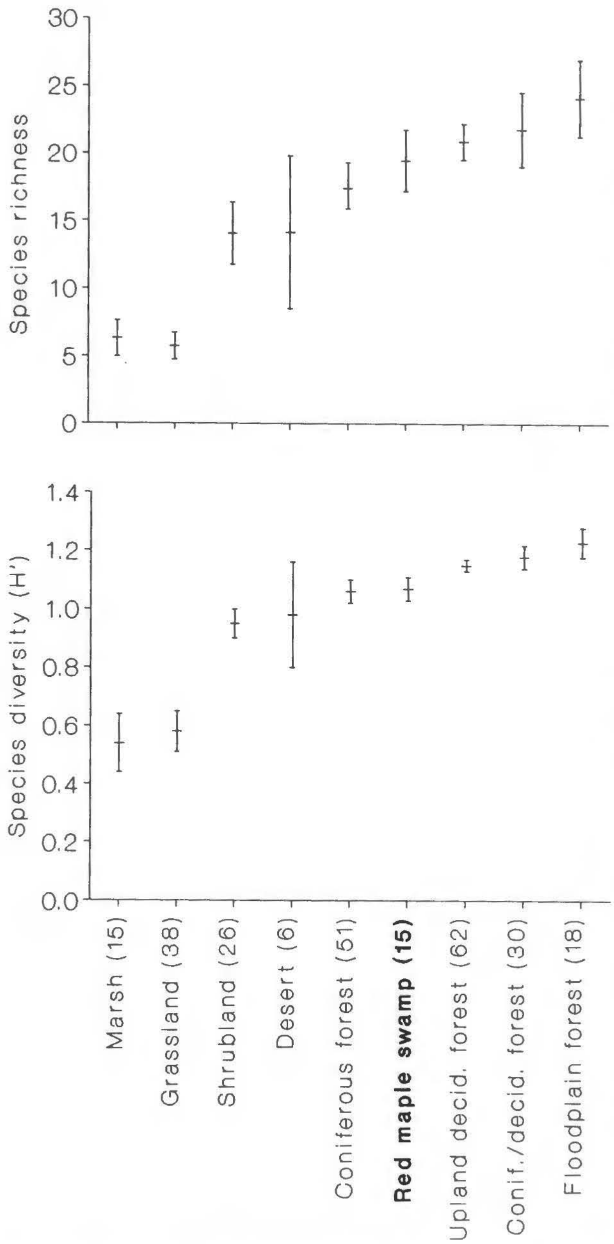

Fig. 7.5. Breeding bird richness and diversity in major North American vegetation types. Means with 2 standard errors are depicted. *Parentheses* indicate the number of censuses included for each vegetation type. Data for all types except red maple swamp are from Tramer (1969). Red maple swamp data were recorded from northeastern U.S. sites greater than 5 ha in size censused by Black and Seeley (1953), Slack et al. (1975), Swift (1980), Meyers et al. (1981), Taylor (1984), and Merrow (1990).

(Melospiza georgiana), and red-winged blackbird (Agelaius phoeniceus).

Over the wide range of structural characteristics measured by Swift et al. (1984) and Merrow (1990), shrub layer structure appeared to be most closely related to avian richness and abundance. Swift et al. (1984) found that stem densities of short shrubs (1–3 m), tall shrubs (3–5 m), and subcanopy trees were positively correlated with breeding species richness, while short shrub density was positively correlated with abundance. Several measures of the tree stratum, including tree height, stem diameter, and crown closure, were negatively correlated with avian richness and abundance. Shrub layer characteristics were strongly related to bird community characteristics in Merrow's (1990) study also. The percentage cover of shrubs less than 2 m tall was positively correlated with the species richness of singing males, and richness generally increased with shrub foliage volume as well. The presence of a dense, extensive shrub layer within red maple forested wetlands appears to add significantly to habitat complexity, providing nest sites, foraging substrates, song perches, and escape cover for a variety of bird species.

Water Regime and Peat Depth

Soil moisture gradients in nonwetland forests have been shown to affect the distribution of breeding birds (Karr 1968; Bertin 1977; Smith 1977). Karr even suggested that surface water is of such great importance that it should be considered equivalent to vegetation strata when describing avian habitats.

In Massachusetts red maple swamps, Swift et al. (1984) found that percent cover of surface water, presence of streams, and peat depth were positively correlated with avian richness and abundance, while the degree of water level fluctuation throughout the summer was negatively correlated with these characteristics. Peat depth was negatively correlated with water level fluctuation and positively correlated with percent surface water; therefore, it was interpreted to be an indicator of site wetness (Swift 1980).

The influence of hydrology on swamp bird communities may be more clearly understood when considered in combination with the effects of vegetation structure. In the eight wetlands studied by Swift et al. (1984), wetter sites also had greater peat depths, denser shrub layers, a less-developed tree stratum, and a larger and more diverse breeding bird community. The swamps studied by Swift et al. spanned a wide range of hydrologic, edaphic, and structural conditions; their results should be interpreted in that light.

Because of the relatively great influence of hydrologic variables on the breeding bird community, Swift et al. (1984) hypothesized that, given similar vegetation structure, avian richness and abundance would increase at sites with deeper organic soils and greater seasonal surface-water coverage. Merrow (1990) verified this hypothesis, to some extent, in his study of 12 mature, relatively homogeneous red maple swamps. Of 20 habitat variables examined, only peat depth was significantly correlated with avian abundance. Surface-water coverage was not an important variable in Merrow's study, most likely because water levels in southern Rhode Island were unusually low during his census period.

Red Maple Swamps as Waterfowl Habitat

Forested floodplains, basin swamps, and beaver flowages of the Northeast are important feeding and resting areas for migrating waterfowl (Moore 1959; Stanton 1965; Rockwell 1970; Kirby 1988). In most years, surface water levels in forested wetlands are highest from late fall through spring, allowing access to these areas by migrating waterfowl. Among the species that frequent flooded swamps during migration are the wood duck, American black duck, mallard (*Anas platyrhynchos*), ring-necked duck (*Aythya collaris*), and hooded merganser (*Lophodytes cucullatus*).

Waterfowl species that breed in northeastern forested wetlands include ground or stump nesters such as American black ducks and mallards, as well as cavity-nesting wood ducks, common goldeneyes (*Bucephala clangula*), common mergansers (*Mergus merganser*), and hooded mergansers (Bellrose 1976).

Impoundments constructed in bottomland hardwoods of the southern and central United States provide important migration and wintering habitat for waterfowl (Yeager 1949; Kadlec 1962; Fredrickson and Taylor 1982). Given the success of this technique in wintering areas, green-timber impoundments were constructed in the mid-1960's at the Montezuma National Wildlife Refuge in central New York. The purpose of the impoundments was to provide both migration and nesting habitat for waterfowl (Thompson et al. 1968). A 120-ha red maple swamp, which was diked and flooded to a depth of 25–30 cm from mid-March through June, was used by 10 species of nesting waterfowl between 1965 and 1969 (Kivisalu et al. 1970). Waterfowl nest density averaged 0.91 per ha over the 5-year period; only six waterfowl nests were found during the same 5 years in 365 ha of unmanaged swamp immediately adjacent to the impoundment. Nest densities in the green-timber impoundment were also higher than those in flooded dead timber and cattail marshes within the refuge (see Cowardin et al. 1967). Mallards accounted for nearly 80% of the 355 nests found (Kivisalu et al. 1970). Other nesting species included wood duck, black duck, Canada goose (*Branta canadensis*), blue-winged teal (*Anas discors*), green-winged teal (*A. crecca*), hooded merganser, gadwall (*A. strepera*), and American wigeon (*A. americana*).

Stumps and tree cavities with openings less than 1 m above the ground accounted for the majority of waterfowl nest sites from 1965 to 1967 at Montezuma (Kivisalu et al. 1970). After a predator-control program was instituted in 1968, the majority of waterfowl nests were built on tree mounds. Raccoons and mink were the primary predators of eggs and incubating hens. Nests were placed an average of 70 cm above the water surface; thus, the need for careful water level management in forested waterfowl impoundments is clear.

Of all the waterfowl species that breed in the Northeast, wood ducks (Fig. 7.6) are the most highly adapted for life in forested wetlands (Johnsgard 1975; Bellrose 1976). Their strong dependence on surface water, cavity-nesting habit, perching ability, and deft maneuverability in flight amidst trees and shrubs are unique adaptations to this habitat. Throughout the southern and central United States, wood ducks breed primarily in floodplain forests and bottomland hardwood stands; red maple swamp is the principal forest type used by breeding wood ducks in the Northeast (McGilvrey 1968). Upland forest stands within 0.3 km of surface water bodies also may be used as nesting areas (Grice and Rogers 1965; McGilvrey 1968).

Grice and Rogers (1965) and McGilvrey (1968) outlined the habitat requirements of breeding wood ducks in detail. Trees at least 40 cm in diameter, with cavities at least 15 cm deep and entrances larger than 9 cm in diameter, appear to be the minimal nesting requirement. Still or slowly moving surface water 8 to 45 cm deep must be present in swamps when ducks are seeking nest sites in March and April, and areas should remain inundated at least halfway through the incubation period. Because of the scarcity of natural cavities in many swamps and the loss of forested wetland habitat, the introduction of artificial nest boxes has significantly increased wood duck breeding populations throughout the eastern United States

Fig. 7.6. Wood duck (*Aix sponsa*). This species uses seasonally flooded and temporarily flooded red maple swamps extensively, both in breeding and in spring and fall migration. *Photo by W. Byrne.*

(McLaughlin and Grice 1952; McGilvrey 1968; Bellrose 1976).

Green-timber impoundments at the Montezuma National Wildlife Refuge provided high quality nesting habitat for wood ducks (Reed 1968; Thompson et al. 1968; Haramis 1975). Water depth was maintained at about 25 cm throughout the nesting season, and the density of natural cavities was relatively high (Reed 1968; Haramis 1975). The introduction of nest boxes dramatically increased population levels of wood ducks for 3 years after the boxes were installed; however, competition for nesting boxes, dump-nesting by hens unable to secure nesting cavities, and increased predation on eggs by woodpeckers (primarily northern flicker, *Colaptes auratus*) lowered wood duck hatching success and increased the frequency of nest desertion (Haramis and Thompson 1985). This trend was reversed in 1978, when flooding of the impoundment was discontinued to reduce stress on the forest community. Without abundant surface water, the forested interior of the impoundment was less attractive for wood duck nesting. As a result, breeding densities declined, but nest success increased.

Black ducks, which breed in a great variety of habitats, are most commonly found in freshwater or estuarine marshes; however, swamps and beaver flowages provide important breeding habitats in many areas of the Northeast (Coulter and Mendall 1968; Reed 1968; Thompson et al. 1968; Ringelman et al. 1982; Kirby 1988). In central Maine, breeding black ducks showed preference, in descending order of importance, for emergent marsh, deciduous forested wetland, and deciduous shrub swamp (Ringelman et al. 1982). Diefenbach and Owen (1989) developed a model of breeding season habitat use in the same area of central Maine and found four habitat variables to be most important in predicting wetland use by black ducks: (1) perimeter of surface water area, (2) area of timber flooded by at least 10 cm of water, (3) presence of beaver, and (4) visibility of occupied human dwellings (negative correlation). Both studies stressed the importance of beaver flowages to breeding waterfowl.

Red maple swamps are not primary brood habitat for waterfowl, mainly because most swamps lack surface water by early summer to midsummer. High-quality food may be scarce as well in many swamps. For these reasons, semipermanently and permanently flooded shrub swamps and emergent wetlands serve as primary brood areas for northeastern waterfowl (McGilvrey 1968; Kivisalu et al. 1970; Ringelman and Longcore 1982; Kirby 1988).

Mammals

Nearly 50 species of mammals are known to live in northeastern red maple swamps (Table 7.4). These species range in size from large animals, such as moose (*Alces alces*), black bears (*Ursus americanus*), and white-tailed deer (*Odocoileus virginianus*), to smaller animals, such as raccoons, river otters, voles, shrews, and bats. Some species, such as beaver, otter, mink, and water shrew (*Sorex palustris*), are wetland dependent, but the great majority of mammals found in northeastern forested wetlands are facultative species (Kirkland and Serfass 1989). Significant research on the mammalian use of red maple swamps has been limited to studies of small mammals and black bears.

Small Mammals

Community Characteristics

Research in New Jersey and Connecticut indicates that the small-mammal community of northeastern red maple swamps often equals or exceeds that of common upland habitats in species richness, diversity, and abundance. Dowler et al. (1985) trapped small mammals in a variety of habitats within the Great Swamp National Wildlife Refuge, Morris County, N.J. Both upland and wetland (red maple–sweet gum) forests had higher numbers of small mammals than did upland grasslands or the edges of freshwater marshes (Table 7.5). White-footed mice and masked shrews (*Sorex cinereus*) were the most abundant species captured in forested wetland. In Connecticut, Miller and Getz (1977a) found that red maple swamps had higher mammal species richness, higher abundance, and higher diversity than either deciduous or coniferous upland forests (Table 7.5). Three species, the woodland jumping mouse (*Napaeozapus insignis*), the star-nosed mole (*Condylura cristata*), and the

Table 7.4. *Wetland dependence of mammals occurring in red maple swamps of the glaciated Northeast (from DeGraaf and Rudis 1986; Kirkland and Serfass 1989).*

Wetland-dependent species
Water shrew
Star-nosed mole
Beaver
Mink
River otter
Facultative species
Virginia opposum
Masked shrew
Smoky shrew
Northern short-tailed shrew
Hairy-tailed mole
Eastern mole
Keen's myotis
Little brown myotis
Indiana myotis
Red bat
Silver-haired bat
Eastern pipistrelle
Big brown bat
Eastern cottontail
New England cottontail
Snowshoe hare
Eastern chipmunk
Woodchuck
Gray squirrel
Red squirrel
Southern flying squirrel
White-footed mouse
Deer mouse
Southern red-backed vole
Meadow vole
Woodland vole
Southern bog lemming
Meadow jumping mouse
Woodland jumping mouse
Porcupine
Coyote
Red fox
Gray fox
Black bear
Raccoon
Fisher
Ermine
Long-tailed weasel
Striped skunk
Mountain lion
Lynx
Bobcat
White-tailed deer
Moose

Table 7.5. *Small-mammal communities in red maple swamps and other habitats of New Jersey (Dowler et al. 1985) and Connecticut (compiled from appendix in Miller and Getz 1977a). Values for individual species are captures per 100 trap-nights.*

Mammal	Red maple swamp	Upland coniferous forest	Upland deciduous forest	Late successional grassland	Early successional grassland	Freshwater marsh edge
New Jersey						
White-footed mouse	7.1		5.6	0.9	0.1	0.1
Masked shrew	4.2		3.2	2.1	2.0	2.3
Northern short-tailed shrew	0.4		1.1	1.7	0.1	0.6
Meadow jumping mouse	0.3		1.2	0.7	0.1	0.4
Meadow vole	0.3		0.3	0.4	1.4	3.1
Eastern chipmunk	0.1		0.1			
Star-nosed mole				0.1		0.2
All species	12.4		11.4	5.8	3.8	6.7
Number of trap-nights	2,100		2,100	2,100	2,100	2,100
Total species richness	6		6	6	5	6
Species diversity (H'_2)	1.44		1.86	2.15	1.51	1.88
Connecticut						
Southern red-backed vole	3.6	0.5	1.2			
White-footed mouse	2.6	4.0	3.1			
Northern short-tailed shrew	0.7	1.1	<0.1			
Masked shrew	0.4	0.2	0.3			
Meadow vole	0.4	0.2	<0.1			
Southern bog lemming	0.1		<0.1			
Woodland jumping mouse	0.1					
Woodland vole	<0.1	0.3	0.9			
Smoky shrew	<0.1	0.1				
Meadow jumping mouse	<0.1		<0.1			
Star-nosed mole	<0.1					
Water shrew	<0.1					
All species	8.0	6.3	6.1			
Number of trap-nights	5,070	1,026	8,283			
Total species richness	12	7	8			
Species diversity (H'_2)	1.61	1.22	1.52			

water shrew, were trapped only in wetland forests. The small-mammal community of red maple swamps was dominated by the southern red-backed vole (*Clethrionomys gapperi*) and the white-footed mouse.

Key Habitat Features

Factors such as vegetation structure, food availability, substrate moisture, and debris cover (large rocks or fallen logs) have been found to influence small mammal populations in upland forests (Dueser and Shugart 1978; Kitchings and Levy 1981), but few studies have examined the factors affecting small-mammal species distribution and abundance in wetland forests. Miller and Getz (1977a) found that red maple swamps with abundant shrub cover had higher mammalian diversity and richness than either upland forests or red maple swamps with a lesser abundance of shrubs. Mammalian species diversity also was positively correlated with the number of tree and shrub species. This relationship was believed to center on food availability, since most small-mammal species that were captured fed primarily on mast and fruit produced by trees and shrubs. Additionally, the authors speculated that a greater variety of tree and shrub leaves in the litter layer might lead to increased richness of invertebrate prey species.

Species composition of trees and shrubs in swamps may be even more important than species richness in explaining the local distributions of certain small mammals. The majority of woody plants in swamps, such as red maple, highbush blueberry, and dewberries *(Rubus* spp.), produce samaras or fleshy fruits, which provide abundant food during summer and fall but are not available for winter consumption. The stable year-round supply of mast in upland oak–hickory forests is a major factor promoting higher numbers of white-footed mice in that habitat than in red maple swamps (Getz 1961b; Batzli 1977; Breidling et al. 1983).

The southern red-backed vole (Fig. 7.7) was the most abundant small mammal species found in Connecticut red maple swamps (Miller and Getz 1973, 1977a, b). This species inhabits most forest types in northern New England, but in southern New England, where upland soils are generally drier, it is apparently restricted to forested wetlands. Getz (1968) showed that the red-backed vole has higher evaporative water loss and less efficient kidneys than other small mammal species. As a result, it must live where standing water or succulent food items are readily available. In red maple swamps, water is available to voles in most of the growing season. Even during exceedingly dry periods, the water table is usually close enough to the surface so that voles can gain access to it by tunnelling along wind-loosened tree roots (Miller and Getz 1972, 1973).

Within forested wetlands, the amount of escape cover provided by low vegetation or debris strongly influences the local distribution and abundance of red-backed voles. Miller and Getz (1972, 1977b) noted that vole abundance and survival rates were markedly lower in areas lacking escape cover, and speculated that the lack of cover allowed higher predation by diurnal avian raptors (e.g., red-shouldered hawk).

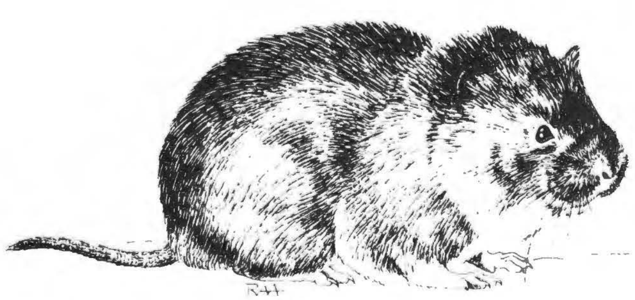

Fig. 7.7. Southern red-backed vole (*Clethrionomys gapperi*), one of the most common small mammals in northeastern red maple swamps. *Drawing by R. Alexander.*

Wildlife residing in seasonally flooded wetlands must be able to adapt to widely fluctuating water levels. Surface inundation in forested wetlands during the spring and fall may make it difficult for some small mammals to move about easily on the forest floor. Water shrews and red-backed voles are efficient swimmers and will enter water more readily than other small mammal species (Getz 1967; Godin 1977). White-footed mice are semiarboreal and thus are able to retreat into trees to avoid surface water. As noted earlier, lower food availability, not seasonal flooding, appears to be responsible for the lower densities of white-footed mice in swamps compared with upland forests (Batzli 1977; Miller and Getz 1977b).

Medium-sized and Large Mammals

In western Massachusetts, black bears show a strong habitat preference for wetlands from mid-April, when they emerge from winter dens, until mid-August (Elowe 1984). Although wetland composed only an average of 11% of the territories of seven radio-equipped female black bears, the bears spent more than one-third of their time in spring and summer in wetlands. Swamps were used most heavily in spring, the season when food was most scarce. Skunk cabbage was the most important food at that time.

Throughout the North American range of black bears, the majority of winter dens are located in upland areas. Swamps are used as denning sites in some areas of the eastern United States, but winter flooding is a major hazard (Alt 1984; Smith 1985; Hellgren and Vaughan 1989). In northeastern Pennsylvania, Alt (1984) found that cub mortality can be as high as 5% due to the flooding of dens by frozen-ground runoff. The highest mortality occurred in excavated or root-cavity dens located in swamps and selected by females during relatively dry autumns; above-average precipitation during fall reduced the selection of potentially dangerous sites because of the presence of water at the time of selection.

In the Northeast, beavers prefer to colonize low-gradient perennial streams in small forested watersheds (Howard and Larson 1985), many of which include red maple swamps. Red maple is a relatively unimportant food species compared with alders, aspens, and willows (Martin et al. 1951; Hodgdon and Hunt 1966), but it may be of significant value where these species are scarce and during the latter years of flowage occupancy. Prolonged flooding eventually kills most trees within the impounded area, but the resulting open-water and marsh habitats are of great value to forest-dwelling amphibians, waterfowl, and mammals.

While there has been little research on the topic, several other species of medium-sized and large mammals are known to make extensive use of red maple swamps. River otters, mink, raccoons, and opossums are most common in swamps containing perennial streams or located along lakeshores. All of these animals feed either in the swamps or in water bodies associated with them. Otters rely heavily on fish, crayfish, and amphibians, while mink eat crayfish, amphibians, muskrats, small mammals, and birds. Raccoons and opossums are omnivorous, feeding on amphibians, crayfish, freshwater clams, birds, bird eggs, and a variety of fruits. Raccoons and opossums commonly den in hollow trees in swamps, while otters and mink generally excavate dens along stream channels or lakeshores.

Gray squirrels (*Sciurus carolinensis*) and red squirrels (*Tamiasciurus hudsonicus*) both inhabit red maple swamps, but the former species is more common in these predominantly deciduous habitats. Their arboreal habits generally insulate squirrels from the effects of seasonal high water. Both eastern cottontails and New England cottontails (*Sylvilagus transitionalis*) are common in deciduous and evergreen forested wetlands, particularly during the winter, when surface water is frozen and travel throughout the swamps is unrestricted. Red maple swamps offer both cover and browse for rabbits.

Red maple swamps are also highly significant habitats for white-tailed deer (Fig. 7.8), particularly in urban areas of the Northeast, where swamps frequently are the wildest, most inaccessible habitats remaining. Swamps provide refuge for deer from dogs and from humans. Forested wetlands along watercourses commonly serve as major travel corridors for deer and other large mammals through areas of otherwise unsuitable habitat (Elowe 1984; Brown and Schaefer 1987).

Fig. 7.8. White-tailed deer (*Odocoileus virginianus*), the most common large mammal in northeastern red maple swamps. *Photo by W. Byrne.*

Vertebrates of Special Concern

Northeastern red maple swamps have no truly endemic vertebrate species; even those species that exhibit a strong affinity for red maple swamps may be found in forested wetlands dominated by other trees. However, red maple swamps provide habitat for numerous rare, threatened, or endangered animals. Appendix D lists 103 vertebrates of special concern known to occur in northeastern red maple swamps, along with their status in each state in the region. Thirty percent of the animals listed in Appendix D are considered of rare, threatened, or endangered status by agencies in five or more northeasternstates.

As noted for plants of special concern (Appendix B), Appendix D should be regarded simply as a potential list of vertebrates of concern. All of the species listed have been observed in northeastern red maple swamps, but many have not been documented in that habitat in states where they are considered rare or endangered. The majority of animals in the list are most frequently found in upland habitats or in wetlands other than red maple swamps.

Chapter 8. Values, Impacts, and Management

Functions and Values of Red Maple Swamps

As previous chapters have shown, relatively little research has been conducted on the hydrologic, edaphic, or ecological characteristics of red maple swamps, despite their abundance in the glaciated Northeast. Similarly, few publications have directly addressed the societal values of these swamps. Many of the functions and values currently recognized for wetlands (e.g., Greeson et al. 1979; Richardson 1981; Adamus and Stockwell 1983; Tiner 1984; Adamus et al. 1987) are nearly universal; that is, they are evident in a wide variety of wetland types, regardless of dominant vegetation or water regime. Despite the lack of documentation, red maple swamps clearly perform many functions that bear directly on public safety, health, and welfare. The great abundance of red maple swamps in the Northeast suggests that the social significance of these functions may be great both locally and regionally.

This section reviews the most obvious functions and values of red maple swamps, noting documentation where it exists, but relying on more general information when necessary. Functions are considered to be processes or actions that the swamps perform; values are the benefits of those functions to society.

Flood Abatement

The ability to reduce the peak level of floods and to delay the flood crest is one of the most widely recognized functions of inland wetlands (Carter et al. 1979; Novitzki 1979b; Tiner 1984). This function is accomplished chiefly through (1) the storage of surface water in wetland basins after snowmelt and major precipitation events, and (2) the reduction in floodflow velocity as water passes through wetland vegetation and over the soil surface. The social significance of the flood abatement function is enormous, particularly if areas downstream from major wetlands are urbanized and vulnerable to flood damage. After a 5-year study of flood control alternatives in the Charles River basin of eastern Massachusetts, the U.S. Army Corps of Engineers (1972) concluded that the least expensive, most effective means of flood control was the preservation of all 3,400 ha of wetlands in the watershed as "natural valley storage areas." Many of those wetlands are red maple swamps. By the late 1980's, all Charles River wetlands had been protected for flood control through either public acquisition or easements (F. W. Colman, U.S. Army Corps of Engineers, Waltham, Mass., personal communication).

The relative contribution of an individual red maple swamp to flood abatement is heavily influenced by its geomorphic setting and land use within its watershed. Swamps with the greatest potential value for flood abatement are those that (1) are located in a well-defined basin capable of storing floodwater, (2) have a relatively large watershed or one that has been extensively altered by humans, and (3) receive floodwaters directly from an overflowing stream or lake (see Ogawa and Male 1983 for a discussion of other factors affecting flood abatement). Hillside seepage swamps, for example, have relatively low flood-control value compared with temporarily or seasonally flooded basin swamps or swamps associated with lower perennial rivers. Trees, shrubs, and herbaceous plants growing in swamps further aid in flood abatement by physically impeding the flow of floodwaters. In this regard, swamps are more effective than open water or nonpersistent emergent wetlands.

Groundwater Functions

As shown earlier, red maple swamps may be isolated from underlying groundwater aquifers or intimately connected to them. Swamps linked to groundwater aquifers may be groundwater recharge areas, groundwater discharge areas, or both. By collecting precipitation and overland flow and recharging the underlying groundwater system, swamps may augment domestic and municipal water supplies. Hydrogeologic studies have shown that heavy pumping of wells located in stratified drift aquifers may induce recharge of water from the surface, or from the soils, of overlying wetlands (Motts and O'Brien 1981; Ozbilgin 1982). While this gain of groundwater may be beneficial from an engineering standpoint, the loss of water from the wetland may be detrimental to fish and wildlife, recreation, and other wetland functions and values.

Except for surface-water depression wetlands that are perched above the regional groundwater table, natural recharge in most red maple swamps is likely to be a relatively brief seasonal phenomenon (O'Brien 1977). It occurs mainly during the late summer or early fall when, due to cumulative evapotranspiration losses, groundwater levels have dropped below the wetland surface, and groundwater discharge has ceased. O'Brien calculated that one red maple swamp in eastern Massachusetts recharged the regional groundwater body with 7 million gallons of water during a 6-week period in the fall; he noted that recharge could be significant during dry periods. In most cases, however, the volume of groundwater recharge in red maple swamps probably is far less than in the surrounding uplands—depending on the slope and soil permeability of the uplands—particularly on an annual basis.

Red maple swamps lying on slopes or in basins that intersect the regional groundwater table are predominantly areas of groundwater discharge. These swamps exist precisely because groundwater is emerging at the surface in the form of springs or seeps. The discharge of groundwater is important in itself because this water supplements public surface-water supplies, maintains fish and wildlife habitats, and improves the water quality of lakes and streams degraded by excess nutrient loads, toxic chemicals, or thermal discharges (Adamus 1986). Groundwater discharge maintains base flow of streams and keeps stream and lake temperatures low during the late summer, when both of these conditions are critical to aquatic invertebrates and cold-water fishes. Note, however, that evapotranspiration losses from swamps may lower base flow of streams during dry periods (Miller 1965).

Aside from recharge and discharge considerations, the spatial association of wetlands and groundwater aquifers is of great significance. Motts and O'Brien (1981) determined that, on an area basis, about two-thirds of Massachusetts wetlands overlie potential high-yield aquifers, and that at least 60 communities in that state obtain water from wells located in or near wetlands. Because the best location for municipal wells, from a purely hydrologic standpoint, is often near wetlands, and because wetlands are often hydrologically linked to underlying aquifers, Motts and O'Brien concluded that the protection of wetlands and their surroundings from pollution should be a integral part of any groundwater management program.

Water Quality Improvement

Since the mid-1970's there has been a great deal of research on the pollution-abatement potential of wetlands (e.g., Tilton et al. 1976; Kadlec and Kadlec 1979; Godfrey et al. 1985; Nixon and Lee 1986). This research has shown that many types of wetlands retain, remove, or transform pollutants and thus improve the quality of surface water. This pollution-abatement function is accomplished through physical settling, plant uptake, adsorption by soil particles, complexing with other chemicals in the soil, and microbial transformation (Burton 1981; Nixon and Lee 1986).

Most of the research on the water quality improvement function of forested wetlands has occurred outside of the glaciated Northeast. Hardwood swamps in various parts of the United States have been shown to significantly reduce concentrations of nitrogen and phosphorus in surface water during periods of inundation (Kitchens et al. 1975; Mitsch et al. 1979; Brinson et al. 1981b), and the potential capacity of forested wetlands for removing pesticides and heavy metals is believed to be high (Winger 1986). Only two papers have reported on the water quality improvement capacity of northeastern red maple swamps. In a comparison of grass- and forest-vegetated filter strips in Rhode Island, Groffman et al. (1991) demonstrated that denitrification rates were significantly greater ($P < 0.05$) in poorly drained soils of red maple swamps than in well drained soils of adjacent upland forests. In a second Rhode Island study, Gold and Simmons (1990) found that removal of nitrate from groundwater generally exceeded 80% in both poorly drained and very poorly drained soils of red maple swamps throughout the year. In almost all cases, nitrate attenuation was significantly higher ($P < 0.05$) in the swamps than in the moist (somewhat poorly drained and moderately well drained) forest soils of the bordering upland. Both studies concluded that forested wetlands are likely to be more effective than upland forests as sinks for nitrate. Prolonged anaerobic soil conditions and high soil organic matter content appear to be mainly responsible for the greater denitrification potential of the swamp soils; at the same time, high water tables bring groundwater contaminants closer to the surface where they may be picked up by plant roots.

Red maple swamps are so abundant in the Northeast, particularly in more urbanized sections such as northern New Jersey, southeastern New York and southern New England, that both point and nonpoint discharges of a wide variety of pollutants into these wetlands have been common occurrences. The most widespread problems are stormwater runoff and resulting goundwater contamination from residential subdivisions, highways, commercial and industrial sites, farms, and construction sites, as well as discharge of effluent from belowground sewage disposal systems into soils bordering wetlands. Judging from the preliminary findings in Rhode Island swamps and research results from wetland forests in other regions, it is reasonable to assume that red maple swamps receiving such pollutants perform a water quality improvement function of value to society. Given the abundance of these wetlands, the overall influence on water quality in the region may be significant.

Wildlife Habitat

The importance of red maple swamps as wildlife habitat was addressed in detail in Chapter 7. These swamps are important as breeding areas, seasonal feeding areas, and year-round habitat for a wide variety of birds, mammals, and amphibians; they may also provide important habitat for certain reptiles and invertebrates, but little research has been done on those taxa. The value of individual red maple swamps for particular wildlife species and for the entire wildlife community depends on several factors, including vegetation structure, water regime, surrounding habitat types, degree of human activity in or near the swamp, wetland size, and proximity to open water bodies and other wetland types (Golet 1976).

While red maple swamps are essential habitat for wetland-dependent species such as the northern waterthrush, they are also of great importance to facultative species, which are often considered upland wildlife. Examples include white-tailed deer, ruffed grouse (*Bonasa umbellus*), crows, American woodcock (*Scolopax minor*), several species of hawks and owls, raccoons, opossums, cottontails, squirrels, and a host of songbirds. In some urban areas, red maple swamps constitute the most significant natural habitat still available to these types of wildlife. The importance of these swamps to upland wildlife will undoubtedly increase as urbanization continues.

The social value of the wildlife habitat function of red maple swamps stems from wildlife-related activities such as hunting, birdwatching, nature study, and wildlife photography. The opportunity to observe wildlife in a natural setting is a vital part of the natural heritage value of wetlands. These pursuits are discussed later in this section.

Wood Products

In the north-central states and in the South, wetland forests are of great commercial value for lumber and pulpwood (Johnson 1979). In the Northeast, the commercial harvest of wood products in wetlands is less intensive, because of both the lower quality of the wood in many wetland forest trees and the greater availability of high-quality upland forest species. Black spruce, northern white cedar, and tamarack are species with significant commercial value, particularly where they occur in large stands. In Maine, black ash and red maple also are considered important timber species in wetlands (Widoff 1988).

The energy crisis of the 1970's in the United States prompted a reassessment of the value of many natural sources of fuel, including cordwood. Braiewa et al. (1985) demonstrated in Rhode Island that average annual biomass production of red maple on moderately well drained to very poorly drained sites (2,382 kg/ha) closely paralleled production of mixed hardwoods on moderately well drained sites (2,316 kg/ha), and greatly exceeded the production of mixed oaks on well drained sites (1,630 kg/ha). They estimated total cordwood production to be 105 cords/ha in a 55-year-old, seed-origin stand of red maple, and 50 cords/ha in a 46-year-old, sprout-origin stand. The authors concluded that southern New England red maple stands on imperfectly drained soils have high biomass production potential and should not be overlooked as a wood resource.

Large-scale commercial harvesting of wood products from northeastern red maple swamps is hindered by the relatively small size of many swamps, the complex pattern of private ownerships, and state and federal wetland protection laws. The impacts of logging on other functions and values of these wetlands, such as wildlife habitat, open space, and recreation, must be carefully considered.

Sociocultural Values

Red maple swamps are also valuable to society for their scenic beauty, their contribution to biotic diversity, and their use as recreation and open-space areas. This collection of wetland values has been variously referred to as sociocultural or heritage values (Niering 1979) and aesthetic, recreational, and landscape values (Smardon 1988).

The scenic or aesthetic value of red maple swamps is most obvious at the landscape level during early fall when the brilliant yellow, red, and orange foliage of the swamps provides striking contrast to the upland vegetation whose foliage has not yet changed from the predominantly green shades of summer. Although red maple has the greatest visual effect because of its predominance, other species such as black gum and ashes may also be striking. Mixed stands of hardwoods and conifers offer a unique contrast in fall foliage in some swamps. Red maple swamps border major highways throughout the Northeast, and each fall these bright autumn colors are seen daily by thousands of motorists. Red maple swamps clearly are a distinctive part of the scenic beauty that characterizes this region.

The aesthetic value of red maple swamps can be appreciated on a more subtle level as well: in the flowers of the spicebush, which form a yellow haze in the understory of hillside seepage swamps and along upland drainageways in early spring; in the curious hoodlike inflorescence and broad green leaves of the skunk cabbage; in the lush growth of cinnamon ferns interspersed with dark pools of water, invoking images of the primeval forest (Fig. 1.1); in the fragrant aroma of sweet pepperbush flowers (Fig. 8.1) in late summer; or in the bright red fruits of the common winterberry throughout fall and winter. These also are common sights along northeastern roads and hiking trails; they are the details that create visual diversity in a predominantly forested landscape.

The public engages in a variety of forms of recreation in red maple swamps. Depending upon the water regime and the proximity of the swamps to open water, hunters may pursue waterfowl, deer, ruffed grouse, rabbits, squirrels, or even ring-necked pheasants (*Phasianus colchicus*) in these habitats. Red maple swamps are frequented by birdwatchers as well, especially during late spring when migrating warblers and other songbirds feed on insects attracted to the flowers and breaking leaf buds of red maple trees. Canoeing, hiking, and photographing nature are other forms of recreation that may be pursued in and along the edges of red maple swamps. Picking native highbush blueberries is another activity that is part of the cultural heritage associated with these forested wetlands.

Biotic diversity, particularly the presence of rare, threatened, unique, or unusual plants and animals, is itself an aspect of our natural heritage to which red maple swamps contribute. As noted previously, many species of plants and animals found in red maple swamps are classified in threatened or endangered conservation status categories by state agencies (see Appendixes B and D). Still, documentation of the flora and fauna (especially invertebrates) in red maple swamps has been limited; more detailed surveys are needed throughout the Northeast.

Pollen preserved for thousands of years in the sediments beneath red maple swamps provides tangible evidence of the changes in climate and plant communities that have occurred in the Northeast since the retreat of the glaciers (Beetham and Niering 1961). Thus, some red maple swamps may have considerable value for research and education.

In highly urbanized areas of the Northeast, red maple swamps also provide a natural, low-cost form of open space. Frequently, the term open space is limited to aesthetics and recreational value, but in many cases its chief value may be in reducing the visual and psychological impacts of urbanization on humans and their quality of life. Public parks, athletic fields, agricultural land, and other undeveloped uplands also provide open space, but wetlands are particularly well suited to this purpose for several reasons: (1) they perform a variety of other functions, such as flood storage and water quality improvement, that are highly valued by society; (2) they are unsuitable for most other land uses because of their wetness; and (3) they are frequently distributed in a linear pattern, paralleling watercourses, which maximizes human contact with undeveloped parts of the landscape. Red maple swamps are especially effective open-space areas (Fig. 8.2); the trees and shrubs provide a tall, visual screen between developed areas and help to reduce noise emanating from

Fig. 8.1. Sweet pepperbush (*Clethra alnifolia*) in flower.

major highways or commercial and industrial zones. For all of the above reasons, the argument to preserve red maple swamps as open-space areas is both logical and compelling.

Human Impacts

Since European settlement of the glaciated Northeast began over 350 years ago, thousands of hectares of wetlands have been filled, drained, impounded, polluted, or otherwise altered. In the core of urban centers such as New York City, Boston, Providence, and Hartford, most natural wetlands probably had been eliminated prior to the late nineteenth century. Except for agricultural effects, which were highly significant in certain parts of the region, wetland losses in most rural areas were less severe until the rapid increase in urbanization that began in the mid-1900's. Passage of state and federal wetlands protection laws and regulations has slowed the rate of conversion, but weak enforcement, minimum legal size limits, and other exemptions have allowed certain wetlands to be altered without a permit. For these reasons, losses of inland wetlands are still occurring at a significant rate in many areas of the Northeast.

Documentation of the extent and causes of inland wetland losses is lacking for most of this region. Statistics are available only for southeastern Massachusetts (Larson et al. 1980; Tiner and Zinni 1988), southern Rhode Island (Golet and Parkhurst 1981), central Connecticut (Tiner et al. 1989), and Pennsylvania (Tiner and Finn 1986).

Fig. 8.2. Red maple swamp providing open space amidst residential and industrial development. Such urban swamps also are important for recreation, nature study, flood storage, water quality improvement, and wildlife habitat. *Outlined areas* labelled "u" represent upland habitats.

Table 8.1. *Examples of gross loss rates for inland vegetated wetlands in the glaciated Northeast. Losses include changes from wetland to nonwetland, wetland to open water, and wetland to farmland (including cranberry bog).*

Location	Percent loss	Study period	Source
Pennsylvania			
Northern Poconos	15	1950's–70's	Tiner and Finn (1986)
Northwestern region	5	1950's–70's	Tiner and Finn (1986)
New Jersey			
Passaic County	15	1940–78	Tiner (1985)
Central Passaic River basin	50	1940–78	Tiner (1985)
Rhode Island			
South Kingstown	1	1939–72	Golet and Parkhurst (1981)
Massachusetts			
Bristol County[a]	7	1951–71	Larson et al. (1980)
Plymouth County[b]	2	1977–86	Tiner and Zinni (1988)
15 communities[c]	4	1951–77	Organ (1983)
Connecticut			
Central region[d]	0.6	1980–86	Tiner et al. (1989)

[a] Only nonforested wetlands were included in this study.
[b] Study area included most of Plymouth County and small sections of Norfolk, Bristol, and Barnstable counties.
[c] Communities were scattered across the state, and represented a wide range of physiographic characteristics and population densities.
[d] Study area included two-thirds of Hartford County and smaller portions of New Haven, Tolland, and Middlesex counties.

Information on losses of forested wetlands is even more scarce. Because forested wetlands predominate throughout the Northeast, the loss of these wetlands is assumed to be at least as great as that for other types of inland wetlands. With minor exceptions, such as timber harvesting, the causes of forested wetland alteration also are similar to those for other inland wetland types.

Rates of Wetland Loss

Loss rates reported for inland vegetated wetlands in the glaciated Northeast vary widely with geographic location and with the geographic scope of individual studies (Table 8.1). The greatest losses have occurred near major metropolitan areas. For example, nearly 50% of the wetland area in the central Passaic River basin of northern New Jersey was destroyed between 1940 and 1978; losses in Passaic County as a whole approached 15% during that period (Tiner 1985). The 4% loss of palustrine vegetated wetland between 1951 and 1977 in 15 communities scattered across the state of Massachusetts (Organ 1983) is probably an average figure for southern New England over that period. In Bristol County, Mass., however, 7% of the inland nonforested wetlands were lost over roughly the same period (1951–71). Recent studies show that the rate of wetland conversion in southeastern Massachusetts—and undoubtedly in other areas of the Northeast as well—remains significant even after implementation of state and federal regulatory programs. Tiner and Zinni (1988), for example, found that over 2% (513 ha) of the palustrine vegetated wetland in the Plymouth County area of Massachusetts was converted to upland, to open water, or to managed cranberry bogs between 1977 and 1986. More than 260 ha of forested wetlands were lost during that 9-year period.

Principal Causes of Wetland Loss

Although documentation is lacking, conversion of wetlands for agriculture, the construction of impoundments for hydropower and water supply, and the cutting of swamp timber for lumber, fence posts, and fuelwood were probably the dominant forms of inland wetland alteration in the Northeast prior to the mid-1800's. Since that time, and especially since World War II, urbanization has emerged as the predominant force impacting wetlands in most parts of this region. The extent and causes of wetland loss have been documented in several areas of southern New England (Table 8.2).

Table 8.2. *Relative importance (% of total loss) of various causes of inland wetland loss in southern New England. Losses include changes from wetland to nonwetland, wetland to open water, and wetland to farmland (including cranberry bog).*

Cause	15 communities, Massachusetts[a] (1951–77)	Bristol County, Mass.[b] (1951–71)	Plymouth County, Mass.[c] (1977–86)	Southern Rhode Island[d] (1939–72)	Central Connecticut[e] (1977–86)
Agriculture	17	20	64		1
Impoundments	1	15	15	2	19
Highway construction	21	12	1	38	14
Residential development	21	9	3	20	10
Commercial development	25[f]	3	4	6	14
Recreational facilities	7	11	4	6	11
Public facilities	2	1	1	10	
Dumps and landfills		10			
Industry	—[g]	8		1	
Mineral extraction	1	1		6	6
Peat harvesting					
Dam removal					6
Other and undetermined	6	9	8	11	19
Total loss (ha) during study period	442	244	513	28	99
Size of study area (km^2)	1,300	1,435	1,641	159	1,997

[a] Study by Organ (1983); communities varied widely in physiography and population density.
[b] Only nonforested wetlands were inventoried (Larson et al. 1980).
[c] Study area included most of Plymouth County and small sections of Norfolk, Bristol, and Barnstable counties (Tiner and Zinni 1988).
[d] Data from South Kingstown, R.I. (Golet and Parkhurst 1981).
[e] Study by Tiner et al. (1989).
[f] Value includes commercial and industrial development.
[g] Included in data for commercial development.

A brief review of the most significant causes of wetland loss follows. All of these agents of change affect red maple swamps throughout the Northeast, but the relative importance of each varies geographically.

Agriculture

Conversion of wetlands for agriculture was a major cause of inland wetland loss in many areas of the Northeast historically, and it is still an important factor today, most notably in New York, New Jersey, and parts of southern New England. As of 1968, the State of New York had more than 14,000 ha of drained mucklands—farmed wetlands with organic soils or mineral soils high in organic matter content (Tiner 1988). The bulk of these drained wetlands are located in the Lake Ontario basin and in southeastern New York. Muckland farming and drainage for pasturage have been significant causes of wetland loss in Middlesex, Sussex, and Warren counties in northern New Jersey as well (Tiner 1985).

Most of the managed cranberry bogs in the Northeast have been developed in former palustrine vegetated wetlands. Larson et al. (1980) found a net increase of 28 ha of cranberry bogs in Bristol County, Mass., between 1951 and 1971. In nearby Plymouth County, 172 ha of vegetated wetlands were converted to cranberry bogs between 1977 and 1986 (Tiner and Zinni 1988). Nearly 100 ha of those new bogs were produced from forested wetlands, the majority of which were red maple swamps (Fig. 8.3). Other forested wetlands in the vicinity were impounded to provide irrigation water for the cranberry bogs. Overall, conversion to agriculture (cranberry bogs or cropland) was responsible for 64% of the wetland loss measured by Tiner and Zinni (Table 8.2). In some areas of New England, where agricultural practices have been abandoned, the lack of maintenance of drainage ditches has caused the land to revert to wetland (Office of Technology Assessment 1984).

Fig. 8.3. Southern New England red maple swamp cleared for cranberry bog expansion.

Construction of Impoundments

Major impacts to vegetated wetlands occurred when thousands of dams were constructed on northeastern streams for hydropower, industrial and public water supply, flood control, and recreation. Where impoundments were small, and associated streams were high-gradient, the losses of wetland probably were small at any single site, but the cumulative impacts of these dams must have been considerable. Where constructed lakes were large, such as Flagstaff Lake in Maine, thousands of hectares of swamp were inundated (Widoff 1988). Widoff estimated that losses of vegetated wetland to impoundments in Maine may exceed 12,000 ha, nearly 30% of the total wetland loss—second only to wetland losses from urbanization. Tiner (1985) listed reservoir construction as a major cause of wetland loss in New Jersey as well. In trend analysis studies of wetlands in southeastern Massachusetts (Larson et al. 1980; Tiner and Zinni 1988), construction of impoundments was found to be responsible for about 15% of vegetated wetland losses. The principal functions of these water bodies were municipal water supply and water storage for irrigation of cranberry bogs.

Highway Construction

Although road construction can be considered one facet of urbanization (see below), it is treated separately here because of its importance. Highway construction represents one of the most significant causes of wetland alteration in the Northeast, both directly through wetland filling and draining, and indirectly by improving access to formerly isolated areas and thus stimulating secondary incursions into wetlands. Construction of interstate highways through northern New Jersey, for example, has filled large areas of wetland and, at the same time, fragmented major wetland complexes, permitting the continued expansion of the New York metropolitan area (Tiner 1985). This same phenomenon can be observed in the vicinity of any of the major urban areas in the Northeast.

In rural areas, filling due to highway construction may represent one of the primary causes of wetland loss. Road-building was the most frequent type of impact identified in a random survey of 100 Vermont wetlands (Wanner 1979). Between 1951 and 1971, nearly 30 ha of inland wetland were directly lost to road construction in Bristol County, Mass.; another 36 ha of wetland were converted from one wetland type to another as the new roads altered wetland water regimes (Larson et al. 1980). In South Kingstown, R.I., road construction accounted for almost 40% of the wetland loss between 1939 and 1972 (Golet and Parkhurst 1981). In Maine, Widoff (1988) estimated that roads were responsible for about 10% of the state's total wetland loss.

Urbanization

In most areas of the Northeast, urbanization (including highway construction) is now responsible for more inland wetland losses than all other causes combined. In major metropolitan areas, it has been the principal factor for decades. The impact of urbanization on wetlands in any geographic area usually is closely related to the population density of that area. Once again, northern New Jersey is a prime example. The Office of Technology Assessment (1984) reported that 20–50% of Troy Meadows and three large swamps (Great Piece, Little Piece, and Hatfield) in the Passaic River basin have been destroyed as a result of highway construction and subsequent commercial, industrial, and residential development. The effects of urbanization are noticeable even in the most rural parts of the Northeast. Construction of interstate highways has spawned a series of resort communities in areas such as the Poconos of northeastern Pennsylvania (Tiner 1984), upstate New York, and the White Mountains of New Hampshire. Significant wetland losses have occurred in some of those areas as a result.

Data gathered in southern New England trend analysis studies (Table 8.2) suggest that residential and commercial development and the development of recreational facilities such as golf courses and athletic fields frequently contribute heavily to wetland losses in rural and suburban areas undergoing rapid population increases. Once again, road construction is an integral part of such urbanization. In Maine, as in much of the Northeast, the impacts of urbanization were historically greatest in coastal wetlands and along major rivers (Widoff 1988). Current losses are most common in small (less than 4 ha) inland wetlands in southern Maine where population growth has been most dramatic. Widoff ranked residential and commercial development as the single most important cause of vegetated wetland loss in Maine; she estimated that urbanization has been responsible for nearly 40% (more than 16,000 ha) of the total losses.

Peat Harvesting

One additional agent of wetland destruction in some areas of the Northeast is the harvesting of peat, primarily for horticultural use. Peat harvesting is a major industry in states such as Minnesota and North Carolina, but it has been practiced to some degree in several of the northeastern states as well. It is an important cause of wetland loss in the Poconos of northeastern Pennsylvania (Tiner 1984). In Maine, this industry peaked during the 1930's and 1940's, but most operations closed down for economic reasons (Widoff 1988). Widoff estimated that 2% (910 ha) of Maine's vegetated wetland loss may be due to peat harvesting.

Peat harvesting for horticulture generally is carried out in *Sphagnum* bogs, which contain large quantities of poorly decomposed fibric peat. This type of peat has the highest moisture retention capacity and so is most valuable as a soil conditioner. Since red maple swamps have mineral soils or well-decomposed (sapric) to moderately well-decomposed (hemic) organic soils, they are of little value as a source of horticultural peat. During the 1970's, when the United States experienced a brief, but severe, shortage of fossil fuels, considerable attention was focused on the possible use of peat as a supplementary energy source. The uncertainty of continued fossil fuel availability suggests that pressures to harvest peat from northeastern wetlands for energy production may increase. Sapric and hemic peats generally have higher energy value per unit of weight than fibric peat (Farnham 1979). For this reason, red maple swamps and other types of forested wetlands with organic soils may be seriously considered as potential sources of energy-producing peat in future years.

Other Forms of Wetland Alteration

Although direct losses clearly have the greatest impact on the wetland resource, other alterations beside total destruction may also significantly affect the structure and functions of wetlands and their value to society. The following paragraphs identify some of these additional forms of alteration.

Tree Cutting

Cutting of wetland trees for fuel and fence posts was common in the Northeast prior to the decline of agriculture in the late nineteenth century. Widoff (1988) noted that timber harvesting is still widespread in Maine wetlands during the winter. In southern Rhode Island (Golet and Parkhurst 1981) and in New Jersey (Tiner 1985), selective cutting of Atlantic white cedar has converted some mixed wetland forests to predominantly red maple. Larson et al. (1980) speculated that much of the shrub swamp and shallow marsh in their southeastern Massachusetts study area was formerly forested wetland that had been cleared for

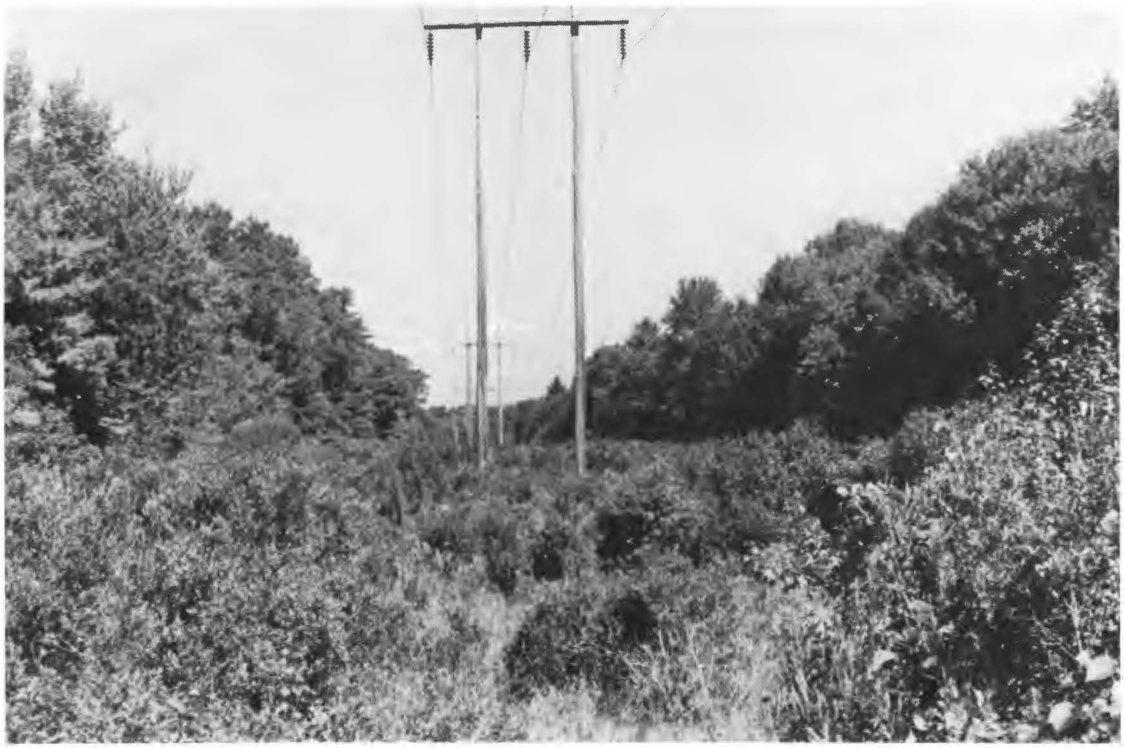

Fig. 8.4. Electric utility lines passing through a former red maple swamp. Forested swamp flanks the powerline on either side while shrub swamp dominates the right-of-way.

agricultural purposes. In northeastern Connecticut, red maple swamps were sometimes clear-cut for fuelwood during the first half of the twentieth century (Grace 1972).

Clearing of forested wetland for utility rights-of-way is a major form of alteration that is growing in importance throughout the Northeast (Fig. 8.4). In a sample of 100 Vermont wetlands surveyed in 1974, 14% had been affected by transmission lines (Wanner 1979). The impacts of cutting usually are compounded by wetland filling for the construction of power line maintenance roads.

The degree of impact of timber removal on wetland functions and values depends on the intensity of cutting. Clear-cuts radically alter habitat values and may result in slightly higher water levels during the summer because of reduced transpiration losses; selective cutting may have far less impact. Timber harvesting for wood products is not currently a major form of alteration in red maple swamps, but increasing energy costs and elimination of upland forests by urbanization may heighten the importance of this activity in the future.

Water Level Manipulation

Human-induced changes in the water regime of a red maple swamp may have major impacts on the floristic composition and structure of the plant community, its habitat values, and its scenic and recreational values. Prior to the passage of wetland protection regulations, changes in wetland water regimes were a common consequence of highway construction. Culverts that were incorrectly designed, improperly installed, or omitted altogether frequently resulted in impoundment of water on the upstream side of the road and a reduction in surface-water flow to the downstream side. Such impoundment commonly converted red maple swamps to marshes or shrub swamps. These impacts are less common today where wetland regulations are strictly enforced; however, sediment accumulation in culverts under roads may cause gradual changes in water regimes with the same ultimate result (Golet and Parkhurst 1981). Nearly 60% of the human-induced changes in inland wetlands of South Kingstown, R.I., between 1939 and 1972 were retrogressive; raised water levels were the cause in most cases.

Groundwater withdrawal by large municipal wells has been a suspected cause of water level declines in a number of swamps in southern New England (D. Albro, Rhode Island Department of Environmental Management, Providence, personal communication; F. Golet, personal observation), but none of these cases has been documented through field measurement. Heavy withdrawal of surface water from streams and lakes for irrigation of crops also may lower water levels in adjacent swamps, particularly in dry summers. Reductions in surface-water hydroperiods in both instances could adversely affect the habitat value of forested swamps for amphibians, waterfowl, and wetland-dependent songbirds such as the northern waterthrush. In some southern New England communities, extensive networks of ditches have been constructed in red maple swamps for the purpose of mosquito control.

Stormwater and Wastewater Discharges

The addition of stormwater runoff and wastewater effluent to red maple swamps may alter both the hydrologic regime and water quality (Fig. 8.5). The volume of storm water runoff entering wetlands from surrounding upland areas may increase dramatically as those areas are urbanized. The increase in impervious surface area (highways, parking lots, rooftops) that accompanies urbanization decreases groundwater recharge and increases runoff. Increased runoff can

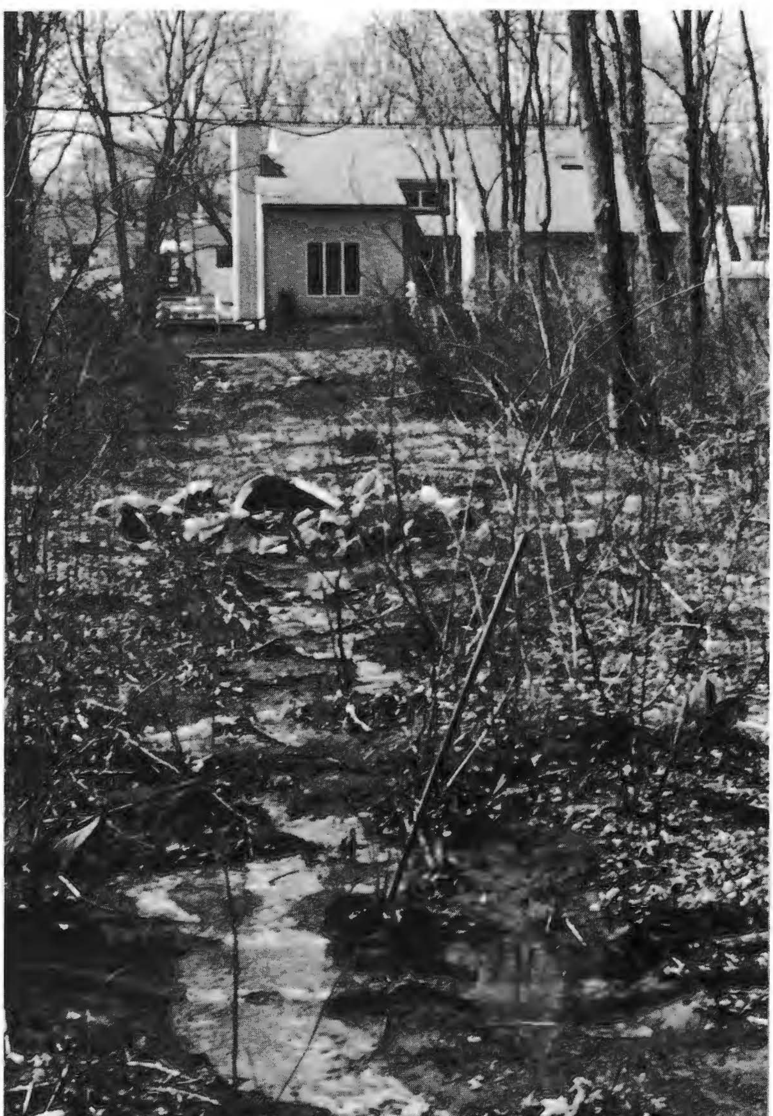

Fig. 8.5. Stormwater discharge in a red maple swamp. Such discharges may alter both water regime and water quality in these wetlands.

be expected to cause more drastic fluctuations in wetland surface-water levels, especially where the wetlands are located in isolated basins with restricted outlets. The greater fluctuation and generally greater volume of surface water entering the wetland may reduce plant productivity and eventually change both the structure and species composition of the plant community; wildlife habitat values may be seriously affected as well. Without proper management of runoff in major land development projects, swamps receiving such waters may become little more than detention basins.

Stormwater runoff may introduce a wide variety of pollutants into wetlands. Highways, parking lots, cropland, animal feedlots, landfills, and sludge disposal sites are some of the land uses that may contribute significantly to surface-water pollution of wetlands. Among the various pollutants are road salt; oil, grease, gasoline, and other petroleum products; suspended sediment; fertilizers; pesticides; heavy metals; and chlorinated hydrocarbons. Runoff from landfills may contain a variety of hazardous wastes. The effects of many of these pollutants on red maple swamps is unknown, but it is highly likely that the accumulation of such substances in wetland soils adversely affects plant growth, invertebrate life in the soil and in surface waters, amphibians, and other forms of wildlife higher in the food chain. Ehrenfeld (1983) demonstrated increased flooding and significant changes in plant species composition and water chemistry in southern New Jersey swamps receiving runoff from urbanized areas.

Discharges of wastewater from sewage treatment facilities or from various industries may have major adverse effects on wetlands. The effects on wetland hydrology and water quality are similar to those from stormwater runoff, but often much more pronounced because of the greater volume of water discharged, the greater concentration of pollutants in the water, and more sustained discharge.

Alteration of Surrounding Uplands

Human activities in upland areas immediately adjacent to red maple swamps (Fig. 8.2) also may adversely affect the functions and values of those wetlands. Clearing of natural vegetation, reduction of groundwater recharge through paving, and installation of belowground sewage disposal systems are common examples.

Natural, undisturbed surroundings may meet some of the habitat requirements of wildlife residing in wetlands. They may help to buffer the direct impacts of human activity (e.g., noise) on wetland wildlife, and may serve as the primary habitat for species such as salamanders, which use swamps for breeding. Clearing of vegetation and other land disturbance near the wetland edge may have a major adverse effect on the value of the wetland to wildlife. Unless provisions are made to artificially recharge the groundwater system when large tracts of land are paved, local water tables may drop in the developed area, which, in turn, may reduce the quantity and duration of groundwater flow to adjacent wetlands, lowering wetland water levels as well. Despite increases in surface-water runoff reaching the wetland, average summer water levels may drop below normal if groundwater inflow formerly was an important component of the wetland's water budget.

Finally, the installation of belowground septic systems near the wetland edge may degrade water quality in wetlands and associated water bodies, particularly if upland soils are low in permeability or have high water tables. Either of these conditions may cause effluent to discharge in the wetland. Septic systems sited close to wetlands in soils with excessively high permeability also represent a significant water-quality threat because of the speed with which effluent can flow toward the wetland, even if the system is properly maintained.

Key Management Issues

Through the regulation of land use in and around northeastern inland wetlands, federal, state, and local regulatory agencies and commissions have assumed the role of wetland resource managers. It is their responsibility to maintain the natural functions and values of wetlands, to prevent wetland loss and degradation, to protect the public from the hazards of development in wetlands, and, in some cases, to mandate restoration of wetlands that have been altered. The task of safeguarding the public interest in wetlands is beset with practical, technical, and philosophical problems. Resolution of these problems is hindered not only by agency staff and budget limitations, but also by a dearth of scientific data on wetland characteristics and values, and a lack of standard procedures for addressing tasks such as wetland identification and delineation, the assessment of wetland functions and values, impact assessment, and mitigation. The following discussion highlights some of the key management issues affecting red maple swamps in the glaciated Northeast.

Boundary Delineation

Wetland identification and delineation are a critical first step in the regulatory process. This step determines which parcels of land are subject to regulation and defines the area within which values and environmental effects will be assessed. In some instances, the transition from wetland to upland is abrupt, the changes in vegetation and soils are obvious, and the location of the wetland boundary is subject to little debate. In other cases, where the slope of the moisture gradient is gradual, no well-defined break may be apparent. The task of boundary location is especially difficult in many red maple swamps because the dominant plants in the swamps are usually facultative species (FACW, FAC, or FACU) that also grow in the adjacent uplands. Swamps located on hillsides or over perched groundwater systems pose a particular problem because changes in surface elevation may not directly correspond to variations in soil moisture.

"Multiparameter" approaches to wetland delineation (e.g., Environmental Laboratory 1987; Federal Interagency Committee for Wetland Delineation 1989) generally assume that vegetation, soils, and hydrologic criteria are perfectly correlated. Actually, empirical data on relations among these three classes of variables are lacking for most wetland types (Allen et al. 1989). Even if the criteria set forth in a particular method are strongly correlated, the accuracy of the method will be limited, if only because the criteria themselves are gross simplifications of nature (Scott et al. 1989).

Allen et al. (1989) tested the agreement between the hydric status of soils, as determined from the national hydric soils list (U.S. Soil Conservation Service 1987), and the average wetland indicator status (Reed 1988) of plants growing in the transition zones of three Rhode Island red maple swamps. They found that herb layer vegetation exhibited the most clearly defined moisture gradient, correlated best with hydric soil status, and permitted the most precise discrimination between upland and wetland. A moisture-related gradient was reflected in the tree layer also, but it was not as consistent as in the herb layer. In the two shrub layers examined, the predominance of facultative species along the entire length of most wetland-to-upland transects obscured moisture-related gradients in vegetation. For this reason, the shrub layers were found to be of little value in locating a wetland–upland vegetation break. Local variations in surface elevation and soil properties often caused the status (wetland vs. upland) of contiguous sample plots to alternate, even in the herb layer; in such instances, the wetland boundary was more aptly represented as a zone, rather than a line. Boundary zones derived from herb layer data ranged in width from 5 to 46 m.

The development of standard hydrologic criteria for wetland delineation is probably unfeasible because of the complex variability in hydrologic conditions over time and the lack of long-term measurements at specific sites. As already noted, boundary determination using only vegetation may be difficult to achieve in many red maple swamps because of the high proportion of facultative species. For these reasons, it seems appropriate to place major emphasis on the hydric status of soil in the delineation of red maple swamps (Allen 1989). This conclusion is consistent with the hierarchy of decisions in the *Federal Manual for Identifying and Delineating Jurisdictional Wetlands* (Federal Interagency Committee for Wetland Delineation 1989). In the Northeast, most hydric soils are very poorly drained or poorly drained (Tiner and Veneman 1987). Consistent inclusion of these two drainage classes of soils within regulated wetlands is logical also from the standpoint of wetland functions and values and hazards to development.

Mitigation by Replacement or Enhancement

Since the mid-1980's, the term "wetland mitigation" has become synonymous with wetland replacement or enhancement (Golet 1986). Replacement entails the creation of new wetland from upland to compensate for the wetland destroyed in a particular project. Enhancement proposals generally seek to compensate for wetland losses by changing a remaining part of the wetland that is to be altered, or changing a nearby wetland, in a manner that enhances certain functions or values. For example, conversion of one area of forested wetland to marsh by artificially raising the water level might be proposed as a means of increasing the wetland's value for waterfowl and compensating for the filling of a second area of wetland for development purposes. Mitigation by replacement and enhancement has been a highly controversial topic in recent years, for both scientific and philosophical reasons (Golet 1986; Larson and Neill 1987; Thompson and Williams-Dawe 1988). Kusler et al. (1988) presented a comprehensive review of mitigation issues, approaches, and policies. Important issues surrounding this topic are outlined below.

The scientific standard for determining whether mitigation is truly replacing the lost wetland should be functional performance (Larson and Neill 1987); that is, the replacement wetland should be able to perform the same functions as the wetland destroyed. Adamus (1988) took the additional step of recommending that replacement wetlands have the same or higher ratings for every function. To fully restore lost habitat values, replacement wetlands should be of the same type as the wetland destroyed, and should be located as near the original wetland as possible so that the benefits of the original wetland are still enjoyed locally.

In the northeastern United States, proposals for mitigation of forested wetland habitat losses usually involve either the creation of new wetland habitats, most commonly ponds or marshes, or the conversion of existing shrub or forested wetland to marsh through manipulation of water levels. Applicants, and sometimes regulatory agencies as well, have attempted to justify such out-of-kind replacement and enhancement by stating that these practices result in greater wildlife habitat diversity, and that marshes are less abundant than swamps and more valuable to wetland-dependent wildlife such as waterfowl. In actuality, out-of-kind replacement and enhancement are the only alternatives available in such cases because it has not been demonstrated that viable forested wetlands can be created from upland. The development of a mature forested wetland would take at least 40–50 years, even under natural conditions where wetland soils were already established. For this reason, both the technical feasibility and the practicality of swamp replacement must be questioned.

Net losses of wetland are characteristic of habitat mitigation projects involving wetland enhancement, because the goal of these projects is to compensate for outright losses of wetland by altering or improving the habitat characteristics of existing wetlands. The use of enhancement methods to mitigate losses of forested wetland habitat is often doubly damaging because forested habitat is lost both during the proposed development project and during the enhancement process (e.g., as wetland forest is converted to marsh).

Protection of Buffer Zones

Regulation of land use in upland areas bordering wetlands is critical to the maintenance of wetland functions and values (Clark 1977; Roman and Good 1986; Brown and Schaefer 1987). Natural, undisturbed surroundings reduce the adverse effects of development on wetlands and contribute directly to certain wetland functions such as wildlife habitat. Where land use in adjacent uplands is restricted by wetland regulatory agencies, these areas are commonly referred to as wetland buffer zones. A wide variety of functions and values have been recognized for wetland buffer zones; some of the major ones are outlined below.

Functions and Values of Buffer Zones

Surrounding uplands are essential habitat for both wetland wildlife species, which reside primarily in the wetland, and upland species, which use the wetland on an occasional basis or for breeding (Golet and Larson 1974; Golet 1976; Porter 1981; Brown and Schaefer 1987). Wood ducks, for example, sometimes nest in the cavities of trees that are located in adjacent upland forests. Upland species such as white-tailed deer and ruffed grouse are commonly observed along the upland edge of forested wetlands where cover is dense. Wetland-dependent upland species, including certain salamanders and toads, reside in upland habitats near swamps most of the year, but require the wetlands for breeding. In addition to providing wildlife habitat directly, undisturbed surrounding uplands also reduce the impact of noise and other human activity on wetland wildlife. Natural buffer zones may provide a refuge for wildlife during periods of exceptionally high water as well (Brown and Schaefer 1987).

Only Husband and Eddleman (1990) have examined wildlife use in upland habitats directly adjacent to red maple swamps. Between March and November in 1989, and March and August in 1990, selected groups of vertebrates were censused in the transition zone extending from red maple swamps into the adjacent upland forest at four sites in southern Rhode Island. During these periods, 14 species of amphibians, 3 species of reptiles, and 14 species of mammals were captured (Table 8.3). The most remote, least disturbed site had the highest number and diversity of reptiles and amphibians, while the most disturbed sites had the highest number and diversity of mammals. Three species of mammals classified as "state-rare" were captured: water shrew, smoky shrew (*Sorex fumeus*), and southern bog lemming (*Synaptomys cooperi*). Forty-nine species of birds were observed during June and July; of these, 19 were Neotropical migrants of potential concern to wildlife management (Table 8.3).

Undisturbed buffer zones perform several important hydrologic functions. They may reduce the velocity of storm-water runoff, thereby allowing infiltration of water into the soil and reducing the volume of runoff entering wetlands during major storm events. This storm water abatement function prevents the drastic fluctuations in wetland water levels that may be hazardous to ground-nesting birds and other wildlife. As noted above, large-scale paving of upland areas surrounding wetlands reduces groundwater recharge, which, in turn, may lower summer water levels in wetlands where groundwater was a major inflow component prior to development. Thus, buffer zones may play an important role in wetland hydrology. Upland areas directly adjacent to wetlands may also serve as supplementary flood storage areas.

While wetlands themselves frequently play an important role in the removal, retention, and transformation of a wide variety of surface-water pollutants, there is undoubtedly a limit to the amount they can process without adverse effects on wildlife, the plant community, and other ecosystem components. For this reason, every attempt should be made to minimize the inflow of pollutants to wetlands. Establishment of natural, undisturbed buffer zones around wetlands helps greatly

Table 8.3. *Birds and mammals observed in the transition zone between red maple swamp and upland forest in Rhode Island (from Husband and Eddleman 1990). See Table 7.2 for amphibians and reptiles.*

Birds
- American crow
- American goldfinch
- American redstart[a]
- American robin
- Belted kingfisher
- Black-and-white warbler[a]
- Black-capped chickadee
- Black-throated green warbler[a]
- Blue jay
- Blue-winged warbler[a]
- Brown creeper
- Brown-headed cowbird
- Canada warbler[a]
- Carolina wren
- Chestnut-sided warbler[a]
- Chipping sparrow
- Common yellowthroat
- Downy woodpecker
- Eastern kingbird[a]
- Eastern phoebe
- Eastern wood-pewee[a]
- European starling
- Gray catbird[a]
- Great crested flycatcher[a]
- Hairy woodpecker
- Hermit thrush
- House wren
- Northern cardinal
- Northern flicker
- Northern mockingbird
- Northern waterthrush[a]
- Ovenbird[a]
- Pine warbler
- Purple finch
- Red-eyed vireo[a]
- Red-winged blackbird
- Rose-breasted grosbeak[a]
- Ruby-crowned kinglet
- Ruffed grouse
- Rufous-sided towhee
- Scarlet tanager[a]
- Song sparrow
- Swamp sparrow
- Tufted titmouse
- Veery[a]
- White-breasted nuthatch
- White-eyed vireo[a]
- Wood thrush[a]
- Yellow warbler[a]

Mammals
- Eastern cottontail
- Long-tailed weasel
- Masked shrew
- Meadow jumping mouse
- Meadow vole
- Northern short-tailed shrew
- Smoky shrew
- Southern bog lemming
- Southern red-backed vole
- Star-nosed mole
- Virginia opposum
- Water shrew
- White-footed mouse
- Woodland jumping mouse

[a] Neotropical migrant.

by capturing sediment, reducing nutrient loads, and filtering other pollutants before they reach the wetland (Brown and Schaefer 1987).

A considerable body of experience has developed on pollution attenuation in artificial buffer strips (Clark 1977). Research on natural systems is more limited, but recent findings are encouraging. For example, forested buffer zones in Maryland and North Carolina have been shown to remove as much as 80% of the excess nitrogen and phosphorus from agricultural runoff (Hall et al. 1986). In a 2-year study conducted in southern Rhode Island, Gold and Simmons (1990) injected a "spike" of nitrate, copper, and a tracer into the ground upgradient from forested upland and red maple swamp monitoring stations at three sites. They found complete attenuation of copper in the groundwater at all stations. Nitrate removal ranged from 14 to 87% in the forested upland, where soils were moderately well drained or somewhat poorly drained; in the swamp, it was almost complete in both poorly drained and very poorly drained soils. The highest attenuation occurred where groundwater levels were closest to the surface. The authors concluded that forested buffer zones can protect wetland and surface-water systems from water quality degradation throughout the year; however, long-term performance may vary because plant uptake and microbial immobilization of nitrate are temporary nutrient sinks.

One of the unique aspects of many buffer zones is the high species richness of both plants and animals (Porter 1981). As a transitional area between wetland and upland, the buffer zone commonly contains species that are representative of both communities (Anderson et al. 1980; Davis 1988). Moisture is characteristically abundant in this zone, but not limiting to plant growth; as a result, forest productivity is often higher there than in more droughty upland soils (Braiewa et al. 1985). Upland habitats along the wetland edge have also been cited as the main source for seeds contributing to the spatial heterogeneity of wetlands (Brown and Schaefer 1987).

The Issue of Buffer Width

One of the most vigorously contested issues in public hearing rooms throughout the Northeast in recent years has been the minimum width of buffer zone required to safeguard wetland ecosystems from the adverse impacts of development. Proposals have ranged widely, from as much as 150 m to as little as 15 m. There has been so little research on the basic characteristics and functions of wetland buffer zones that the development of scientifically valid criteria for determining buffer zone width has been difficult (Jordan and Shisler 1988). As a result, buffer zone widths established by regulatory agencies often have been arbitrary.

The Rhode Island Freshwater Wetlands Act (G.L., Chap. 2-1, Sect. 18 et seq.), passed in 1971, was the first inland wetlands law to include a buffer; all land within 15 m of the edge of ponds, marshes, swamps, and bogs is considered part of those wetlands and is regulated accordingly. New Jersey's Freshwater Wetlands Protection Act (NJ S.A. 13:9B-1 et seq.), which was passed in 1987, contains the most sophisticated treatment of buffer zones (termed transition areas in the law) to date. The act requires that all freshwater wetlands be classified as exceptional, intermediate, or ordinary. Exceptional wetlands, which provide habitat for threatened or endangered species or which border trout production waters, have a 46-m transition area. Transition areas are not required for ordinary wetlands, which include ditches, swales, detention basins, and isolated wetlands less than 465 m^2 in area with development along at least 50% of their borders. All other wetlands, which are considered to be of intermediate value, have 15-m transition areas.

A major contribution toward the development of buffer zone criteria was made by researchers in the New Jersey pinelands (Roman and Good 1985). In their buffer delineation model, buffer width is determined by numerically rating both the natural quality, values, and functions of a wetland and the potential for site-specific, cumulative, and watershed-wide impacts of development. Indices for relative wetland quality and relative environmental effects are averaged, and the resulting buffer index is translated into a buffer width by using a conversion table. This is the only quantitative procedure that rates both wetland values and impacts.

Working in the Wekiva River Basin of central Florida, Brown and Schaefer (1987) also developed quantitative criteria for buffer delineation. Key functions addressed were water quality maintenance, water quantity maintenance, and wildlife habitat. Buffer width was determined from existing scientific data on soil erodibility, depth to the water table, and the habitat requirements of representative wildlife species known to inhabit the area. Buffer zone widths were calculated for each function, and the largest width was considered to be controlling in any given area. Buffer widths

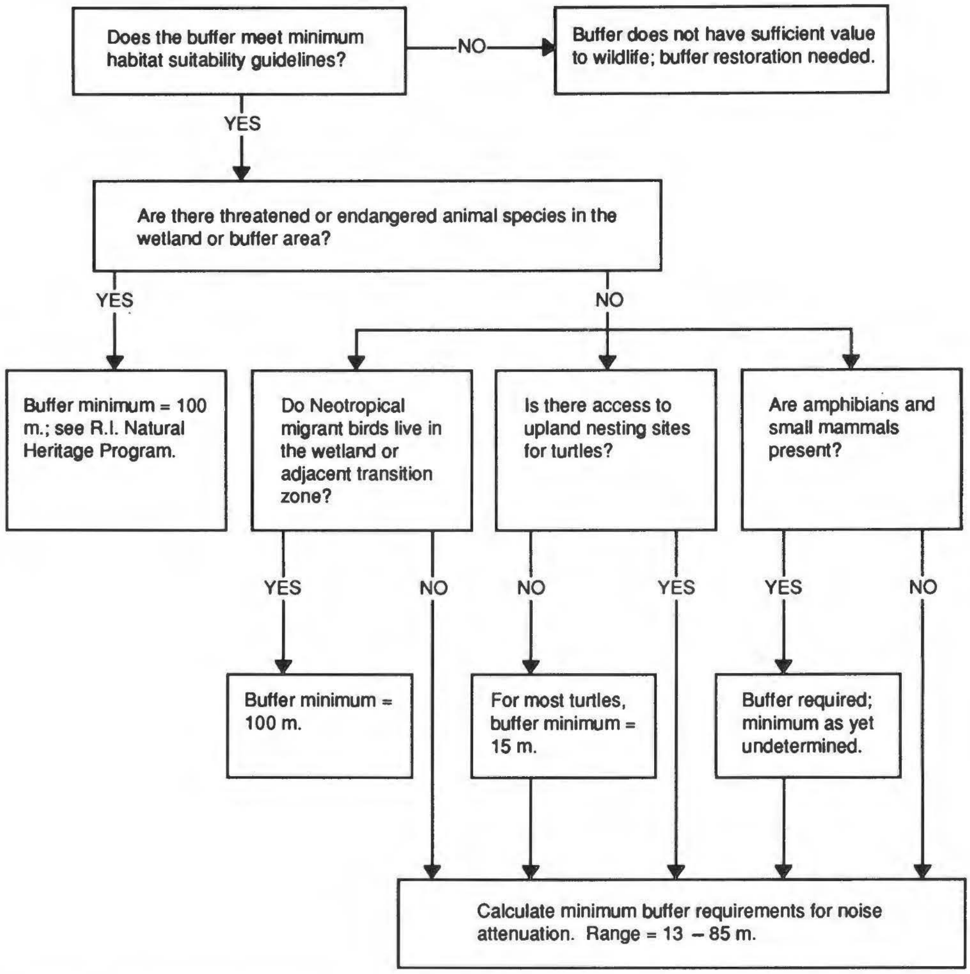

Fig. 8.6. Wetland buffer width model developed for wildlife habitat functions in Rhode Island red maple swamps (after Husband and Eddleman 1990).

ranged from as little as 13 m for water quality maintenance in areas with low slope and low soil erodibility to as much as 163 m for individual wetland-dependent animals of most species living in the watershed.

Husband and Eddleman (1990) developed a preliminary buffer width model for Rhode Island red maple swamps using four wildlife habitat factors outlined in the Wekiva River basin study (Brown and Schaefer 1987): (1) habitat suitability, (2) wildlife spatial requirements, (3) access to upland or transitional habitats, and (4) noise impacts on wildlife life functions. Buffer widths calculated for these four variables ranged from 13 m for noise attenuation under optimal conditions (i.e., forested buffer and residential noise) to 100 m for spatial requirements of forest interior bird species, small mammals, and reptiles and amphibians. A buffer exceeding 100 m was recommended for swamps with threatened or endangered species. Figure 8.6 outlines the decisions leading to a final buffer width determination in the Rhode Island model.

Exempted Wetlands

One additional problem hindering wetland protection is the wetland loss that results from exemptions on the basis of wetland size or type. As noted earlier in this report, several northeastern states have size minima for protection. In Rhode Island, swamps smaller than 1.2 ha are not regulated as stringently as larger swamps (G.L., Chap. 2-1, Sect. 20). In New York, the minimum size limit for all regulated wetlands is 5 ha unless the wetland can be shown to be of unusual local importance (Riexinger 1986). In Maine, inland wetlands are protected only if they are 4 ha or larger (Title 38, M.R.S.A., Sect. 480A). Research by Merrow (1990) on breeding-bird communities in red maple swamps demonstrated that swamps as small as 0.5 ha support wetland-dependent species such as the northern waterthrush. Swamps smaller than the size minima listed above clearly may have significant public value for flood storage, water quality improvement, wildlife habitat, scenic value, and open space, particularly in urban areas. And, although individual losses of small wetlands may seem minor, the cumulative effects on flood levels, water quality, wildlife populations, and the quality of human life may be highly significant.

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Appendix A. Sources of Floristic Data for Northeastern Red Maple Swamps

Zone I: Southern New England Upland, Seaboard Lowland, and Coastal Plain

Anderson et al. (1980)
Baldwin (1961)
Braiewa (1983)
Buell and Wistendahl (1955)
Cain and Penfound (1938)
Conard (1935)
Damman and Kershner (1977)
Davis (1988)
Davis, R. B. (University of Maine, Orono, unpublished data)
Deland (1986)
Egler and Niering (1967)
Fosberg and Blunt (1970)
Goodwin and Niering (1975)
Grace (1972)
Greller (1977)
Hale (1965)
Hanks (1985)
Harper (1917)
Holland and Burk (1984)
Hunter, M. L., and J. Witham (University of Maine Holt Research Forest, Aroosik, unpublished data)
Kershner (1975)
Laundre (1980)
Lowry (1984)
Messier (1980)
Metzler (1982)
Metzler and Tiner (1992)
Moore (1959)
National Wetlands Inventory Field Data (U.S. Fish and Wildlife Service, Newton Corner, Mass.)
Nichols (1915, 1916)
Niering (1953)
Niering and Goodwin (1962, 1965)
Nowell, H. (New Hampshire Fish and Game Department, Concord, personal communication)
Osvald (1970)
Profous and Loeb (1984)
Sorrie, B. A. (Massachusetts Natural Heritage Program, Boston, personal communication)
Swift (1980)
Tiner (1985, 1989b)
Vogelmann (1976)
Wistendahl (1958)
Wright (1941)

Zone II: Great Lakes and Glaciated Allegheny Plateau

Bray (1915)
Brooks et al. (1987)
Brooks and Tiner (1989)
Cowardin (1965)
Golet (1969)
Goodwin (1942)
Huenneke (1982)
Malecki et al. (1983)
McVaugh (1958)
National Wetlands Inventory Field Data (U.S. Fish and Wildlife Service, Newton Corner, Mass.)
Paratley and Fahey (1986)
Phillips (1971)
Reschke (1990)
Reed (1968)
Shanks (1966)
Stewart and Merrell (1937)
Thompson et al. (1968)
Van Dersal (1933)

Zone III: St. Lawrence Valley and Lake Champlain Basin

Bray (1915)
Goodwin and Niering (1975)
Marshall, E. (Vermont Natural Heritage Program, Burlington, personal communication)
National Wetlands Inventory Field Data (U.S. Fish and Wildlife Service, Newton Corner, Mass.)
Thompson (1988)
Thompson, E. (Vermont Natural Heritage Program, Burlington, personal communication)
Vogelmann, H. W. (University of Vermont, Burlington, personal communication)
Vosburgh (1979)

Zone IV: Northeastern Mountains

DeGraaf and Rudis (1990)

National Wetlands Inventory Field Data (U.S. Fish and Wildlife Service, Newton Corner, Mass.)

Calcareous Seepage Swamps

McVaugh (1958)
Metzler (1982)
Metzler and Tiner (1992)
New Hampshire Natural Areas Program (1983)
Rawinski (1984)
Reschke (1990)
The Nature Conservancy (Eastern Regional Office, Boston, unpublished data)
Thompson, E. (Vermont Natural Heritage Program, Burlington, personal communication)
Sorrie, B. A. (Massachusetts Natural Heritage Program, Boston, personal communication)

Appendix B. Plants of Special Concern That Have Been Observed in Northeastern Red Maple Swamps[a]

Species[d]	State[b] and conservation status[c]								
	Maine	N.H.	Vt.	Mass.	R.I.	Conn.	N.Y.	Pa.	N.J.
Trees									
Abies balsamea						S1			
Betula papyrifera									S2
Carya cordiformis	SU								
Carya laciniosa							S1		
Chamaecyparis thyoides	S2						S3	SX	
Fraxinus nigra					S2				
Larix laricina					S1				
Liquidambar styraciflua						S2/S3			
Liriodendron tulipifera			SH						
Magnolia virginiana				S1			S1	S2	
Nyssa sylvatica			S2						
Picea mariana						S2			
Picea rubens						S2			S2
Platanus occidentalis	SH								
Quercus coccinea	SH		S1						
Quercus imbricaria									S1
Quercus macrocarpa		SU		S3		S1			
Sassafras albidum	S2		S3						
Thuja occidentalis				S1		S1			S1
Ulmus rubra	SH				S1				
Erect shrubs and woody vines									
Acer pensylvanicum					S1				
Acer spicatum						S1			
Betula pumila	S3/S4	S1	S1	S2		S2	S2		S3
Celastrus scandens					S1				
Celtis occidentalis		S2							
Clethra alnifolia	S1								
Ilex glabra	S1					S1		SX	
Ilex laevigata	S2		SU						
Kalmia latifolia	S3/S4		S3						
Ledum groenlandicum					S1/S2		S3	SX	
Leucothoe racemosa								S3	
Lindera benzoin	S2		S3						
Lonicera dioica	S1				S1				
Lyonia ligustrina			S3						
Menispermum canadense		S1							
Myrica gale								S2	
Potentilla fruticosa								S1	
Rhamnus alnifolia								SU	S3

Appendix B. *Continued.*

Species[d]	State[b] and conservation status[c]								
	Maine	N.H.	Vt.	Mass.	R.I.	Conn.	N.Y.	Pa.	N.J.
Rhododendron canadense						S3	S2		S1
Rhododendron maximum	S1	S2	S2	S2		S3			
Rhododendron periclymenoides		S1			S1				
Rhododendron viscosum	S1	S2							
Ribes hirtellum					S1				S3
Ribes lacustre				S3		SH		S2	
Ribes triste				S3		SH		S1	SU
Rosa virginiana								SU	
Staphylea trifolia		S3							
Taxus canadensis					S1				S2
Vaccinium myrtilloides						SH			
Viburnum lantanoides					S1				
Viburnum trilobum									S2
Zanthoxylum americanum		S1			SU				
Ferns, clubmosses, and horsetails									
Equisetum fluviatile					S1				
Lycopodium complanatum			S1				SH		
Lygodium palmatum		SH	S1	S3	S2	S2	S1	S2	S2
Matteuccia struthiopteris					S2				
Thelypteris simulata			S1						
Woodwardia areolata	SX	S1							
Woodwardia virginica			S1						
Graminoids									
Carex disperma								S2	S2
Carex flava								S2	
Carex grayi			S2	S2					
Carex laxiculmis			S1						
Carex lonchocarpa			S3						
Carex pseudocyperus			S2			SH		S1	S1
Carex rostrata									S2
Carex seorsa	S1	S1					S1		
Carex tenuiflora	S2		S2				SH		
Carex tetanica				S3		S2/S3		S2	
Cinna arundinacea			S3						
Cinna latifolia									S1
Cladium mariscoides								S2	
Glyceria obtusa								S1	
Muhlenbergia glomerata									S3
Scirpus microcarpus						SU			S1
Forbs and trailing shrubs									
Actaea rubra					S1				
Anemone canadensis						SU			SX
Angelica atropurpurea					SH				
Aster divaricatus	S3/S4								
Aster macrophyllus					S1				
Aster novi-belgii								S2	
Aster prenanthoides				S3		SH			S2
Bartonia virginica			S1						

Appendix B. *Continued.*

Species[d]	State[b] and conservation status[c]								
	Maine	N.H.	Vt.	Mass.	R.I.	Conn.	N.Y.	Pa.	N.J.
Cardamine bulbosa		S1	SH						
Cardamine pratensis var. *palustris*		S1		S2				SU	S2
Chimaphila maculata	S2		S2						
Circaea alpina					S2				
Cirsium muticum			S3						
Claytonia virginica			S1	S2	SX				
Conioselinum chinense				S3		S3/S4		S2	S1
Corallorhiza trifida					S1	S1			S2
Cornus canadensis									S2
Cypripedium calceolus var. *parviflorum*		S1	S3	S1	S1			S1	
Cypripedium reginae	S2	S1	S3	S3		S1		S2	SH
Epilobium leptophyllum									S3
Epilobium palustre			SH		S1	SH		S2	
Eupatoriadelphus dubius	SX								
Geum rivale									S3
Hydrophyllum canadense			S1	S1					S1
Hydrophyllum virginianum		S2				S2			
Hypericum denticulatum							S1	SX	
Impatiens pallida	S2								
Lilium canadense					S1				
Lilium philadelphicum			S3		S2				S3
Lilium superbum		S1							
Liparis loeselii		S2	S3		S1				
Lobelia siphilitica	SX			S2					
Lycopus rubellus		S2	SU	S2			SH	S2	S2
Lycopus virginicus			S2						
Lysimachia thyrsiflora		S2							S3
Malaxis monophyllus									SH
Malaxis monophyllus var. *brachypoda*	S1/S2	S1	S2	S2		S1		S2	
Mikania scandens	SX	S2							
Mitella nuda						S3		SX	
Monarda didyma									S2/SE
Pedicularis lanceolata				S1		S2/S3			
Penthorum sedoides					S1				
Peltandra virginica	S2		S1						
Petasites palmatus		S1	S1	S2		S1			
Platanthera grandiflora								S3	
Platanthera psycodes					S2				S3
Podophyllum peltatum			S1						
Prenanthes trifoliata		S3	S1						
Pyrola asarifolia	S3/S4	S2	S1						
Rudbeckia laciniata					S1				
Sanguinaria canadensis					S2				
Saururus cernuus				SH	S1	S1			
Saxifraga pensylvanica	S2				S1				
Solidago patula		SU	S2						
Sphenopholis pensylvanica				S2			SH		S2
Streptopus amplexifolius					S1				S1

Appendix B. *Continued.*

Species[d]	State[b] and conservation status[c]								
	Maine	N.H.	Vt.	Mass.	R.I.	Conn.	N.Y.	Pa.	N.J.
Streptopus roseus					S1				S1
Tiarella cordifolia									S1
Trillium cernuum			S1						
Trillium erectum					S1				
Trillium grandiflorum	SX								
Trollius laxus						S1	S2/S3	S1	S1
Viola brittoniana	SX			S2		S1		S1	S3
Viola incognita					S1				S3
Zizea aurea					S2				

[a] The plant species in this table have been observed in red maple swamps somewhere in the glaciated Northeast (see Table 3.3), and have been given special status by at least one northeastern state. None of these species is restricted to red maple swamps, and many are more common in other habitats. Several subspecies or varieties of species listed in Table 3.3 are listed by various states, but only those that have been reported from red maple swamps are in this appendix.

[b] Sources for each state are:
Maine—Maine Natural Heritage Program, Topsham, October 1989.
N.H.—New Hampshire Natural Heritage Inventory, Concord, July 1989.
Vt.—Vermont Nongame and Natural Heritage Program, Waterbury, February 1990.
Mass.—Massachusetts Natural Heritage Program, Boston, May 1989.
R.I.—Rhode Island Natural Heritage Program, Providence, March 1990.
Conn.—Connecticut Natural Diversity Data Base, Hartford, July 1990.
N.Y.—New York Natural Heritage Program, Latham (Clemants 1989).
Pa.—Pennsylvania Natural Diversity Inventory, Harrisburg, July 1990.
N.J.—New Jersey Natural Heritage Program, Trenton, November 1989.

[c] Codes for status are as follows; detailed definitions may be obtained from the above sources: S1—critically endangered, S2—endangered, S3—threatened, S4—apparently secure, SE—exotic, SH—historically occurred, SU—status uncertain, SX—apparently extirpated.

[d] Taxonomy according to the *National List of Scientific Plant Names* (U.S. Soil Conservation Service 1982). Common names are given in Table 3.3.

Appendix C. Vertebrates That Have Been Observed in Northeastern Red Maple Swamps

Taxonomy of amphibians and reptiles according to Collins (1990), birds according to AOU (1983), and mammals according to Jones et al. (1986).

Amphibians

American toad	*Bufo americanus*
Blue-spotted salamander	*Ambystoma laterale*
Bullfrog	*Rana catesbeiana*
Dusky salamander	*Desmognathus fuscus*
Eastern newt	*Notophthalmus viridescens*
Four-toed salamander	*Hemidactylium scutatum*
Fowler's toad	*Bufo woodhousii fowleri*
Gray treefrog	*Hyla versicolor*
Green frog	*Rana clamitans*
Jefferson salamander	*Ambystoma jeffersonianum*
Marbled salamander	*Ambystoma opacum*
Mink frog	*Rana septentrionalis*
Mountain dusky salamander	*Desmognathus ochrophaeus*
Northern leopard frog	*Rana pipiens*
Northern slimy salamander	*Plethodon glutinosus*
Northern two-lined salamander	*Eurycea bislineata*
Pickerel frog	*Rana palustris*
Redback salamander	*Plethodon cinereus*
Silvery salamander	*Ambystoma* X *platineum*[a]
Spotted salamander	*Ambystoma maculatum*
Spring peeper	*Pseudacris crucifer*
Spring salamander	*Gyrinophilus porphyriticus*
Tremblay's salamander	*Ambystoma* X *tremblayi*[a]
Wood frog	*Rana sylvatica*

Reptiles

Bog turtle	*Clemmys muhlenbergii*
Brown snake	*Storeria dekayi*
Common garter snake	*Thamnophis sirtalis*
Copperhead	*Agkistrodon contortrix*
Eastern box turtle	*Terrapene carolina*
Eastern ribbon snake	*Thamnophis sauritus*
Five-lined skink	*Eumeces fasciatus*
Milk snake	*Lampropeltis triangulum*
Northern water snake	*Nerodia sipedon*
Painted turtle	*Chrysemys picta*
Racer	*Coluber constrictor*
Rat snake	*Elaphe obsoleta*
Redbelly snake	*Storeria occipitomaculata*
Ringneck snake	*Diadophis punctatus*
Smooth green snake	*Opheodrys vernalis*
Snapping turtle	*Chelydra serpentina*
Timber rattlesnake	*Crotalus horridus*
Wood turtle	*Clemmys insculpta*

Birds

Acadian flycatcher	*Empidonax virescens*

American black duck	*Anas rubripes*
American crow	*Corvus brachyrhynchos*
American goldfinch	*Carduelis tristis*
American redstart	*Setophaga ruticilla*
American robin	*Turdus migratorius*
American woodcock	*Scolopax minor*
American wigeon	*Anas americana*
Barred owl	*Strix varia*
Belted kingfisher	*Ceryle alcyon*
Black-and-white warbler	*Mniotilta varia*
Black-billed cuckoo	*Coccyzus erythropthalmus*
Black-capped chickadee	*Parus atricapillus*
Black-throated green warbler	*Dendroica virens*
Blue jay	*Cyanocitta cristata*
Blue-gray gnatcatcher	*Polioptila caerulea*
Blue-winged teal	*Anas discors*
Blue-winged warbler	*Vermivora pinus*
Broad-winged hawk	*Buteo platypterus*
Brown creeper	*Certhia americana*
Brown-headed cowbird	*Molothrus ater*
Bufflehead	*Bucephala albeola*
Canada goose	*Branta canadensis*
Canada warbler	*Wilsonia canadensis*
Carolina chickadee	*Parus carolinensis*
Carolina wren	*Thryothorus ludovicianus*
Cerulean warbler	*Dendroica cerulea*
Chestnut-sided warbler	*Dendroica pensylvanica*
Chipping sparrow	*Spizella passerina*
Common goldeneye	*Bucephala clangula*
Common grackle	*Quiscalus quiscula*
Common merganser	*Mergus merganser*
Common yellowthroat	*Geothlypis trichas*
Cooper's hawk	*Accipiter cooperii*
Dark-eyed junco	*Junco hyemalis*
Downy woodpecker	*Picoides pubescens*
Eastern kingbird	*Tyrannus tyrannus*
Eastern phoebe	*Sayornis phoebe*
Eastern screech-owl	*Otus asio*
Eastern wood-pewee	*Contopus virens*
European starling	*Sturnus vulgaris*
Evening grosbeak	*Coccothraustes vespertinus*
Gadwall	*Anas strepera*
Golden-crowned kinglet	*Regulus satrapa*
Gray catbird	*Dumetella carolinensis*
Great blue heron	*Ardea herodias*
Great crested flycatcher	*Myiarchus crinitus*
Great gray owl	*Strix nebulosa*
Great horned owl	*Bubo virginianus*
Green-winged teal	*Anas crecca*
Hairy woodpecker	*Picoides villosus*
Hermit thrush	*Catharus guttatus*
Hooded merganser	*Lophodytes cucullatus*
Hooded warbler	*Wilsonia citrina*
House wren	*Troglodytes aedon*
Indigo bunting	*Passerina cyanea*
Kentucky warbler	*Oporornis formosus*
Long-eared owl	*Asio otus*
Louisiana waterthrush	*Seiurus motacilla*
Mallard	*Anas platyrhynchos*

Mourning warbler	*Oporornis philadelphia*
Nashville warbler	*Vermivora ruficapilla*
Northern bobwhite	*Colinus virginianus*
Northern cardinal	*Cardinalis cardinalis*
Northern flicker	*Colaptes auratus*
Northern goshawk	*Accipiter gentilis*
Northern mockingbird	*Mimus polyglottos*
Northern oriole	*Icterus galbula*
Northern parula	*Parula americana*
Northern saw-whet owl	*Aegolius acadicus*
Northern shrike	*Lanius excubitor*
Northern waterthrush	*Seiurus noveboracensis*
Orchard oriole	*Icterus spurius*
Ovenbird	*Seiurus aurocapillus*
Peregrine falcon	*Falco peregrinus*
Philadelphia vireo	*Vireo philadelphicus*
Pileated woodpecker	*Dryocopus pileatus*
Pine grosbeak	*Pinicola enucleator*
Pine siskin	*Carduelis pinus*
Pine warbler	*Dendroica pinus*
Prairie warbler	*Dendroica discolor*
Prothonotary warbler	*Protonotaria citrea*
Purple finch	*Carpodacus purpureus*
Red-bellied woodpecker	*Melanerpes carolinus*
Red-eyed vireo	*Vireo olivaceus*
Red-headed woodpecker	*Melanerpes erythrocephalus*
Red-shouldered hawk	*Buteo lineatus*
Red-tailed hawk	*Buteo jamaicensis*
Red-winged blackbird	*Agelaius phoeniceus*
Ring-necked duck	*Aythya collaris*
Rose-breasted grosbeak	*Pheucticus ludovicianus*
Ruby-crowned kinglet	*Regulus calendula*
Ruby-throated hummingbird	*Archilochus colubris*
Ruffed grouse	*Bonasa umbellus*
Rufous-sided towhee	*Pipilo erythrophthalmus*
Rusty blackbird	*Euphagus carolinus*
Scarlet tanager	*Piranga olivacea*
Sharp-shinned hawk	*Accipiter striatus*
Solitary vireo	*Vireo solitarius*
Song sparrow	*Melospiza melodia*
Swamp sparrow	*Melospiza georgiana*
Tufted titmouse	*Parus bicolor*
Turkey vulture	*Carthartes aura*
Veery	*Catharus fuscescens*
Warbling vireo	*Vireo gilvus*
Whip-poor-will	*Caprimulgus vociferus*
White-breasted nuthatch	*Sitta carolinensis*
White-eyed vireo	*Vireo griseus*
White-throated sparrow	*Zonotrichia albicollis*
Wild turkey	*Meleagris gallopavo*
Winter wren	*Troglodytes troglodytes*
Wood duck	*Aix sponsa*
Wood thrush	*Hylocichla mustelina*
Yellow warbler	*Dendroica petechia*
Yellow-bellied sapsucker	*Sphyrapicus varius*
Yellow-billed cuckoo	*Coccyzus americanus*
Yellow-rumped warbler	*Dendroica coronata*
Yellow-throated vireo	*Vireo flavifrons*
Yellow-throated warbler	*Dendroica dominica*

Mammals

Beaver	*Castor canadensis*
Big brown bat	*Eptesicus fuscus*
Black bear	*Ursus americanus*
Bobcat	*Lynx rufus*
Coyote	*Canis latrans*
Deer mouse	*Peromyscus maniculatus*
Eastern chipmunk	*Tamias striatus*
Eastern cottontail	*Sylvilagus floridanus*
Eastern mole	*Scalopus aquaticus*
Eastern mountain lion	*Felis concolor cougar*
Eastern pipistrelle	*Pipistrellus subflavus*
Ermine	*Mustela erminea*
Fisher	*Martes pennanti*
Gray fox	*Urocyon cinereoargenteus*
Gray squirrel	*Sciurus carolinensis*
Hairy-tailed mole	*Parascalops breweri*
Indiana myotis	*Myotis sodalis*
Keen's myotis	*Myotis keenii*
Little brown myotis	*Myotis lucifugus*
Long-tailed weasel	*Mustela frenata*
Lynx	*Lynx canadensis*
Masked shrew	*Sorex cinereus*
Meadow jumping mouse	*Zapus hudsonius*
Meadow vole	*Microtus pennsylvanicus*
Mink	*Mustela vison*
Moose	*Alces alces*
New England cottontail	*Sylvilagus transitionalis*
Northern short-tailed shrew	*Blarina brevicauda*
Porcupine	*Erethizon dorsatum*
Raccoon	*Procyon lotor*
Red bat	*Lasiurus borealis*
Red fox	*Vulpes vulpes*
Red squirrel	*Tamiasciurus hudsonicus*
River otter	*Lutra canadensis*
Silver-haired bat	*Lasionycteris noctivagans*
Smoky shrew	*Sorex fumeus*
Snowshoe hare	*Lepus americanus*
Southern bog lemming	*Synaptomys cooperi*
Southern flying squirrel	*Glaucomys volans*
Southern red-backed vole	*Clethrionomys gapperi*
Star-nosed mole	*Condylura cristata*
Striped skunk	*Mephitis mephitis*
Virginia opposum	*Didelphis virginiana*
Water shrew	*Sorex palustris*
White-footed mouse	*Peromyscus leucopus*
White-tailed deer	*Odocoileus virginianus*
Woodchuck	*Marmota monax*
Woodland jumping mouse	*Napaeozapus insignis*
Woodland vole	*Microtus pinetorum*

[a] Scientific name follows the Eastern Heritage Task Force data base, The Nature Conservancy, Boston, Mass.

Appendix D. Vertebrates of Special Concern That Have Been Observed in Northeastern Red Maple Swamps[a]

Species[d]	State[b] and conservation status[c]								
	Maine	N.H.	Vt.	Mass.	R.I.	Conn.	N.Y.	Pa.	N.J.
Amphibians									
Blue-spotted salamander			S3	S3		S3			S1
Dusky salamander						S3/S4			
Four-toed salamander			S2	S3	S3				S3
Jefferson salamander		S2	S3	S3		S3			S3
Marbled salamander		S1	SH	S2	S2				S3
Mountain dusky salamander			SH						SH
Northern leopard frog					S2	S3/S4			
Northern slimy salamander		SH				S2			
Spring salamander				S3	S2	S2			S3
Silvery salamander		SU	SU	S3					S3
Spotted salamander			SU						S3
Tremblay's salamander			SU	S3					S1
Reptiles									
Bog turtle[e]				S1		S1	S2	S2	S3
Copperhead				S1		S3	S3		
Eastern box turtle	SX	S1		S3					
Eastern ribbon snake					S3	S3/S4			
Five-lined skink			S1	SX		S1	S3		S3
Racer	S2		S1						
Rat snake			S2	S3	S2				
Redbelly snake					S3				
Smooth green snake						S3/S4			S3
Timber rattlesnake	SX	S1	S1	S1	SX	S1	S3	S3/S4	S2
Wood turtle			S3	S3	S3				
Birds									
Acadian flycatcher		S2		S2	S1	S3/S4	S3		
American black duck						S3			
American wigeon			SN	S1		SN	S3		SN
Barred owl									S3
Blue-gray gnatcatcher		S2							
Blue-winged teal					S1	S2			
Blue-winged warbler		S3	S3	S3					
Bufflehead			SN	SN		SN			SN
Carolina wren			SA						
Cerulean warbler			S1		SN	S3			
Common goldeneye				SN		SN	S2		SN
Common merganser			SN	S2		S3			
Cooper's hawk	S2	S2	S2	S3	S1	S1/S2		S3	S2
Dark-eyed junco					S2				S3

Appendix D. *Continued.*

Species[d]	State[b] and conservation status[c]								
	Maine	N.H.	Vt.	Mass.	R.I.	Conn.	N.Y.	Pa.	N.J.
Eastern screech-owl		S3							
Evening grosbeak				SA		SA			SN
Gadwall			SN	S1	S1	S2	S3		
Golden-crowned kinglet				S2	S1	S2			
Great blue heron		S3	S2	S2	S1	S3		S3	S2
Great gray owl			SN			SA			
Green-winged teal		S3	SN	S2	S1	SN	S3		SN
Hooded merganser		S3		S3	S1	S3		S2	SN
Hooded warbler				S2					
Kentucky warbler						S2	S2		
Long-eared owl		SU	SU	S2	S1	S1	S3	S1	S3
Mourning warbler				S1		SN			SN
Nashville warbler									S3
Northern bobwhite		SH							
Northern goshawk				S3	S1	S3/S4		S2	S2
Northern parula				S2	SH	SH/SN	S3/S4		S3
Northern saw-whet owl				S3	S1	S2/S3	S3		SN
Northern shrike			SN	SN		SN			SN
Orchard oriole	S1	S2	S3	S3	S2				
Peregrine falcon[f]	S1	S1	S1	S1	SH	SH	S2	SX	S2
Philadelphia vireo			S3	SN		SN	S3		SN
Pileated woodpecker					S1				
Pine grosbeak			SN	SN		SN			SN
Pine siskin				S3		SA			SN
Prairie warbler			S3						
Prothonotary warbler				S3		SA	S2	S2	S3
Purple finch						S3/S4			
Red-bellied woodpecker				S2	S1				
Red-headed woodpecker		S1	S2	S3	S1	S1			S3
Red-shouldered hawk	S3	S3		S3	S3				
Ring-necked duck		S2	SN	SA		SN	S3		SN
Ruby-crowned kinglet				S2		SN	S3		SN
Rusty blackbird			S3	SA		SN	S3		SN
Sharp-shinned hawk				S3	SH	S1/S2		S3	SN
Solitary vireo									S3
Tufted titmouse			S3						
Turkey vulture		S3	S2/S3	S3	S2				
Whip-poor-will			S3					S3/S4	
White-eyed vireo			SA						
White-throated sparrow					S1				SN
Winter wren					S1				
Yellow-bellied sapsucker									SN
Yellow-rumped warbler									SN
Yellow-throated warbler						SA/SN	S1		
Mammals									
Black bear						SH			S3
Bobcat					S3	S2		S3	S3
Coyote								S3/S4	
Deer mouse						S3			SU

Appendix D. *Continued.*

Species[d]	State[b] and conservation status[c]								
	Maine	N.H.	Vt.	Mass.	R.I.	Conn.	N.Y.	Pa.	N.J.
Eastern mountain lion[f]	SH	SH	SH	SH		SH	SX	SX	SX
Eastern pipistrelle	SU	S2							SN
Ermine									SN
Fisher					S1	S1		SH	SX
Hairy-tailed mole									SU
Indiana myotis[f]			S1	SH		SH	S1	S1	
Keen's myotis								S2/S3	
Lynx[e]	S2	S1	SH					SX	
Moose				SH		SX	S1	SX	
New England cottontail[e]	S3	S3	SU		S2		S3	SU	SU
Red bat									SU
River otter								S3	
Silver-haired bat			SN	SU		S3		SU	SU
Smoky shrew					S3				SU
Snowshoe hare									SH
Southern bog lemming			S2	S2	S1	S3			S2
Southern red-backed vole								S2/S3	
Water shrew				S3	S1	S3/S4		S1/S3	SU

[a] Species or subspecies in this table are known to occur in red maple swamps of the Northeast (see references in Chapter 7), and have been given special status by at least one northeastern state. None of these animals is restricted to red maple swamps, and many are more common in other habitats.

[b] Sources for each state are:
Maine—Maine Natural Heritage Program, Topsham, June 1989.
N.H.—New Hampshire Natural Heritage Inventory, Concord, September 1990.
Vt.—Vermont Nongame and Natural Heritage Program, Waterbury, April 1990.
Mass.—Massachusetts Natural Heritage and Endangered Species Program, Boston, May 1990.
R.I.—Rhode Island Natural Heritage Program, Providence, May 1989.
Conn.—Connecticut Natural Diversity Data Base, Hartford, March 1990.
N.Y.—New York Natural Heritage Program, Latham, May 1990.
Pa.—Pennsylvania Natural Diversity Inventory, Harrisburg, December 1988.
N.J.—New Jersey Natural Heritage Program, Trenton, July 1989.

[c] Codes for status are as follows; detailed definitions may be obtained from the above sources: S1—critically endangered, S2—endangered, S3—threatened, S4—apparently secure, SA—accidental (sporadic breeder), SH—historically occurred, SN—nonbreeding migrant, SU—status uncertain, SX—apparently extirpated.

[d] Scientific names are given in Appendix C.

[e] Proposed for listing by the U.S. Fish and Wildlife Service as an endangered or threatened species. Current status is category C2: taxon may be appropriate for listing, but additional data on biological vulnerability and threats are needed.

[f] Formally listed as an endangered species by the U.S. Fish and Wildlife Service.

A list of current *Biological Reports* follows.

1. The Ecology of Humboldt Bay, California: An Estuarine Profile, by Roger A. Barnhart, Milton J. Boyd, and John E. Pequegnat. 1992. 121 pp.
2. Fenvalerate Hazards to Fish, Wildlife, and Invertebrates: A Synoptic Review, by Ronald Eisler. 1992. 43 pp.
3. An Evaluation of Regression Methods to Estimate Nutritional Condition of Canvasbacks and Other Water Birds, by Donald W. Sparling, Jeb A. Barzen, James R. Lovvorn, and Jerome R. Serie. 1992. 11 pp.
4. Diflubenzuron Hazards to Fish, Wildlife, and Invertebrates: A Synoptic Review, by Ronald Eisler. 1992. 36 pp.
5. Vole Management in Fruit Orchards, by Mark E. Tobin and Milo E. Richmond. 1993. 18 pp.
6. Ecology of Band-tailed Pigeons in Oregon, by Robert L. Jarvis and Michael F. Passmore. 1992. 38 pp.
7. A Model of the Productivity of the Northern Pintail, by John D. Carlson, Jr., William R. Clark, and Erwin E. Klaas. 1993. 20 pp.
8. Guidelines for the Development of Community-level Habitat Evaluation Models, by Richard L. Schroeder and Sandra L. Haire. 1993. 8 pp.
9. Thermal Stratification of Dilute Lakes—Evaluation of Regulatory Processes and Biological Effects Before and After Base Addition: Effects on Brook Trout Habitat and Growth, by Carl L. Schofield, Dan Josephson, Chris Keleher, and Steven P. Gloss. 1993. 36 pp.
10. Zinc Hazards to Fishes, Wildlife, and Invertebrates: A Synoptic Review, by Ronald Eisler. 1993. 106 pp.
11. In-water Electrical Measurements for Evaluating Electrofishing Systems, by A. Lawrence Kolz. 1993. 24 pp.

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