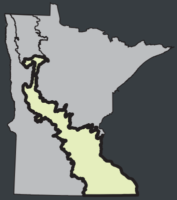
Field Guide to the
NATIVE PLANT COMMUNITIES *of* MINNESOTA



The Eastern Broadleaf Forest Province

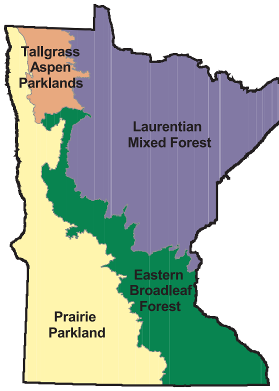
ECOLOGICAL SYSTEM SUMMARIES

Ecological Land Classification Program
Division of Forestry

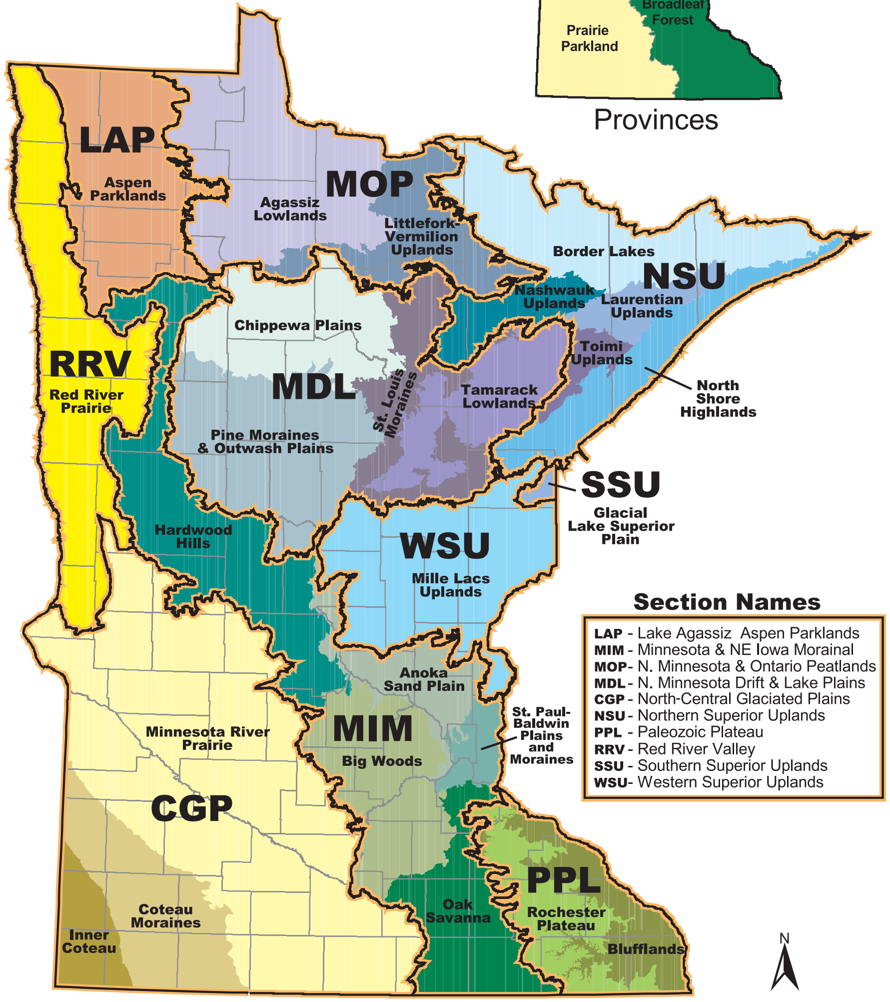
Minnesota County Biological Survey
Division of Ecological Resources

Natural Heritage and Nongame Research Program
Division of Ecological Resources

Ecological Provinces, Sections, & Subsections of Minnesota



Provinces



Section Names

LAP - Lake Agassiz Aspen Parklands
MIM - Minnesota & NE Iowa Morainal
MOP - N. Minnesota & Ontario Peatlands
MDL - N. Minnesota Drift & Lake Plains
CGP - North-Central Glaciated Plains
NSU - Northern Superior Uplands
PPL - Paleozoic Plateau
RRV - Red River Valley
SSU - Southern Superior Uplands
WSU - Western Superior Uplands

Sections and Subsections

Minnesota's Native Plant Community Classification: System Groups, Systems, and Classes

A. Upland Forests and Woodlands

Fire-Dependent Forest/Woodland System

FDn12 Northern Dry-Sand Pine Woodland
FDn22 Northern Dry-Bedrock Pine (Oak) Woodland
FDn32 Northern Poor Dry-Mesic Mixed Woodland
FDn33 Northern Dry-Mesic Mixed Woodland
FDn43 Northern Mesic Mixed Forest

FDc12 Central Poor Dry Pine Woodland
FDc23 Central Dry Pine Woodland
FDc24 Central Rich Dry Pine Woodland
FDc25 Central Dry Oak-Aspen (Pine) Woodland
FDc34 Central Dry-Mesic Pine-Hardwood Forest

FDs27 Southern Dry-Mesic Pine-Oak Woodland
FDs36 Southern Dry-Mesic Oak-Aspen Forest
FDs37 Southern Dry-Mesic Oak (Maple) Woodland
FDs38 Southern Dry-Mesic Oak-Hickory Woodland

FDw24 Northwestern Dry-Mesic Oak Woodland
FDw34 Northwestern Mesic Aspen-Oak Woodland
FDw44 Northwestern Wet-Mesic Aspen Woodland

Mesic Hardwood Forest System

MHn35 Northern Mesic Hardwood Forest
MHn44 Northern Wet-Mesic Boreal Hardwood-Conifer Forest
MHn45 Northern Mesic Hardwood (Cedar) Forest
MHn46 Northern Wet-Mesic Hardwood Forest
MHn47 Northern Rich Mesic Hardwood Forest

MHc26 Central Dry-Mesic Oak-Aspen Forest
MHc36 Central Mesic Hardwood Forest (Eastern)
MHc37 Central Mesic Hardwood Forest (Western)
MHc38 Central Mesic Cold-Slope Hardwood-Conifer Forest
MHc47 Central Wet-Mesic Hardwood Forest

MHs37 Southern Dry-Mesic Oak Forest
MHs38 Southern Mesic Oak-Basswood Forest
MHs39 Southern Mesic Maple-Basswood Forest
MHs49 Southern Wet-Mesic Hardwood Forest

MHw36 Northwestern Wet-Mesic Hardwood Forest

B. Wetland Forests

Floodplain Forest System

FFn57 Northern Terrace Forest
FFn67 Northern Floodplain Forest

FFs59 Southern Terrace Forest
FFs68 Southern Floodplain Forest

Wet Forest System*

WFn53 Northern Wet Cedar Forest
WFn55 Northern Wet Ash Swamp
WFn64 Northern Very Wet Ash Swamp

WFs55 Southern Wet Aspen Forest
WFs57 Southern Wet Ash Swamp

WFw54 Northwestern Wet Aspen Forest

Forested Rich Peatland System*

FPn62 Northern Rich Spruce Swamp (Basin)
FPn63 Northern Cedar Swamp
FPn71 Northern Rich Spruce Swamp (Water Track)
FPn72 Northern Rich Tamarack Swamp (Eastern Basin)
FPn81 Northern Rich Tamarack Swamp (Water Track)
FPn82 Northern Rich Tamarack Swamp (Western Basin)

FPs63 Southern Rich Conifer Swamp

FPw63 Northwestern Rich Conifer Swamp

Acid Peatland System*

APn80 Northern Spruce Bog
APn81 Northern Poor Conifer Swamp

*Occurs in System Groups B & D.

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C. Upland Grasslands, Shrublands, and Sparse Vegetation

Cliff/Talus System

CTn11 Northern Dry Cliff
CTn12 Northern Open Talus
CTn24 Northern Scrub Talus
CTn32 Northern Mesic Cliff
CTn42 Northern Wet Cliff

CTu22 Lake Superior Cliff

CTs12 Southern Dry Cliff
CTs23 Southern Open Talus
CTs33 Southern Mesic Cliff
CTs43 Southern Maderate Cliff
CTs46 Southern Algific Talus
CTs53 Southern Wet Cliff

Rock Outcrop System

ROn12 Northern Bedrock Outcrop
ROn23 Northern Bedrock Shrubland

ROs12 Southern Bedrock Outcrop

Lakeshore System

LKi32 Inland Lake Sand/Gravel/Cobble Shore
LKi43 Inland Lake Rocky Shore
LKi54 Inland Lake Clay/Mud Shore

LKu32 Lake Superior Sand/Gravel/Cobble Shore
LKu43 Lake Superior Rocky Shore

River Shore System

RVx32 Sand/Gravel/Cobble River Shore
RVx43 Rocky River Shore
RVx54 Clay/Mud River Shore

Upland Prairie System

UPn12 Northern Dry Prairie
UPn13 Northern Dry Savanna
UPn23 Northern Mesic Prairie
UPn24 Northern Mesic Savanna

UPs13 Southern Dry Prairie
UPs14 Southern Dry Savanna
UPs23 Southern Mesic Prairie
UPs24 Southern Mesic Savanna

D. Wetland Grasslands, Shrublands, and Marshes

Acid Peatland System*

APn90 Northern Open Bog
APn91 Northern Poor Fen

Open Rich Peatland System

OPn81 Northern Shrub Shore Fen
OPn91 Northern Rich Fen (Water Track)
OPn92 Northern Rich Fen (Basin)
OPn93 Northern Extremely Rich Fen

OPp91 Prairie Rich Fen
OPp93 Prairie Extremely Rich Fen

Forested Rich Peatland System*

FPn73 Northern Rich Alder Swamp

Wet Forest System*

WFn74 Northern Wet Alder Swamp

Wet Meadow/Carr System

WMn82 Northern Wet Meadow/Carr

WMs83 Southern Seepage Meadow/Carr
WMs92 Southern Basin Wet Meadow/Carr

WMp73 Prairie Wet Meadow/Carr

Marsh System

MRn83 Northern Mixed Cattail Marsh
MRn93 Northern Bulrush-Spikerush Marsh

MRu94 Lake Superior Coastal Marsh

MRp83 Prairie Mixed Cattail Marsh
MRp93 Prairie Bulrush-Arrowhead Marsh

Wetland Prairie System

WPn53 Northern Wet Prairie

WPs54 Southern Wet Prairie

Wetland Prairie System

(WPn) Region (Figure WP-1). Only the WPs Region is well-represented in the EBF Province. Communities of the WPn Region are present in the northern end of the province, but are rare enough that they are not described in this guide. Differences between the floristic regions are subtle. The composition of the dominant graminoids is remarkably constant throughout the WP System, but there are some differences in the composition of forbs and less-important graminoids. In addition, shrubs are more common in WPn communities.

Most of the species that are restricted to the WPs Region occur in only part of the region; restriction to the southeastern corner of the state is the most frequent pattern. Table WP-1 lists the most geographically widespread species with at least moderately high fidelity to one of the floristic regions. None of the indicators for the WPs Region has high frequency for communities in that floristic region because the species occurs in only part of the region, or because it is uncommon, or both. Low frequency values for indicators of the WPn Region are mostly attributable to the second factor. Species that are reliably present in WP communities in one floristic region tend to be present with high frequency in communities of the other region as well. Tufted hair grass *(Deschampsia cespitosa)*, which has high frequency only in the WPn Region, is a notable exception. These facts raise questions about the validity of these two floristic regions. Additional data and analysis may support moving the boundary or creating different floristic regions. Another possibility is the elimination of floristic regions within the WP System. Rather than being an indication of ecologically coherent regions, the geographic variation in species composition of WP communities may be best interpreted as simply the result of independently determined range limits of some of the component species.

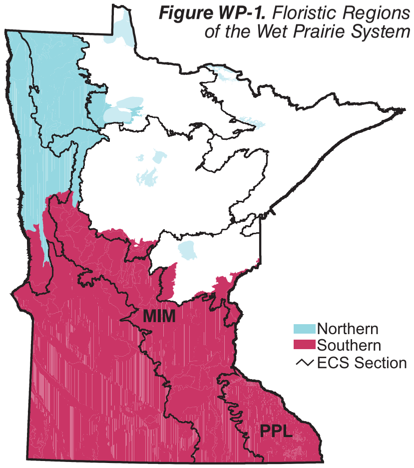

Figure WP-1. *Floristic Regions of the Wet Prairie System*

Table WP-1. *Plants useful for differentiating the Northern and Southern Floristic Regions of the Wetland Prairie System.*

	Common Name	Scientific Name	frequency (%)	
			UPn	UPs
Northern Floristic Region	Seaside arrowgrass	*Triglochin maritima*	27	6
	Bebb's willow	*Salix bebbiana*	43	10
	Crawe's sedge	*Carex crawei*	12	2
	Slender willow	*Salix petiolaris*	54	10
	Kalm's lobelia	*Lobelia kalmii*	20	-
	White aster-like goldenrod	*Solidago ptarmicoides*	20	-
	Bog birch	*Betula pumila*	43	-
	Tufted hair grass	*Deschampsia cespitosa*	64	-
Southern Floristic Region	Gray-headed coneflower	*Ratibida pinnata*	-	27
	Canada tick trefoil	*Desmodium canadense*	-	22
	Skyblue aster	*Aster oolentangiensis*	-	22
	Wild garlic	*Allium canadense*	-	16
	Cup plant	*Silphium perfoliatum*	-	12
	Tussock sedge	*Carex stricta*	1	24
	Veiny pea	*Lathyrus venosus*	1	18
	Prairie phlox	*Phlox pilosa*	4	33

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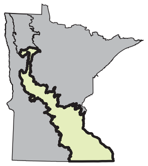

The Eastern Broadleaf Forest Province

Ecological System Summaries

This material is excerpted from: *Field guide to the native plant communities of Minnesota: The Eastern Broadleaf Forest Province.* Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. Minnesota Department of Natural Resources, St. Paul. 2005.

User’s Guide to Ecological System Summaries

The ecological system summaries provide information on the fifteen ecological systems recognized in the Minnesota Department of Natural Resources’ native plant community (NPC) classification. These summaries originally appeared in three field guides to the native plant communities of Minnesota, which are organized by Minnesota’s four ecological provinces (the Laurentian Mixed Forest, the Eastern Broadleaf Forest, the Prairie Parkland, and the Tallgrass Aspen Parklands provinces, with the last two provinces combined in one field guide). Although each of the three versions differs somewhat in content, there is much overlap.

Each summary typically contains a brief general description of the system, a discussion of the major ecological process or processes that influence the system, some of the characteristic plant adaptations to these processes, and information on distinctions between the floristic regions in the system (where applicable) or variation among the NPC classes in the system. The system summaries were developed to provide context and background information when using keys to the ecological systems or comparing NPC classes within a system.

In each system summary, the general description contains information on the basic structure and composition of the vegetation, on landscape setting, and on distribution of the system in the province. The major ecological processes most commonly discussed in the system summaries are nutrient cycling, moisture regime, and disturbance regime. In some system summaries, the treatment of ecological processes may include discussion of processes that span several systems (such as formation of peatlands) or successional relationships among systems. The information presented on plant adaptations includes some of the most prominent or illustrative adaptive responses of plants to the ecological processes that characterize the system.

Most of the systems are divided into floristic regions that reflect the distribution of Minnesota’s plant species into characteristically northern, northwestern, central, southern, and prairie flora, or groups. Floristic region maps in the system summaries show the general ranges of floristic regions in the system. These maps were constructed by amalgamating the distribution maps of the NPC classes in the system. The boundaries between floristic regions are usually more diffuse than represented by boundary lines on the maps; floristic regions may overlap by 50 miles or more along some boundaries.

For systems that have been documented with substantial vegetation plot data, tables are provided listing species useful in differentiating the floristic regions. These tables can be used to help with decisions at dichotomies in keys to NPC classes that represent divisions between classes in different floristic regions. Some of the wooded systems also have tables with historical tree species compositions and disturbance regimes for the NPC classes in the system. The data presented in the tables come from analyses of Public Land Survey records from the late 1800s and early 1900s. Tree species followed by “(C)” in the tables are canopy trees and are present in the system at heights greater than 10 meters (33 feet) tall; trees followed by “(U)” are present in the understory and are less than 10 meters tall.

Notes:

► Measures of height, distance, and area in the system summaries are given in both English and metric units. English and metric equivalents are approximate because most original measurements were imprecise.

► For wooded systems, ages derived in analyses of historical growth stages and disturbance regimes are generally rounded to the nearest five years.

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hand, during drier periods, wetland prairies provided superior forage and were probably preferentially grazed. It is not known whether the long-term absence of grazing will result in the disappearance of species from WP communities.

Soil-moisture conditions in WP communities are intermediate between those in UP and WM communities. WP communities typically receive surface runoff but are subjected to only brief, periodic inundation. Although the water table usually persists in the lower part of the rooting zone for much of the growing season, most of the plant rooting zone is not saturated except for brief periods during snowmelt or after heavy rains. As a result, anoxic conditions rarely persist long enough to cause mortality in plants incapable of transporting oxygen to their roots. In some situations, upward seepage of groundwater is enough to keep the surface soil permanently moist but not enough to saturate it. Moisture stress is an infrequent experience for plants in WP communities in the EBF Province. In the western part of the state where evapotranspiration regularly exceeds precipitation, translocated salts concentrate in many low areas, making water uptake by plants difficult. A distinctive variant of wet prairie occupies these saline places, but no occurrences of this have been documented in the EBF Province. Soils that support WP communities are classified as mollisols (very dark, base-rich mineral soils). Textures vary, including clays, silts, loams, and sands. At present, no floristic differences associated with these textural variations are recognized, but additional data collection and analysis may support subdivision based on this factor.

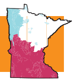
Plant Adaptations

Adaptations to frequent fire are prominent in the flora of the WP System. First, is the overwhelming predominance of herbaceous plants that, unlike woody plants, do not lose much investment when fire destroys their aboveground parts. However, shrubs are more important in WP communities than in UP communities, as greater productivity resulting from greater availability of water allows shrubs to maintain their root structure despite frequent destruction of above-ground parts. The perennating organs of most of the plants—buds, tubers, root collars, or other tissue from which new growth originates—are generally deep enough below the soil surface to escape damage in prairie fires. Although this is not as true of shrubs, the moist soil conditions provide some buffering of high temperatures at the soil surface during fires, increasing their chances for survival. In general, plants in WP communities invest heavily in belowground growth: biomass below ground in tallgrass prairies is estimated to be two to four times that above ground. There are several selective forces that produce this result, but sequestering nitrogen—a limiting nutrient in tallgrass prairies—from loss in fire is probably one. Related to this is sequestration of nutrient and energy reserves to support rapid regrowth following grazing. The graminoid life form is itself an adaptation to grazing, as the meristematic tissue from which new growth arises is at the base of the plant where it is inaccessible to grazers, which consume only easily replaceable leaf tissue.

Because severe water limitation is not frequent in WP communities in the EBF Province, adaptations to cope with this are not common in plants of this system. Saline wet prairies are an exception, as the salinity of the soil water makes its uptake by plants difficult, but these are not known to occur in the EBF Province. Although water is seldom limiting, the dominant graminoids of the WP System are C_4 grasses, indicating that its efficient use is still favored. (In WM communities, in contrast, where conditions are wetter, the dominant graminoids are usually less-water-efficient C_3 sedges.) The challenge in wetter systems—that of providing oxygen to roots in water-logged soil—is also not a significant force in shaping the composition of WP communities. Consequently, most of the plants of this system have no adaptations to cope with soil anoxia.

Floristic Regions

WP communities in Minnesota are grouped into two floristic regions based on differences in species composition, the Southern Floristic (WPs) Region and the Northern Floristic



broad band of outwash flanking the Mississippi River, where shallow, braided channels in the outwash surface were occupied by WP communities and the channel bars by UP communities. The larger body of the Anoka Sand Plain away from the valley train was dominated by savannas, brushlands, and woodlands; the wetlands here were probably predominantly Wet Meadow/Carr (WM) communities associated with the shallow water table. WP communities, however, were probably not uncommon, especially on the margins of the wet meadows. Elsewhere in the EBF Province, WP communities were mostly confined to its western edge, adjacent to the continuous prairie of the Prairie Parkland (PPA) Province, although they extended more deeply into the EBF Province at a few places towards its north end. Very little native wetland prairie remains today; conversion to cropland, succession to woodland and forest, and urban and suburban development have destroyed more than 99 percent of the wetland prairies present in the EBF Province before Euro-American settlement.

Natural History

Frequent fire (with return intervals less than 10 years) is critical for the occurrence of wetland prairies. The association of wetland prairies with larger upland prairies noted above is explained by their dependence upon proximity to upland prairies for a fire regime adequate to establish and maintain them, as their limited size and the increased influence of wet conditions reduces the likelihood of ignition and spread within them.

Fire frequency is responsive to climate and to landscape properties. The most important factors are the frequency and intensity of drying events that create flammable conditions, and the absence of topographic and water features that impede the spread of fire. Vegetation itself may facilitate or impede the spread of fire: deciduous forests are much more resistant to fire than grasslands, which burn readily. The size of a fire-prone landscape is also an important influence on the fire return interval at points within it, as ignition events generally increase with area, as does the average extent of individual fires. The combination of a drier climate and a topographically subdued landscape with few lakes in the PPA Province west of the EBF Province resulted in the strong dominance of the entire PPA Province by prairie communities. Increasingly moist climatic conditions eastward, together with greater topographic relief and much higher density of lakes dramatically altered the fire environment in most of the EBF Province, which was dominated by woodland and forest communities. The distribution of prairie communities in the EBF Province noted above reflects the location of fire-prone landscapes in the province. In the Anoka Sand Plain Subsection of the MIM, UP communities were primarily savannas rather than open prairies, probably reflecting this subsection's isolation by surrounding forests from more extensive prairie regions and consequently from fires originating in them. All fires in this subsection had to originate within its relatively small area. In contrast, there was no significant barrier to the spread of fires into the Oak Savanna Subsection of the MIM from the prairie-dominated region of the PPA Province to the west and south, increasing the frequency of fires in this part of the EBF Province sufficiently that open prairies rather than savannas predominated.

WP communities were historically subject to grazing and browsing by large mammals including bison, elk, and deer. The role these animal activities played in shaping WP communities is unclear, but they probably influenced relative abundances of plant species through their effects on regeneration and competitive interactions. Mechanical disturbance of the soil by hooves provided a regeneration niche for short-lived species that depend on frequent germination from seed to persist in the community. Reduction in the height and density of the canopy of tall grasses from grazing prevented competitive exclusion of smaller-stature plant species. Large grazers can produce greater disturbance in WP communities than in UP communities, as wet soils are vulnerable to greater mechanical disturbance by the hooves of these heavy animals than are drier soils. However, bison and elk may have avoided wetland prairies when soils were soft, as there would have been ample upland prairie available. On the other

► Common names of vascular plants are used throughout the text of each summary. Scientific names are included with common names in tables. Scientific names are also included with common names at the first mention of a species in the text, with two exceptions. Trees are listed by common name only and rushes and sedges are always listed by both common and scientific name.

► Names of Ecological Classification System sections are abbreviated in the summaries. The full names are:
LAP – Lake Agassiz Aspen Parklands
MIM – Minnesota and Northeast Iowa Morainal
MOP – Northern Minnesota and Ontario Peatlands
MDL – Northern Minnesota Drift and Lake Plains
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FD Fire-Dependent Forest/Woodland System


photo by Sarah Vest, MN DNR

St. Croix Savanna Scientific and Natural Area, Washington County, MN

General Description

The Eastern Broadleaf Forest (EBF) Province historically was characterized by extensive forests of mesic hardwood tree species common to much of the eastern United States. In Minnesota, the western border of the province was bounded by expansive prairies. Numerous and sometimes large areas of prairie were also present within the province. Between the prairies, which burned regularly, and the mesic hardwood forests, which rarely burned, are lands that burned occasionally during droughts or exceptionally dry falls and springs. These lands burned often enough to prevent large expanses of forests from forming but not enough to favor development of prairies. The vegetation of these lands was predominantly brush, consisting of shrubs and of trees stunted by fire or resprouting after fire. The pattern of trees, brush, and grassland in these areas was described in the 1800s by land surveyors as barrens, savanna, openings, thickets, groves, or parkland. Natural remnants of this vegetation have developed into woodlands or forests following the decline in fire frequency that came with Euro-American settlement in the region. The descriptions of Fire-Dependent Forest/Woodland (FD) communities in this guide are based largely on current examples of these previously more fire-prone communities. The majority of these examples are on sandy, gravelly, or otherwise droughty sites where succession to closed-canopy Mesic Hardwood Forest (MH) communities has been slowed by harsh growing conditions.

As the name implies, FD communities are or have been strongly influenced by wildfires. In the past, fires in the deciduous woodlands of the EBF Province were capable of killing stands of trees and other aboveground vegetation under the right climate, fuel, and topographic settings. However, even intense fires in these deciduous woodlands did not generate the kinds of conflagrations possible in closed-canopy coniferous forests of the Laurentian Mixed Forest (LMF) Province, where crown fires generate enough heat to totally consume branches of live trees, coarse woody debris, litter, and even some soil organic matter. By comparison, fires in the deciduous woodlands of the EBF Province were more regenerative than destructive. The typical cycle involved top-killing of plants and vegetative recovery by resprouting. Plant mortality was primarily due to attrition rather than consumption in a single fire. These fires did enhance plant reproduction by exposing mineral soil, triggering seed dispersal, breaking seed

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WP Wetland Prairie System


photo by F.S. Harris MN DNR

Blue Earth County, MN

General Description

Wetland Prairie (WP) communities are herbaceous plant communities dominated by graminoid species with a forb component that can approach codominance with the graminoids. The tall grasses big bluestem *(Andropogon gerardii)* and prairie cordgrass *(Spartina pectinata)* are the most important graminoids. The most common associates are Indian grass *(Sorghastrum nutans)* and switchgrass *(Panicum virgatum)*, also tall grasses, and mat muhly grass *(Muhlenbergia richardsonis)*, a short-stature species. Sedges *(Carex* spp.) are common in WP communities but are typically a subordinate component; woolly sedge *(C. pellita)* is the most important. Shrubs are often present, usually sparse in southern Minnesota but becoming abundant northward. These include prairie rose *(Rosa arkansana)*, a low semi-shrub, and taller shrubs such as red-osier dogwood *(Cornus sericea)* and several willows *(Salix* spp.). The main vegetation layer is usually less than 40in (1m) high, although some forbs and the flowering stalks of many of the grasses elongate well above this height as the season progresses.

The herbaceous dominance of WP communities is closely tied to the frequent occurrence of fire. In circumstances where fire frequency or intensity is reduced, more fire-tolerant shrubs and trees can persist, forming wet brush-prairie communities that are considered members of the WP system. Wet brush-prairies are characterized by an abundance of shrubs—and of suckers and saplings of quaking aspen and balsam poplar—that alters the aspect from that of grassland to shrubland or brushland, although herbaceous prairie plants remain a major component of the vegetation. In the absence of fire, wet brush-prairies rapidly succeed to woodland. Today, most wet brush-prairies occur in the Tallgrass Aspen Parklands Province of northwestern Minnesota.

WP communities almost always occur in association with Upland Prairie (UP) communities, usually as inclusions in landscapes dominated by the latter. Historically, they were common in the Eastern Broadleaf Forest (EBF) Province in the prairie- and savanna-dominated Oak Savanna Subsection of the MIM and in the Rochester Plateau Subsection of the PPL, becoming uncommon to rare in the more dissected Blufflands Subsection of the PPL, where UP communities occur mainly on steep slopes in a woodland- and forest-dominated landscape. WP communities were also common in the Anoka Sand Plain Subsection of the MIM, notably in the Mississippi valley train, a correlated with degree of exposure to wave action. MRn83 typically occurs in ponds, bays of lakes, or sluggish streams where vegetation is at least partially protected from wave action or strong currents. MRn83 is dominated by cattails and sedges *(Carex* spp.) and has forb species such as star-duckweed *(Lemna trisulca),* common bladderwort *(Utricularia vulgaris),* and marsh bellflower (*Campanula aparinoides*). MRn93 occurs along wave-washed lakeshores, on sandbars, and in stream channels and is dominated by bulrushes *(Scirpus* spp.), spikerushes *(Eleocharis* spp.), broad-leaved arrowhead *(Sagittaria latifolia)*, and grasses such as northern manna grass *(Glyceria borealis)*. Water depth may also be important in distinguishing the two classes, but there are not enough data on marshes in the MRn Region to assess the influence of water depth on species composition

Succession

Marshes can develop from submerged or floating-leaved aquatic communities if water depth is reduced by deposition of sedimentary peat, siltation, or draining, which enables persistent emergent plants to become established at the site. Conversely, marshes are converted to aquatic communities in settings where water levels increase for sustained periods, drowning emergent species and favoring submerged or floating-leaved species. Increases in water level are caused most often by increased precipitation and runoff or by construction of beaver dams. Muskrats also commonly decimate marsh vegetation, leading to areas within marshes that are open and aquatic in character. If water levels drop within marsh communities and they are subjected to regular seasonal drawdowns, characteristic emergent marsh species such as cattails are replaced in dominance by sedges, and affiliated submerged and floating-leaved species are eliminated, resulting in conversion to WM communities. Marshes can develop from wet forests, peatland communities, or even upland forests in areas flooded by beaver impoundments. The creation and eventual draining of beaver ponds often result in formation of wetland complexes that contain MR communities mixed with transitional stages of other wetland communities, especially WM and aquatic communities. MR communities also sometimes develop following fire in peatlands, where peat “burn-outs” leave depressions that fill with standing water.

dormancy, and increasing light and heat conditions on the ground. The fires prevented accumulation of litter and humus, thus affecting nutrient cycling, nutrient availability, and soil-forming processes linked to humus.

In the EBF Province, the native plant community classes in the FD System occur on distinctive sites and soils. In the past, when fires were more frequent, landscape context was more important than inherent site characteristics in determining where FD communities occurred. Local relief, the distribution of water bodies, slope, aspect, soil texture, and the vegetation itself were all contributing factors. In general, hummocky topography, steep slopes, numerous lakes and wetlands, north and east aspects, and fine soil textures favored MH communities. Flat, lakeless, and sandy landscapes favored Upland Prairie (UP) communities, as did very steep, south- to west-facing slopes with shallow soils over bedrock in southeastern Minnesota. FD communities developed in areas intermediate or transitional between these two extremes. At present, the EBF Province is highly developed for agriculture and urban uses. The context that created the mosaic of FD, MH, and UP communities is gone. Prairies no longer serve as an ignition source for the wildfires that maintained FD communities and that limited MH communities to the most protected sites. Gone also are herds of bison and elk, which probably supplemented fire in shaping the composition and structure of FD communities.

The EBF Province is an ecotone between subhumid prairie and humid forest climates and experiences modest fluctuations between these climate regimes over cycles of tens to hundreds of years. The pattern, structure, and composition of vegetation in the province in the past were sensitive to these fluctuations in climate. Although fire was the most immediate cause of vegetation patterns in the province, fuel conditions and the probability of fire were influenced by climate cycles. As a result of fluctuation in climate and its effect on fire probability, any given site in the province could cycle among vegetation types over time, causing temporal variation in soil development on the site. For this reason, soils in the province often have mixed grassland, woodland, and forest characters, and differences in the soils associated with FD, MH, and UP communities are not strong. In general, in the current climate and the absence of wildfire, any terrestrial site in the province will succeed toward communities of the MH System. (This is in strong contrast to the LMF Province, where FD communities are strongly correlated with droughty, often sandy, poor soils that tend to become even poorer over time under the regime of catastrophic fires characteristic of conifer-dominated FD communities).

Plant Adaptations

Plants that occur in FD communities have seeds or vegetative structures that can survive fire and are good at colonizing burned sites. Many FD plants are opportunists that can take advantage of the short periods following fire when nutrients are relatively abundant and light levels are high. Such plants must also survive frequent drought and potentially long periods between fires when light levels decrease beneath increasingly dense shrub and tree canopies. The most evident characteristic of FD plants in this region of Minnesota is their ability to sprout prolifically. The trees, shrubs, and many of the herbs are capable of storing considerable amounts of carbohydrates belowground in roots, rhizomes, or other specialized organs and then sprouting vigorously after aerial stems are destroyed by fire. These plants seem to be particularly plastic in allocating resources to underground or aboveground tissues, depending on the impact of fire on their overall vigor.

At present, FD communities in the EBF Province have a mixture of species with life history traits and morphological features that are generally associated with either UP communities or MH communities. This is because the composition of FD communities includes plants adapted to the historic, fire-prone conditions of the sites on which they occur as well as plants adapted to the current shadier conditions. As an example, FD communities tend to have graminoid cover dominated by sedges, as is true for MH communities, but also have grass species that are equally at home in prairies. In addition, the flora of FD communities includes ferns, which are common in MH communities and rare in UP communities, but the ferns in FD communities are limited to the most widespread species such as lady fern, rattlesnake fern, and bracken. Many additional fern species common in MH communities are absent from FD communities. Several other kinds of species of FD communities that are shared with UP communities are summer- and fall-blooming herbs, shrubs with spines and prickles, shrubs with fleshy fruits, half-shrubs, annual plants, and plants with sticky, animal-dispersed seeds.

The dominant trees of FD communities are oaks and aspen. Bur oak is by far the most common tree species, but northern pin oak, white oak, and northern red oak (as well as black oak in southeastern Minnesota) are dominant in some stands. The oaks and aspen are well adapted to repeated burning because of their ability to store resources in their root systems and resprout after fire. The oaks develop peculiar growth forms (often referred to as “grubs”) when subjected to fire. When the tree trunk or stem is killed, a callus develops over the top of an enlarged root mass near the ground surface. These trees continue to send up sprouts from the root collar at the margin of the mass, forming a ring of stems. Such rings commonly achieve 3-foot diameters, and individual stems up to 5 feet apart may be connected to the same rootstock. These sprouts grow quickly at first, but growth eventually slows, especially when the stems are overtopped by aspens or by adjacent trees that survived the fire.

Quaking aspen survives repeated burning by forming suckers that sprout from an extensive network of roots. This produces a dispersed, thicketlike growth of new sprouts. These sprouts, like those of the oaks, often seem stunted, with growth of individual stems slowing after a rapid initial burst. It is significant that in the EBF Province land surveyors in the 1800s commonly listed aspen and oak as “underbrush” rather than “timber.” Aboveground, the FD communities of the province were incredibly dynamic, with the density and height of woody plants ever changing in response to fires. Belowground, however, were massive rootstocks of oaks, aspens, and many of the common shrub species. These rootstocks can attain great age, and there is every reason to believe that oak grubs, aspen clones, and colonies of shrubs could continuously occupy a site for centuries.

Floristic Regions

FD communities in Minnesota are grouped into four floristic regions, based on general differences in species composition (Fig. FD-1). Two of these floristic regions are represented in the EBF Province: the Southern Floristic (FDs) Region and the Central Floristic (FDc) Region. FDs communities are common throughout the province, whereas FDc communities are rare, being limited to a few areas along the boundary of the EBF Province with the Laurentian Mixed Forest (LMF) Province. Communities of the Northwestern Floristic (FDw) Region and Northern Floristic (FDn) Region are not known to occur in the EBF Province.

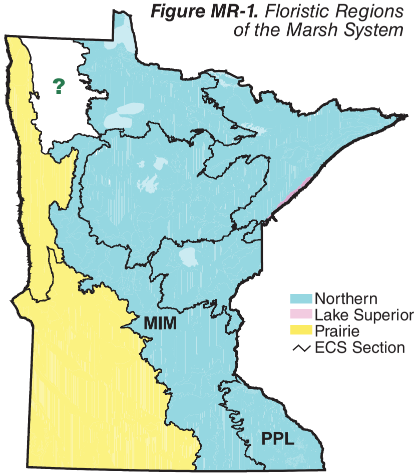
Given the paucity and localized occurrence of FDc communities, the EBF Province is essentially a single floristic region of fire-dependent vegetation (FDs) that is functionally quite different from the conifer-dominated forests and woodlands of the LMF Province, where FDn and FDc communities are prevalent. Most noticeable is that the plants growing in the FD communities of the EBF Province are generally not dependent on fire at any stage of their life cycles but are clearly tolerant of fire. Fire may alter the growth form of these plants and influence the allocation of resources among roots, stems, bark, leaves, or fruits, but most of these species can be found in habitats that lack any direct evidence of fire. In fact, there are many herbaceous plants that are widespread in FD communities in the EBF Province that never occur on sites in the LMF Province that burn

species germinate only when seeds buried in sediments are exposed following water-level drawdowns. These include annuals such as beggarticks *(Bidens* spp.) and smartweeds *(Polygonum* spp.) that germinate rapidly and profusely on freshly exposed substrates. Reflooding of exposed substrates, however, usually eliminates annuals from the site—either drowning them if water levels rise high enough or preventing them from germinating on sites that remain inundated—or restricts them to floating mats. Perennial emergent species, once established at a site, can expand rapidly by extensive rhizomes as water levels rise. Therefore, the dominant plants in most marshes are emergent species, especially those with vegetative and flowering structures that extend well above the water level and can withstand short periods of abnormally high water. These species include cattails *(Typha* spp.), bulrushes *(Scirpus* spp.), and arrowheads *(Sagittaria* spp.). Persistently high water levels typically eliminate shorter emergent species not able to remain above the water level, and favor floating species such as duckweeds *(Lemna* spp. and *Spirodela polyrhiza)* and common white water-lily *(Nymphaea odorata)*. With sustained high water levels, submerged species such as bladderworts *(Utricularia* spp.), common coontail *(Ceratophyllum demersum)*, and Canadian elodea *(Elodea canadensis)* become more frequent. These plants have little resistance to desiccation, however, and are usually eliminated during the next cyclic drawdown. In settings where water levels are stable because of steady inputs of groundwater, MR communities often become dominated by a single species, and species diversity declines.

Floristic Regions

MR communities in Minnesota are grouped into three floristic regions, the Northern Floristic (MRn) Region, the Lake Superior Floristic (MRu) Region, and the Prairie Floristic (MRp) Region (Fig. MR-1). Only the MRn Region is represented in the EBF Province. In general, differences in species composition among the floristic regions are subtle, with regional climatic influences appearing to be less important than differences in water chemistry, especially in MR communities with deeper water levels where differences in alkalinity (i.e., hard water versus soft water) may cause greater variation in species composition among marshes within a given floristic region than are observed between floristic regions. Additional data are needed to understand the most important factors in regional variation among MR communities.

Figure MR-1. *Floristic Regions of the Marsh System*



The MRn Region is characterized by relatively high precipitation, low evaporation rates, and infrequent drought, so marshes in the region can be present in basins fed by precipitation and surface runoff as well as by groundwater. (In comparison, in the MRp Region to the south and west, relatively low precipitation, high evaporation rates, and more frequent drought cause marshes to be more restricted to settings with steady inputs of groundwater.) There are two plant community classes in the MRn Region, Northern Mixed Cattail Marsh (MRn83) and Northern Bulrush-Spikerush Marsh (MRn93). There is much variability in species composition within these two classes, while floristic differences between the classes are subtle. They are distinguished from one another mainly by differences in dominant plant species, which appear to be

MR Marsh System


photo by D.S. Wovcha MN DNR

Wabasha County, MN

General Description

Communities of the Marsh (MR) System are tall forb- and graminoid-dominated wetland communities that have standing or, in the case of riverine marshes, slow-flowing water present through most of the growing season. The vegetation is characterized by perennial emergent plants such as cattails *(Typha* spp.), bulrushes *(Scirpus* spp.), and arrowheads *(Sagittaria* spp.), mixed with annual forbs during low-water periods when substrates are exposed, and floating-leaved and submergent aquatic plants in settings with persistent standing water. MR communities occur statewide and are common throughout the Eastern Broadleaf Forest (EBF) Province in wetland basins, along sheltered lakeshores, near stream mouths, and in river backwaters or sluggish streams. The maximum water depth is typically sustained at 20–60 inches (50–150cm) but may be higher, especially in marshes where the vegetation is rooted on floating mats. Water levels are fairly stable in settings supplied by significant groundwater inputs and variable where water is supplied predominantly by precipitation and surface runoff. If water-level drawdown occurs, it coincides with drought cycles and is not seasonal as in Wet Meadow/Carr (WM) communities.

Nutrient levels are typically high in MR communities, particularly following drawdowns, which allow for oxidation of organic material in sediments and release of nutrients. Because most of the EBF Province is underlain by calcareous glacial deposits, the pH of water in MR communities in the province is typically circumneutral to basic with high dissolved mineral content. Substrates in MR communities range from mineral soil to sedimentary peat to floating peaty root mats. Organic matter can be abundant in substrates not exposed regularly to wave action, river currents, ice scouring, or drawdowns and episodes of oxidation.

Plant Adaptations

The dominant plants in MR communities are tolerant of persistently deep water levels. Like many wetland plants, they have stems, leaves, and roots that contain intercellular air spaces (aerenchyma) that store oxygen and diffuse it from above-water structures to roots during waterlogged conditions. Variation in species composition over time is common in marshes in response to changes in hydrological conditions. Many marsh

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with any regularity. These plants have life history strategies—such as shade tolerance, seedling banks, and storage organs—that are most often associated with plants common in communities of the MH and Floodplain Forest (FF) systems.

FDs communities are predominantly deciduous, with very dense shrub layers and low abundance of grasses. They are not inherently flammable and tend to develop structures and fuels that make them less likely to burn as they age. In the past, however, they were subject to creeping surface fires because they occurred next to prairies. In some instances, these fires killed shrubs and small trees, thereby creating dry woody fuels for subsequent, more intense fires.

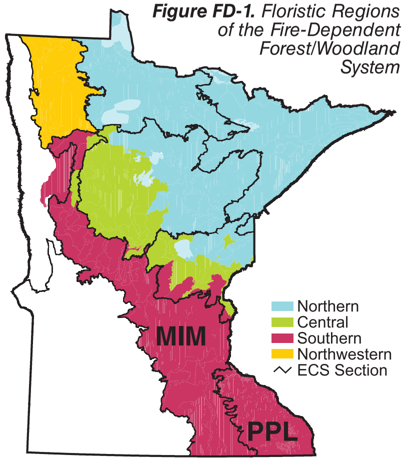

Figure FD-1. *Floristic Regions of the Fire-Dependent Forest/Woodland System*

Statewide, FDs communities occur in habitats that are much richer and slightly moister than those of FDc communities. Several geologic and soil properties are consistent with FDs sites being richer than FDc sites. Most impressive is that 83% of the FDs vegetation samples used in developing this classification occur on calcareous drift, sediment, or loess from the Red River, Des Moines, and Grantsburg glacial lobes. Eighty-four percent of FDc samples occur on noncalcareous or slightly calcareous drift or outwash from the Superior, Rainey, and Wadena glacial lobes. Surprisingly, with the exception of nutrient status, the soil characteristics commonly associated with calcareous and noncalcareous landscapes are not so divergent between FDs and FDc sites. There is broad overlap in soil texture in the coarse soil-texture classes. Only those FDs communities present on loess occur on consistently fine-textured soils. Free carbonates tend to occur deep within the soil for both FDs communities and FDc communities. In FDs communities, free carbonates are usually present about 42in (105cm) below the soil surface. In FDc communities, free carbonates are often absent or about 49in (125cm) deep when present. The upper soil horizons in FDs communities have 1.3–3.3% organic matter content while FDc communities have 1.0–2.5% organic matter. Rooting zone pH tends to be slightly acid or near neutral for both FDs communities (5.9–7.2) and FDc communities (5.0–6.7).

The four native plant community classes in the FDs Region are distinctive and geographically separated from one another—arguably, the classes could be separated by geography and substrate alone. Southern Dry-Mesic Oak-Aspen Forests (FDs36) occur on till plains and moraines in the Hardwood Hills Subsection in Polk and Mahnomen counties. Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) occur on sandy and gravelly soils throughout the Hardwood Hills Subsection south of Mahnomen County and across the Anoka Sand Plain and St. Paul Baldwin Plains and Moraines Subsections. Southern Dry-Mesic Oak (Maple) Woodlands occur also on steep slopes along the Minnesota River with excessively drained gravelly till. Southern Dry-Mesic Pine-Oak Woodlands (FDs27) and Southern Dry-Mesic Oak-Hickory Woodlands (FDs38) are restricted to the Paleozoic Plateau Subsection, with the former occurring on sandy alluvial bottoms and the latter on loess-covered bedrock in association with bedrock bluff prairies.

The four FDs community classes arrived at similar vegetative conditions by different pathways. In the Paleozoic Plateau, mesic forests of oak, elm, maple, basswood, and ironwood developed in the early Holocene Epoch, about 9,000 years ago, and persisted until about 5,500 years ago. Except at the most protected sites, these forests were replaced by prairie at that time, and prairie persisted until about 3,000 years ago. At about 3,000 years ago, woodland vegetation began to develop, possibly with communities analogous to Southern Dry-Mesic Pine-Oak Woodlands (FDs27) forming on sites occupied by sand prairies and barrens, and Southern Dry-Mesic Oak-Hickory Woodlands (FDs38) encroaching on sites occupied by bluff prairies. This pattern appears to have remained fairly stable until recent times, when some areas of fire-dependent woodland began to succeed to mesic forest.

At sites where Southern Dry-Mesic Oak-Aspen Forests (FDs36) are now present, boreal species such as spruce, birch, and some (jack) pine persisted into the very early Holocene Epoch, until about 8,500 years ago. These woodlands were then replaced by prairie, with oak also appearing in the landscape. This condition persisted until about 4,000 years ago, when forests of mesic and fire-dependent hardwood trees developed that are similar to those present today. Southern Dry-Mesic Oak-Aspen Forests (FDs36) most likely began replacing the patches of prairie or brush prairie and continue to occupy drier sites in the landscape.

Curiously, the sites on which Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) occur have topography and soil parent material similar to sites on which FDc communities occur in the LMF Province across the border from the EBF Province. The differences between Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) and FDc communities seem to be related to their paleohistory, which is virtually identical until the late Holocene Epoch, from 3,000 to 300 years ago. Forests or woodlands of jack pine and perhaps red pine formed on these sites in the early Holocene Epoch, about 10,000 years ago. Dry upland prairies replaced these pine forests about 8,000 years ago. Beginning about 4,000 years ago, pines started to reclaim these lands and have been doing so until modern times. Pine forests formed on sites now occupied by Central Poor Dry Pine Woodlands (FDc12) about 3,500 years ago, on sites now occupied by Central Dry Pine Woodlands (FDc23) and Central Dry-Mesic Pine-Hardwood Forests (FDc34) about 2,000 years ago, on sites occupied by Central Rich Dry Pine Woodlands (FDc24) about 300 to 600 years ago, and not at all on sites occupied by Southern Dry-Mesic Oak (Maple) Woodlands (FDs37). Thus, Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) differ from FDc communities only in that they occur on sites that were not reinvaded by jack pine (and associated ground-layer plants).

Plant Indicators of FDc vs. FDs Communities

Plant species with high fidelity for FDc communities relative to FDs communities are listed in Table FD-1. Many of these plants are strongly associated with the coniferous forests abundant throughout the adjacent LMF Province. Most occur in upland pine forests, but others occur in both upland and wetland settings where conifers are present. These plants tend to be evergreen or have overwintering leaves, such as wintergreen *(Gaultheria procumbens)*, pipsissewa *(Chimaphila umbellata)*, bearberry *(Arctostaphylos uva-ursi)*, and round-leaved pyrola *(Pyrola rotundifolia)*. Another guild of plants common in FDc communities but not in FDs communities are plants of UP communities. Presumably plants like hoary puccoon *(Lithospermum canescens)*, big bluestem *(Andropogon gerardii)*, and smooth blue aster *(Aster laevis)* occur in FDc communities because these communities were prairies before jack pine invaded these sites in the late-Holocene Epoch. Given the proximity of FDs communities with prairies along the prairie-forest border and in the blufflands, one might have expected prairie plants to be more prevalent in FDs communities than FDc communities. Apparently these sun-loving plants are not successful beneath the canopy of deciduous trees and dense shrub layer that is currently typical of FDs forests and woodlands.

Plants with high fidelity for FDs communities relative to FDc communities appear in Table FD-2. Nearly all of these plants reach their peak presence in floodplain forests

Table WM-2 *Plants useful for differentiating the Southern from the Northern Floristic Region of the Wet Meadow/Carr System.*

				frequency (%)	
	Layer	Common Name	Scientific Name	WMn	WMs
Southern Floristic Region	Forb	Sunflower	*Helianthus* spp.*	1	29
		Stemless blue violets	*Viola nephrophylla* and similar *Viola* spp.	2	24
		Tall meadow-rue	*Thalictrum dasycarpum*	5	24
		Rough bugleweed	*Lycopus asper*	3	23
		Flat-topped aster	*Aster umbellatus*	5	22
		Virginia mountain mint	*Pycnanthemum virginianum*	1	21
		Swamp thistle	*Cirsium muticum*	3	18
		Spotted water hemlock	*Cicuta maculata*	2	17
		Swamp lousewort	*Pedicularis lanceolata*	1	14
		Germander	*Teucrium canadense*	-	11
		Starry false Solomon's seal	*Smilacina stellata*	-	10
		Clasping dogbane	*Apocynum sibiricum*	1	8
		Autumn sneezeweed	*Helenium autumnale*	-	8
		Great lobelia	*Lobelia siphilitica*	-	7
		Golden alexanders	*Zizia aurea*	-	5
	Graminoid	Slough sedge	*Carex atherodes*	5	29
		Prairie cordgrass	*Spartina pectinata*	-	23
		Fowl manna grass	*Glyceria striata*	4	23
		Woolly sedge	*Carex pellita*	1	22
		Redtop	*Agrostis stolonifera*	1	17
		Porcupine sedge	*Carex hystericina*	3	17
		Whitetop	*Scolochloa festucacea*	-	13
		Sartwell's sedge	*Carex sartwellii*	3	13
		Hairy-fruited sedge	*Carex trichocarpa*	-	5
		Crested sedge	*Carex cristatella*	1	5
	Tree & Shrub	Box elder (U)	*Acer negundo*	1	10
		Poison ivy	*Toxicodendron rydbergii*	-	7

(U) = understory tree *Helianthus giganteus, H. grosseserratus,* or *H. nuttallii*

Succession

WM communities can develop from Wet Forest (WF) communities in areas flooded by beaver activity or from FP communities following catastrophic fires during severe droughts. WM communities can also develop from Marsh (MR) communities when siltation, accumulation of sedimentary peat, development of floating root mats, or lowering of water tables (commonly following disintegration of beaver dams or other natural or artificial dams) effectively lowers the water level in relation to the substrate surface; this promotes invasion and dominance by sedges over emergent aquatic plants such as cattails (*Typha* spp.) or bulrushes (*Scirpus* spp.). In WM communities invaded by peat-producing bryophytes (particularly *Sphagnum*), nutrient levels decline, and the dominant broad-leaved sedge species are replaced by fine-leaved sedges, causing conversion to Open Rich Peatland (OP) communities. In some cases, invasion by *Sphagnum* occurs so quickly that the site appears to succeed directly from a WM community to an Acid Peatland (AP) community. This happens primarily when the dominant sedges, with the exception of the most deeply rooted, are eliminated by rapid expansion of level *Sphagnum* carpets that lack significant development of hummocks and hollows. In this situation, the characteristic OP plants do not become established on the site before water chemistry turns acidic and nutrient poor, favoring plants characteristic of AP communities. WM communities can also succeed to WF communities if hydrological changes result in lowering of the water table, followed by an increase in dominance of shrubs and eventual establishment of tree seedlings.

Table WM-1 *Plants useful for differentiating the Northern from the Southern Floristic Region of the Wet Meadow/Carr System.*

	Layer	Common Name	Scientific Name	frequency (%)	
				WMn	WMs
Northern Floristic Region	Forb & Fern	Marsh cinquefoil	*Potentilla palustris*	39	-
		Three-cleft or small bedstraw	*Galium trifidum* or *G. tinctorium*	46	10
		Arrow-leaved tearthumb	*Polygonum sagittatum*	28	2
		Marsh St. John's wort	*Triadenum fraseri*	23	-
		Crested fern	*Dryopteris cristata*	24	3
		Northern blue flag	*Iris versicolor*	22	4
		Broad-leaved arrowhead	*Sagittaria latifolia*	21	5
		Big-leaf white or Northern white violet	*Viola blanda* or *V. macloskeyi*	12	-
		Mad dog skullcap	*Scutellaria lateriflora*	13	1
		Yellow loosestrife	*Lysimachia terrestris*	10	-
		Wild calla	*Calla palustris*	9	-
		Spinulose shield fern	*Dryopteris carthusiana*	6	-
		Dotted smartweed	*Polygonum punctatum*	7	1
	Graminoid	Fen wiregrass sedge	*Carex lasiocarpa*	29	5
		Silvery sedge	*Carex canescens*	6	-
		Creeping sedge	*Carex chordorrhiza*	5	-
	Tree & Shrub	Paper birch (U)	*Betula papyrifera*	8	-
		Speckled alder	*Alnus incana*	24	1
		Meadowsweet	*Spiraea alba*	23	4
		Bog willow	*Salix pedicellaris*	9	-
		Balsam willow	*Salix pyrifolia*	7	-
		Steeplebush	*Spiraea tomentosa*	5	-
		Leatherleaf	*Chamaedaphne calyculata*	6	-

(U) = understory tree

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in the FF System and in wet-mesic hardwood forests in the MH System. Shagbark hickory and tall thimbleweed *(Anemone virginiana)* are the only plants in this list with peak presence in FD communities. These two species and golden alexanders *(Zizia aurea)* are the only plants in this list to occur in habitats that burned regularly. The remaining plants are clearly not dependent on fire, because they most commonly occur in habitats that rarely burn. Either they are tolerant of fire and are a natural component of FDs communities, or they have invaded the sites on which FDs communities occur as a result of fire-suppression in modern times. Floodplain forests, wet-mesic hardwood forests, and FDs communities have in common a forest floor with low light levels, soils

Table FD-1. *Plants useful for differentiating the Central from the Southern Floristic Region of the Fire-Dependent Forest/Woodland System.*

		Common Name	Scientific Name	frequency (%)	
				FDc	FDs
Central Floristic Region	Evergreen or over-wintering leaves	Wintergreen	*Gaultheria procumbens*	41	-
		One-sided pyrola	*Pyrola secunda*	39	5
		Pipsissewa	*Chimaphila umbellata*	26	5
		Bearberry	*Arctostaphylos uva-ursi*	24	-
		Jack pine (U)	*Pinus banksiana*	22	1
		Round-leaved pyrola	*Pyrola rotundifolia*	16	-
		Balsam fir (U)	*Abies balsamea*	16	-
		Red pine (U)	*Pinus resinosa*	15	-
		Twinflower	*Linnaea borealis*	15	-
		Bunchberry	*Cornus canadensis*	14	-
	Prairie affinity	Hoary puccoon	*Lithospermum canescens*	27	3
		Big bluestem	*Andropogon gerardii*	23	2
		Smooth blue aster	*Aster laevis*	21	2
		Slender wheatgrass	*Elymus trachycaulus*	17	-
		Gray goldenrod	*Solidago nemoralis*	15	1
		Oval-leaved milkweed	*Asclepias ovalifolia*	11	-
		Kalm's brome	*Bromus kalmii*	11	-
		Virginia ground cherry	*Physalis virginiana*	11	-
		Wood betony	*Pedicularis canadensis*	10	2
	Other	Lowbush blueberry	*Vaccinium angustifolium*	81	8
		Prickly or smooth wild rose	*Rosa acicularis* or *R. blanda*	71	17
		Pale vetchling	*Lathyrus ochroleucus*	51	10
		Prairie willow	*Salix humilis*	49	-
		Veiny pea	*Lathyrus venosus*	46	7
		False melic grass	*Schizachne purpurascens*	41	3
		American vetch	*Vicia americana*	35	1
		Pussytoes	*Antennaria* spp.	31	7
		Yarrow	*Achillea millefolium*	28	5
		Harebell	*Campanula rotundifolia*	28	5
		Poverty grass	*Danthonia spicata*	26	2
		Hairy goldenrod	*Solidago hispida*	24	2
		Sharp-pointed rice grass	*Oryzopsis pungens*	23	-
		Pin cherry	*Prunus pensylvanica*	22	3
		Balsam ragwort	*Senecio pauperculus*	20	-
		Cow wheat	*Melampyrum lineare*	19	-
		Kalm's hawkweed	*Hieracium kalmii*	18	1
		Bluebead lily	*Clintonia borealis*	17	1
		Fringed brome	*Bromus ciliatus*	16	2
		Blue giant hyssop	*Agastache foeniculum*	16	-
		Sand cherry	*Prunus pumila*	16	-
		Sand or dog violet	*Viola adunca* or *V. conspersa*	15	-
		Clustered muhly grass	*Muhlenbergia glomerata*	13	-

(U) = understory tree

with comparatively high amounts of incorporated organic matter, and little or no humus on the surface. These conditions are characteristic in floodplain forests because floodwaters tend to remove organic matter on the soil surface and bury organic surfaces under fresh alluvium. In modern wet-mesic hardwood forests, earthworms exotic to Minnesota have accomplished much the same thing by totally mixing the humus into the mineral soil. Frequent surface fires in FDs communities (see below) prevent accumula-

Table FD-2. *Plants useful for differentiating the Southern from the Central Floristic Region of the Fire-Dependent Forest/Woodland System.*

		Common Name	Scientific Name	frequency (%) FDc	FDs
Southern Floristic Region	Mesic Hardwood Forest Affinity	Clayton's sweet cicely	*Osmorhiza claytonii*	19	82
		Pointed-leaved tick trefoil	*Desmodium glutinosum*	6	70
		Lopseed	*Phryma leptostachya*	2	66
		Common enchanter's nightshade	*Circaea lutetiana*	2	51
		Wild geranium	*Geranium maculatum*	4	43
		Prickly gooseberry	*Ribes cynosbati*	8	43
		Rattlesnake fern	*Botrychium virginianum*	2	31
		White snakeroot	*Eupatorium rugosum*	-	26
		Red elm (U)	*Ulmus rubra*	3	21
		White oak (U)	*Quercus alba*	1	19
		Bitternut hickory (U)	*Carya cordiformis*	1	18
		Black raspberry	*Rubus occidentalis*	2	18
		Rugulose or yellow violet	*Viola canadensis* or *V. pubescens*	4	18
		Bottlebrush grass	*Elymus hystrix*	3	17
		Elliptic pyrola	*Pyrola elliptica*	2	16
		Agrimony	*Agrimonia* spp.	-	15
		Zigzag goldenrod	*Solidago flexicaulis*	2	15
		Elm-leaved goldenrod	*Solidago ulmifolia*	-	14
		Bloodroot	*Sanguinaria canadensis*	1	14
		Climbing bittersweet	*Celastrus scandens*	2	13
		Blue cohosh	*Caulophyllum thalictroides*	-	12
		Shining bedstraw	*Galium concinnum*	-	12
		American spikenard	*Aralia racemosa*	1	12
		Red-berried elder	*Sambucus pubens*	1	10
		Tail-leaved aster	*Aster urophyllus*	2	10
	Floodplain Forest Affinity	Prickly ash	*Zanthoxylum americanum*	1	64
		Wild grape	*Vitis riparia*	3	63
		American elm (U)	*Ulmus americana*	8	45
		Box elder (U)	*Acer negundo*	2	43
		Missouri gooseberry	*Ribes missouriense*	-	29
		Honewort	*Cryptotaenia canadensis*	-	28
		Nannyberry	*Viburnum lentago*	2	28
		White avens	*Geum canadense*	-	21
		Stickseed	*Hackelia* spp.	2	19
		Hackberry (U)	*Celtis occidentalis*	-	17
		Gregarious black snakeroot	*Sanicula gregaria*	-	17
		Greenbriar	*Smilax hispida*	3	15
		Aniseroot	*Osmorhiza longistylis*	1	12
		Kidney-leaved buttercup	*Ranunculus abortivus*	-	11
	Other	Lady fern	*Athyrium filix-femina*	5	33
		Shagbark hickory (U)	*Carya ovata*	-	18
		Eastern red cedar (U)	*Juniperus virginiana*	-	15
		Side-flowering aster	*Aster lateriflorus*	3	14
		Golden alexanders	*Zizia aurea*	-	13
		Jack-in-the-pulpit	*Arisaema triphyllum*	-	11
		Virginia thimbleweed	*Anemone virginiana*	2	10

(U) = understory tree

[Calamagrostis canadensis]) form dense tussocks that elevate rootlets above the water surface. These tussock-formers account for the hummocky topography characteristic of WM communities. Other species, such as willows, develop roots from stems or root collars (adventitious roots) that provide access to oxygen when other roots are submerged. Plants in WM communities must also minimize desiccation during periods of drawdown; this is accomplished by development of roots that extend deeply into permanently wet or moist substrates and by hard-walled cells (sclerenchyma) on outer surfaces of roots and rhizomes that reduce water loss. Although floating-leaved and submerged aquatic species may temporarily invade WM communities during periods of high water, they lack adaptations to prevent desiccation and are eliminated during low-water periods.

Because minerals and nutrients are plentiful in WM communities, growth of vegetation is typically luxuriant although not usually diverse. The characteristic sedges are wide-leaved species such as lake sedge *(Carex lacustris)* and tussock sedge *(C. stricta)* that form monotypic stands and produce dense thatch. In WM communities with dense cover of the strongly rhizomatous species lake sedge *(C. lacustris)*, regular oscillations in water level and thick thatch limit plant diversity by reducing habitats available for forb species. In comparison, WM communities dominated by tussock-forming species, such as tussock sedge *(C. stricta)*, usually have higher vascular species diversity, with forbs growing between tussocks and on the exposed roots of uprooted tussocks.

Floristic Regions

Based on general differences in species composition, WM communities in Minnesota are grouped into three floristic regions: the Northern Floristic (WMn) Region, the Prairie Floristic (WMp) Region, and the Southern Floristic (WMs) Region (Fig. WM-1). Only the WMn and WMs regions are represented in the EBF Province. WMn communities are prevalent in the EBF Province and in the Laurentian Mixed Forest Province, both of which are characterized by dependable precipitation and low evapotranspiration rates. WMs communities, although present in the EBF Province, are infrequent; they are much more common in the Prairie Parkland and Tallgrass Aspen Parklands provinces, where precipitation is sporadic and evapotranspiration rates are higher. Species that help to differentiate the WMn and WMs regions are presented in Tables WM-1 and WM-2.

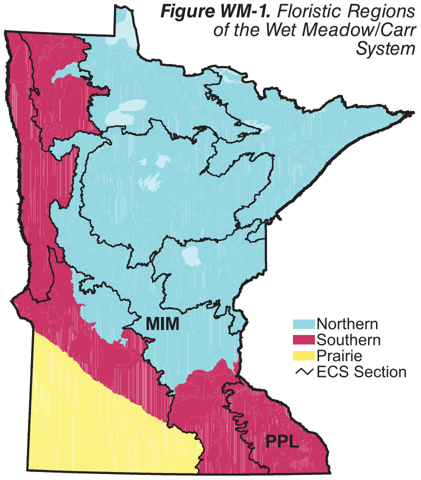

Figure WM-1. *Floristic Regions of the Wet Meadow/Carr System*

Variation Within Floristic Regions

Currently, only one native plant community class is recognized in the WMn Region, Northern Wet Meadow/Carr (WMn82). Future collection and analysis of environmental data along with vegetation data will likely lead to delineation of several WMn classes based on average or maximum water depth or length of inundation. There are two native plant community classes in the WMs Region. Southern Seepage Meadow/Carr (WMs83) develops in settings fed by groundwater and is characterized by relatively constant water supply. Southern Basin Wet Meadow/Carr (WMs92) occurs in settings where water is supplied by precipitation and surface runoff. WMs92 is characterized by distinct wet and dry cycles.

WM Wet Meadow/Carr System

photo by E.R. Rowe MN DNR

Becker County, MN

General Description

Wet Meadow/Carr (WM) communities are graminoid- or shrub-dominated wetlands that are subjected annually to moderate inundation following spring thaw and heavy rains and to periodic drawdowns during the summer. The dominant graminoids are broad-leaved species such as lake sedge *(Carex lacustris)*, tussock sedge *(C. stricta)*, and bluejoint *(Calamagrostis canadensis)*. Shrubs such as willows *(Salix* spp.) and dogwoods *(Cornus* spp.) are likely to be dominant on drier sites. Peak water levels are high and persistent enough to prevent trees (and often shrubs) from becoming established. However, there may be little or no standing water present during much of the growing season. As a result, the substrate surface alternates between aerobic and anaerobic conditions. Any organic matter that accumulates over time is usually oxidized during periodic drawdowns and may even burn during severe droughts. Soils range from mineral soils to muck and peat. Silt from flooding sometimes is intermixed with organic matter in muck or peat soils. Although WM communities can be present on deep peat, they are not "peat-accumulating" communities. Rather, the peat was usually formed previously on the site by a peat-producing community, such as a Forested Rich Peatland, that was flooded by beaver activity and converted to a WM community. Deep peat may also be present in some WM communities because of debris that has been transported into the wetland, forming sedimentary peat. Because surface water is derived from runoff, stream flow, or groundwater, it is circumneutral (pH 6.0–8.0) and has high mineral and nutrient content. WM communities are present statewide and are common throughout the Eastern Broadleaf Forest (EBF) Province in wetland basins, along streams and drainage ways, in drained beaver ponds, in shallow bays, or as semifloating mats along sheltered lake shorelines.

Plant Adaptations

The characteristic plants of WM communities have adaptations that allow them to survive waterlogged conditions, although they are generally intolerant of prolonged inundation or high (> 20in [50cm]) water levels. Like many wetland plants, they have stems, leaves, and roots that contain intercellular air spaces (aerenchyma) that store oxygen and transport it from above-water structures to roots during waterlogged periods. In addition, some sedges and grasses (e.g., tussock sedge *[Carex stricta]* and bluejoint

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tion of thick humus layers, and these forests, like wet-mesic hardwood forests, have a long history of earthworm activity.

Natural History and Fire Regimes of FDc vs. FDs Communities

The natural rotation periods of fires in FDc and FDs communities are similar (Table FD-3). In the past, communities in both floristic regions were far more likely to experience surface fires than catastrophic fires that killed existing trees and caused regeneration of forest stands. In general, FDc communities have rotations of 30 years for surface fires, and rotations of 110–130 years for catastrophic fires. Central Dry Oak-Aspen (Pine) Woodlands (FDc25) are somewhat exceptional among FDc communities, with rotations of just 10 years for surface fires. FDs communities have rotations of 10–20 years for surface fires, and 100–150 years for catastrophic fires. The chances of any fire resulting in significant mortality of canopy trees ranges from about one in four for FDc communities to about one in ten for FDs communities. This contrasts strongly with FDn communities, where catastrophic fires were roughly as frequent as surface fires.

Both FDc and FDs communities are remnants of what the land surveyors described in the late 1800s as "upland brush with scattered timber." At present, their structure

Table FD-3. *Historic tree species composition and disturbance regimes in FDc and FDs communities*

	Historic Tree Species Frequency by Class and Stand Age						Historic Disturbance Rotation Periods by Class (in years)			
	young forest age	young forest species	mature forest age	mature forest species	old forest age	old forest species	Stand-Regenerating Fire	Moderate Surface Fire	All Fires	Catastrophic Windthrow
Central Floristic Region						ranges ⟶	80-130	10-30	10-25	>1000
FDc24	0 - 55 yrs	**jack pine**	75 - 155 yrs	**jack pine** red pine	> 155 yrs	**jack pine** *(white pine)*	130	30	23	>1000
FDc25	0 - 55 yrs	bur oak quaking aspen *(jack pine)* *(northern pin oak)*	55-135 yrs	**bur oak** *(northern pin oak)*	> 135 yrs	jack pine bur oak	80	10	9	--
FDc34	0 - 55 yrs	quaking aspen* red pine *(white pine)* *(jack pine)*	95-135 yrs	**red pine** *(white pine)*	>195 yrs	**white pine** *(red pine)*	110	30	23	>1000
Southern Floristic Region						ranges ⟶	110-150	10-20	10-20	>1000
FDs27	0+ yrs	**bur oak** *(black oak)* *(northern pin oak)*	--	--	--	--	135	15	14	--
FDs36	0-35 yrs	**quaking aspen** *(bur oak)*	75-135 yrs	**bur oak** *(quaking aspen)*	>175 yrs	**bur oak** *(American elm)* *(white pine)*	100	20	18	>1000
FDs37	0-75 yrs	**bur oak** *(northern red oak)*	>75 yrs	**bur oak** white oak *(northern red oak)*	--	--	110	10	9	>1000
FDs38	0-55 yrs	**bur oak** *(northern red oak)*	55-135 yrs	**bur oak**	>135 yrs	**bur oak** *(white oak)*	150	15	11	>1000

bold = >50% normal = 25-50% *(italics)* = 10-25% *includes big-toothed aspen is better described as woodland or even forest. Before Euro-American settlement, the number of trees per acre in FDc communities was about one-third that of MH communities in the same general region (i.e., MHc communities). For FDs communities, historic density was about a third or a fourth that of MHs communities. Today, there is no difference in tree density between FDc or FDs communities and MHc or MHs communities, respectively. A clear consequence of fire suppression has been for tree canopies to develop in FDc and FDs communities, filling the gaps created in the past by frequent surface fires. The effect of tripling the density of pines in FDc communities is to make them more flammable and capable of carrying crown fires. The effect of tripling or quadrupling the density of bur oak, aspen, and birch in FDs communities is to create a less flammable community composed mostly of deciduous trees and shrubs. The mean cover of woody trees and shrubs in FDs communities is 163%, meaning that these communities have nearly double canopies of woody vegetation, which maintain humid subcanopy conditions and provide enough shade to stifle the production of herbaceous fine fuels.

There is no reason to assume that colonies of hazelnuts, dogwoods, or other native deciduous woodland shrub species in Minnesota are much more likely to burn as they age. It is also unlikely that they would burn much hotter because of accumulated fuel or because of intrinsic properties such as the accumulation of flammable chemicals in living tissue that occurs in some species of western shrubs. Rather, in the past Minnesota's native shrubs likely formed the dominant vegetation layer in uplands where the fire regime was imposed on the landscape by context more than site properties or the developmental stage of these brushlands. FDc and FDs communities probably burned frequently because they were next to or surrounded areas of prairie. Where there were extensive areas of FDs communities in the historic landscape, it almost always appears they were in areas between prairies and true forests. Where there were extensive areas of FDc communities, they almost always contained areas of prairies, sandy river terraces, or perennial Indian settlements. Grasslands and wet hay meadows within short distances of forests were of great value to Indians and European settlers alike. These openings attracted game and provided food for the settlers' horses and livestock. These grasslands consistently produced dried fine fuel, people commonly set them ablaze, and they commonly brought fire to the edge of FDc and FDs communities. Under dry conditions the fires burned through FDc and FDs communities, while under wetter conditions they did not.

The spatial configuration of trees and brush in historic FDc and FDs communities is difficult to reconstruct from Public Land Survey (PLS) records. Raw estimates based on distances of bearing trees to survey corners suggest there were about 14 trees per acre in FDc communities and about 9 trees per acre in FDs communities. However, the same calculations for communities where densities of trees should have been unaffected by fire (e.g., MH communities) suggest that PLS reconstructions underestimate tree density by five to as much as ten times. Such calculations are misleading because they suggest there were trees on almost every acre of land. Direct descriptions are more useful. For both FDc and FDs communities, the surveyors described about half of the land survey corners as some kind of forest or woodland. The remaining corners were variously described as scattered timber, savanna, thickets, barrens, openings, groves, brush, or prairie. It is interesting that vast areas of Minnesota were surveyed with rather casual mention of the upland vegetation; it was simply described as either forest or prairie. In the EBF Province, where the forest and prairie biomes meet, the surveyors' vocabulary flourished. They were clearly attempting to describe something of great spatial complexity. Detailed maps of the trees referenced in the PLS notes indicate that trees grew on sites where they escaped fire or where the fires were of low intensity. Topography and surface water determined the pattern of such sites. Fluctuations in climate, especially as it affected lake levels and water tables, determined just how protected from fire these sites were from year to year.

Non-Mineotrophic Peatland Species

Because only those species listed below can persist in the ombrotrophic conditions of bogs, the occurrence of any other species can be considered an indicator of minerotrophic conditions. However, some seedlings, particularly of tree species, can germinate in bogs but are short-lived and should not be considered as minerotrophic indicators.

	Common Name	Scientific Name
Tree	Tamarack	*Larix laricina*
	Black spruce	*Picea mariana*
	Jack pine	*Pinus banksiana*
Low Shrub	Bog rosemary	*Andromeda glaucophylla*
	Leatherleaf	*Chamaedaphne calyculata*
	Creeping snowberry	*Gaultheria hispidula*
	Bog laurel	*Kalmia polifolia*
	Labrador tea	*Ledum groenlandicum*
	Lowbush blueberry	*Vaccinium angustifolium*
	Velvet-leaved blueberry	*Vaccinium myrtilloides*
	Small cranberry	*Vaccinium oxycoccus*
	Lingonberry	*Vaccinium vitis-idaea*
	Dwarf misletoe	*Arceuthobium pusillum*
Forb	Stemless lady's slipper	*Cypripedium acaule*
	Round-leaved sundew	*Drosera rotundifolia*
	Heart-leaved twayblade	*Listera cordata*
	Indian pipe	*Monotropa uniflora*
	Pitcher plant	*Sarracenia purpurea*
	Three-leaved false Solomon's seal	*Smilacina trifolia*
Graminoid	Bog wiregrass sedge	*Carex oligosperma*
	Few-flowered sedge	*Carex pauciflora*
	Poor sedge	*Carex paupercula*
	Three-seeded bog sedge	*Carex trisperma*
	Tussock cottongrass	*Eriophorum spissum*
	Tawny cottongrass	*Eriophorum virginicum*

OP
-continued-

Open Rich Peatland System

Table OP-2 *Plants useful for differentiating the Prairie from the Northern Floristic Region of the Open Rich Peatland System.*

				frequency (%)	
	Layer	Common Name	Scientific Name	OPn	OPp
Prairie Floristic Region	Shrub	Sage-leaved willow	*Salix candida*	12	48
		Shrubby cinquefoil	*Potentilla fruticosa*	8	34
	Forb	Grass-leaved goldenrod	*Euthamia graminifolia*	-	43
		Kalm's lobelia	*Lobelia kalmii*	10	41
		Spotted Joe pye weed	*Eupatorium maculatum*	9	37
		Swamp lousewort	*Pedicularis lanceolata*	4	35
		Stemless blue violets	*Viola* spp.*	5	34
		Eastern panicled aster	*Aster lanceolatus*	2	33
		Swamp milkweed	*Asclepias incarnata*	3	32
		Cut-leaved bugleweed	*Lycopus americanus*	1	32
		Flat-topped aster	*Aster umbellatus*	5	31
		Sunflower	*Helianthus* spp.**	-	30
		Canada goldenrod	*Solidago canadensis*	2	26
		American grass-of-Parnassus	*Parnassia glauca*	3	23
		Rough bugleweed	*Lycopus asper*	1	22
		Swamp thistle	*Cirsium muticum*	-	22
		Northern bedstraw	*Galium boreale*	-	20
		Common mint	*Mentha arvensis*	1	18
		Lesser fringed gentian	*Gentianopsis procera*	1	18
		Riddell's goldenrod	*Solidago riddellii*	-	18
		Marsh arrowgrass	*Triglochin palustris*	-	16
		Virginia mountain mint	*Pycnanthemum virginianum*	-	13
		Prairie loosestrife	*Lysimachia quadriflora*	-	12
		Silverweed	*Potentilla anserina*	-	12
		Germander	*Teucrium canadense*	-	11
		Spotted water hemlock	*Cicuta maculata*	-	11
		Poor gerardia	*Agalinis purpurea*	-	10
	Graminoid	Narrow reedgrass	*Calamagrostis stricta*	6	78
		Buxbaum's sedge	*Carex buxbaumii*	4	51
		Tall cottongrass	*Eriophorum polystachion*	7	44
		Sterile sedge	*Carex sterilis*	1	29
		Mat muhly grass	*Muhlenbergia richardsonis*	-	28
		Rigid sedge	*Carex tetanica*	-	25
		Sartwell's sedge	*Carex sartwellii*	1	24
		Tufted hair grass	*Deschampsia cespitosa*	-	22
		Big bluestem	*Andropogon gerardii*	-	19
		Baltic rush	*Juncus arcticus*	-	14
		Woolly sedge	*Carex pellita*	-	10

**Viola nephrophylla* and similar *Viola* spp. *******Helianthus giganteus, H. grosseserratus,* or *H. nuttallii*

other sources are sufficient to compensate their removal by *Sphagnum*, succession to AP communities may be stopped or slowed. In comparison with OP communities, AP communities have very little contact with groundwater, have *Sphagnum* in hollows as well as on hummocks, and lack rich minerotrophic species (see page EBF-OP6) for an explanation of minerotrophic versus bog species). The predominance of calcareous till and the marginal climatic conditions in the EBF Province limit the development of *Sphagnum* to isolated basins with stable water tables and small watersheds, so succession of OP communities to AP communities is uncommon in the province.

MH

Mesic Hardwood Forest System

MN DNR

Wolsfeld Woods Scientific and Natural Area, Hennepin County, MN

General Description

Mesic Hardwood Forest (MH) communities are present in the Eastern Broadleaf Forest (EBF) Province on upland sites with soils that retain water and in settings where wildfires are infrequent. These forests are characterized by continuous, often dense canopies of deciduous trees. Beneath the main canopy are successively shorter strata composed of shade-adapted seedlings, shrubs, and herbs. Basswood, sugar maple, and northern red oak are the most common canopy dominants, but MH communities are characteristically mixtures of at least four species. Other associated or occasionally dominant tree species include American elm, bur oak, paper birch, quaking aspen, white oak, black ash, red elm, green ash, bitternut hickory, black cherry, hackberry, and big-toothed aspen.

Plants in MH communities have access to predictable supplies of water and nutrients, but growth of understory plants is limited by light because of dense forest canopies. Typical sites are buffered from seasonal drought by fine-textured soils capable of holding or perching rainfall. At the same time, soils are well drained and are water logged or saturated only after spring snowmelt or heavy, prolonged rains. Consequently, plants in MH communities rarely experience diminished respiration due to soil anoxia. Essential nutrients, especially nitrogen, are mineralized from decaying organic matter at relatively high rates (twice those of Fire-Dependent Forest/Woodland (FD) and of Wet Forest (WF) communities). As a result, in MH communities nutrients in dead plant material quickly become available again for uptake by plants during the spring and early summer months. Overall, resource availability in MH communities follows a predictable annual or seasonal pattern (in comparison with FD communities, where nutrients and carbon are released episodically by burning). Tree mortality in older MH communities is rather constant, with stand-regenerating disturbances such as wildfires and catastrophic windthrow uncommon. The death of established canopy trees is most often caused by windthrow or disease affecting individual trees or small patches of trees or by other fine-scale disturbances.

Plant Adaptations

Competition for light has a strong influence on the species composition and structure of MH communities. Older forests commonly have several, nearly closed layers of woody plants, including a well-defined forest canopy, subcanopy, and shrub layer. These layers combine to produce continuous, if not overlapping, cover. Thus, most sunlight is filtered and attenuated before it reaches herbaceous plants and seedlings on the forest floor. Measurements of light intensity have been reported on forest floors in closed-canopy sugar maple stands of just 0.1% to 2% of direct sunlight. The plants of MH communities have strategies that appear to be adapted to the low intensity of light in these forests. For example, herbs and tree seedlings in the ground layer have enzyme stores and accessory pigments that allow for rapid photosynthesis as flecks of sunlight briefly pass over them, thereby minimizing the cost of maintaining the large stores of enzymes typical of plants growing in full sunlight. Another adaptive strategy to low light levels in MH communities is exemplified by the presence of herbaceous ground-layer species that develop rapidly in the spring, capturing and storing most of their annual energy needs before trees become fully leaved. There are varying degrees of this strategy, but for several common species in the EBF Province, this pattern of rapid early development has evolved to the point where aboveground stems develop completely, produce flowers and seeds, and die back before the leaves of canopy trees fully expand in May or early June.

In addition to light intensity, the quality (i.e., wavelength) of light changes as light is transmitted, absorbed, or reflected as it passes through the canopy to the forest floor. Light quality affects the production of the hormones in plants that control growth and form. Some woody plants are extremely plastic in form in response to the varied light conditions in MH communities. For example, red elm and pagoda dogwood *(Cornus alternifolia)* are often decumbent under low light levels, spreading horizontally beneath the duff and producing many small aerial stems. Upon reaching a light gap or after the death of an overhead tree, a single aerial stem will become dominant to form a tree or shrub with the classic upright growth form. Often, the common canopy trees have large colonies of offspring beneath them, forming banks of seedlings that remain in the understory for years until a gap opens in the canopy. For example, sugar maple trees commonly produce numerous offspring that can persist for 20 to 30 years in deep shade as knee-high seedlings with just a pair of leaves and then begin to grow up to several feet per year in response to change in light intensity should the canopy open above them.

In MH communities, nutrients and organic matter accumulate at the soil surface in leaf litter and humus. (This contrasts with FD communities, for example, where nutrients are leached deeply into the soil, and the humus layer is periodically consumed by fire, and with WF and Floodplain Forest (FF) communities, which are sinks for nutrients transported from uplands in groundwater or runoff.) Deeply rooted plants in MH communities extract base elements such as calcium, magnesium, and potassium from deep in the mineral soil and deposit them on the surface in plant litter. Species such as sugar maple, basswood, and elm, which are abundant in many stands, shed leaves with high amounts of nutrients, contributing to high nutrient content in the humus. As a result, much of the plant activity in MH forests is concentrated in the soil surface and rich humus layer. Many herbaceous plants are rooted almost entirely in humus, and many woody plants have a high proportion of their roots near the surface. Sugar maple is especially noteworthy for its ability to form secondary roots or risers that grow upward from deep roots and spread prolifically through the humus layer.

Landscape Setting, Soils, and History

The distribution of MH communities in the EBF Province is strongly influenced by landscape and soil features that provide protection from wildfires. Most important is topography. Within the EBF Province, MH communities occur most often on rugged terrain where the spread of fire is interrupted by irregular ground-level air currents and by frequent presence of relatively moist, shaded north-facing slopes. The flatter areas

Table OP-1 *Plants useful for differentiating the Northern from the Prairie Floristic Region of the Open Rich Peatland System.*

	Layer	Common Name	Scientific Name	frequency (%)	
				OPn	OPp
Northern Floristic Region	Tree	Tamarack (C, U)	*Larix laricina*	32	8
		Black spruce (U)	*Picea mariana*	14	2
		White cedar (U)	*Thuja occidentalis*	6	-
	Tall Shrub	Speckled alder	*Alnus incana*	27	-
		Balsam willow	*Salix pyrifolia*	18	-
	Low Shrub	Leatherleaf	*Chamaedaphne calyculata*	41	-
		Bog rosemary	*Andromeda glaucophylla*	34	-
		Small cranberry	*Vaccinium oxycoccos*	27	-
		Labrador tea	*Ledum groenlandicum*	14	-
		Large cranberry	*Vaccinium macrocarpon*	11	-
		Bog laurel	*Kalmia polifolia*	5	-
	Forb	Buckbean	*Menyanthes trifoliata*	36	5
		Round-leaved sundew	*Drosera rotundifolia*	34	-
		Intermediate bladderwort	*Utricularia intermedia*	30	3
		Pitcher plant	*Sarracenia purpurea*	29	3
		Scheuchzeria	*Scheuchzeria palustris*	16	-
		Three-leaved false Solomon's seal	*Smilacina trifolia*	12	-
		Spatulate-leaved sundew	*Drosera intermedia*	11	-
	Fern	Northern marsh fern	*Thelypteris palustris*	51	10
		Water horsetail	*Equisetum fluviatile*	34	7
		Crested fern	*Dryopteris cristata*	18	-
	Graminoid	Creeping sedge	*Carex chordorrhiza*	43	1
		Candle-lantern sedge	*Carex limosa*	32	5
		Lake sedge	*Carex lacustris*	27	5
		Beaked sedge	*Carex utriculata*	23	-
		White beak rush	*Rhynchospora alba*	19	-
		Slender cottongrass	*Eriophorum gracile*	17	1
		Bristle-stalked sedge	*Carex leptalea*	14	-
		Silvery sedge	*Carex canescens*	11	-
		Slender sedge	*Carex echinata*	11	-
		Chamisso's cottongrass	*Eriophorum chamissonis*	10	1

(C) = canopy tree (U) = understory tree

Succession

OP communities can develop from WM communities if conditions become suitable for accumulation of organic matter and rooting contact with mineral soil is reduced. If peat continues to accumulate over time, the peat surface and water table become elevated, and the rate of water flow and inputs of minerals to the plant-rooting zone are gradually reduced. Conditions then become favorable for invasion by minerotrophic *Sphagnum* species. Once *Sphagnum* is present, it further reduces available minerals by absorbing them—particularly calcium—and replacing them with hydrogen ions, causing the peat surface to become increasingly acidic. The site then becomes suitable for more acid-tolerant *Sphagnum* species, and pH continues to fall. Below pH 5.5, the water chemistry changes from a bicarbonate-buffered system to a humic–acid buffered system. Subsequent production of humic acids by peat decomposition and living *Sphagnum* accelerates the acidification process. The higher parts of hummocks rapidly become more acidic and boglike, while hollows usually retain more minerotrophic water chemistry and brown mosses. Eventually, the brown moss species in the hollows are replaced by oligotrophic *Sphagnum* species, completing transformation of the OP community to an AP community. However, if inputs of minerals via groundwater or and are subject to fires and water stress during periods of drought. Therefore, they lack some of the characteristic OP species that are less tolerant of drought, including ericaceous shrubs such as leatherleaf, bog rosemary, and small cranberry *(Vaccinium oxycoccos);* insectivorous plants such as pitcher plant, sundews, and bladderworts; and ferns and fern allies such as crested fern *(Dryopteris cristata)* and water horsetail *(Equisetum fluviatile),* all of which are typically present in communities in the OPn Region (Table OP-1). On the other hand, OPp communities have species common in the drier and more fire-prone landscapes of western Minnesota that are not present in the OPn Region. Examples of these species are grass-leaved goldenrod *(Euthamia graminifolia)*, Buxbaum's sedge *(Carex buxbaumii)*, and narrow reedgrass *(Calamagrostis stricta)* (Table OP-2).

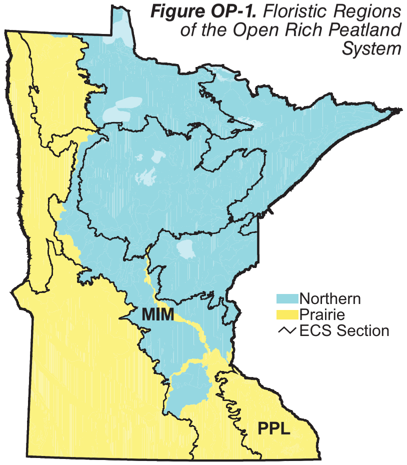

Figure OP-1. *Floristic Regions of the Open Rich Peatland System*

Variation Among Classes

The plant community classes in the OPn Region are divided into two groups based on differences in topography, substrate, and hydrology. Classes in the first group—Northern Shrub Shore Fen (OPn81) and Northern Rich Fen (Basin) (OPn92)—form in basins underlain by fine-textured substrates with relatively low hydraulic conductivity. As a result, these peatlands are influenced primarily by stagnant (rather than flowing) groundwater. They are characterized by level or slightly concave peat surfaces and are common where irregular topography allows the development of poorly drained, isolated peat-filled depressions. They also form on floating mats adjacent to lakes, ponds, and rivers and in lagg zones between larger peatlands and adjacent uplands. The two community classes in this group differ from one another primarily in frequency of inundation by surface runoff or rising lake levels. Northern Shrub Shore Fens are occasionally inundated (and as a result are somewhat similar to WM communities), whereas Northern Rich Fens (Basin) are less frequently inundated.

The classes in the second group of OPn communities—Northern Extremely Rich Fen (OPn93) and Northern Rich Fen (Water Track) (OPn91)—form on flat or slightly sloping surfaces, such as broad glacial lake plains. These communities are associated with lenses of sandy substrates that have high hydraulic conductivity. Because of the porosity of the subterranean sands, these peatlands are influenced by inputs of groundwater that create surface water flow and the formation of water tracks on the peatland surface. The elongated water tracks slope gently in the direction of drainage and sometimes form characteristic ribbed fen patterns visible on aerial photos. The water track communities differ from one another in mineral concentrations and pH. Northern Extremely Rich Fens are fed by highly calcareous groundwater and have characteristic calciphilic plants, whereas Northern Rich Fens (Water Track) have circumneutral water chemistry and lack calciphilic species.

Plant communities in the OPp Region are divided into two classes based on differences in hydrology and water chemistry. Prairie Extremely Rich Fens (OPp93) develop at highly calcareous groundwater discharge points and have characteristic calciphilic plants. Prairie Rich Fens (OPp91) occur in glacial drainages that are influenced by lateral movement of groundwater, and lack calciphilic species.

in the province tended to burn regularly in the past and are more likely to support FD or Upland Prairie (UP) communities. (In comparison, in the Laurentian Mixed Forest (LMF) Province, MH communities often occur on level to rolling landscapes with fine-textured soils that retain or pond water.) Most MH communities in the EBF Province are on high stagnation moraines and stream-dissected blufflands. On especially steep or tall slopes in these landscapes, MH communities usually occur on shaded north or east aspects or on moist lower slopes. In contrast, FD and UP communities tend to occur on upper south- to west-facing slopes in these landscapes. Streams, rivers, and lakes also historically provided protection from wildfires. Along the southwestern border of the EBF Province, patches of MH communities occurred on the northeast sides of water bodies because fires started most frequently in the prairies to the west and were spread by southwesterly winds. Rugged terrain and water-related firebreaks could act alone or in concert to produce habitats that were isolated, moist, pocked with vernal pools, and experienced diminished wind speeds. These effects helped to reduce the probability of fire, but no site in the EBF Province was completely safe from fire during periods of extreme drought or unusual wind.

Another determinant of where MH communities occur within the EBF Province is the presence of sites with clayey, compacted, or cemented soil horizons about 20 to 30 inches (50 to 75cm) below the ground surface. These dense layers tend to impede the drainage of snowmelt and rainfall. As a result, in the spring the soil is saturated above these horizons, keeping the humus wet and promoting rapid green-up of the ground-layer plants, both of which help to deter fires. In the EBF Province, about 60% of all MH communities occur on soils with dense lower horizons that perch water. Interestingly, about 85% of all soils with impermeable subsurface horizons in Minnesota's forested regions are occupied by MH communities. This suggests rather strongly that in Minnesota MH communities have played a role in the genesis of soils with impermeable layers, and once established, MH communities tend to persist on these sites.

When land surveyors and Euro-American settlers described the EBF Province and its plant communities in the mid-1800s, the general consensus was that fires, originating in the prairie regions, were spreading into and destroying a large, rather solid block of MH communities that occupied much of the province. Scientists of the era, relying mostly on description and intuition, supported this view of the region's vegetative history, and it was widely accepted that these forests were Minnesota's expression of the deciduous broadleaf forest that formed the climax vegetation across much of the eastern United States. Subsequent pollen diagrams and soil surveys from the region suggest, however, that MH communities and other wooded communities were expanding their range into the prairies at about the time the first Europeans arrived in Minnesota. The following paragraphs describe in more detail the development of vegetation in the EBF Province in the period following the melting of the last glaciers in Minnesota.

About 6,000 to 8,000 years ago, during the warmest and driest period following the recession of the glaciers, the EBF Province was mostly prairie. Wooded vegetation was limited to sites extremely well protected from fire. It is unlikely that MH communities as described in this guide were present at the time, but some species characteristic of MH communities probably occurred in areas of wooded vegetation. Such sites are recognizable today by well-developed forest soils with highly leached surface horizons and thick subsoil horizons enriched with clay. The climate in the province became cooler and moister about 4,000 years ago, initiating an expansion of woody vegetation containing oak species, birch, hazel, and ironwood. Areas that today have soils with features characteristic of both forest soils and prairie soils probably became forested at this time. At the most protected sites (i.e., those sites that were wooded even during the warmest and driest period 6,000 to 8,000 years ago), a case can be made for modest increases in basswood, ironwood, elm, and ash at this time. Sites throughout the EBF Province and the southwestern edge of the LMF Province also show change in vegetation beginning about 1,000 years ago in some cases and about 500 to 300 years ago in others. These dates coincide roughly with the warm Medieval Climatic Anomaly (about 750 to 1,100 years ago) and the cooler and moister Little Ice Age Anomaly (beginning about 750 years ago and culminating about 300 to 500 years ago). In each of these climate anomalies, the response of vegetation in the EBF Province was an increase in the presence of the fire-sensitive tree species typical of MH communities. These climatic events most likely encouraged sugar maple, basswood, elm, and ash to expand to their current ranges. The contemporary presence of oak-dominated MH communities on soils with virtually none of the features associated with long occupation by deciduous forest indicates that these forests were almost certainly established in response to these most recent climatic events.

Thus, the general trend of vegetation history in the EBF Province is the spread of MH communities across the glaciated portions of the landscape for the past 4,000 years. The sequence of prairies, followed by oak-aspen (and ironwood) woodlands, followed by dry-mesic oak forests, and eventually by forests dominated by sugar maple, basswood, ash and elm is evident in nearly all pollen diagrams in the region. The change in vegetation toward increasingly mesic, fire-sensitive species and forest structure may well be explained by a decrease in fire frequency caused by an increasingly moist and possibly cooler climate. Perhaps as important in promoting change toward mesic forest vegetation was the conversion of prairie soils to forest soils once wooded vegetation became established on sites, because forest soils retain water more effectively than prairie soils, thereby reinforcing even modest increases in precipitation. The sequence of development of forest soils in the EBF Province began with the formation of closed-canopy oak forests, followed by the loss of prairie grasses due to shade, the buildup of deciduous leaf litter and humus, the acidification and decalcification of the upper soil horizons, and the eventual movement of clays from upper to lower soil horizons. The lower soil horizons, because of their increased clay content and structure, tend to perch rainfall and snowmelt, causing forest soils to retain moisture more readily than prairie soils. There are some exceptions to this pattern of soil development in the EBF Province, most notably on the Anoka Sand Plain and the loess-covered Paleozoic Plateau, where the parent material has very little clay, and the presence of forest communities does not lead to the formation of typical forest soils with their characteristic clayey or dense subsoil horizons.

Floristic Regions

MH communities in Minnesota are grouped into four floristic regions based on general differences in species composition (Fig. MH-1). Three of these floristic regions are represented in the EBF Province: the Northern Floristic (MHn) Region, the Central Floristic (MHc) Region, and the Southern Floristic (MHs) Region. MHn communities are rare and generally limited to wet-mesic habitats in Polk, Mahnomen, and Clearwater counties and possibly to deep ravines in northernmost Washington County. MHc communities are prevalent in the northern extent of the EBF Province from Polk County to Stearns County. Southeast of Stearns County, MHc communities are rare and limited to cool microhabitats or unusual habitats that contain populations of northern plants. MHs communities occur throughout the EBF Province and are especially prevalent from Stearns County to the southeastern border of Minnesota. Communities of the fourth region, the Northwestern Floristic (MHw) Region, do not occur in the EBF Province.

The floristic variation among MH communities follows a geographic trend common to other systems in this classification. In general, common plants in northeastern Minnesota reach their southwestern range limits in the coolest and wettest local habitats. Conversely, plants widespread in the Great Plains and southwestern Minnesota tend to reach their northeastern range limits in dry, warm habitats, such as sandy riparian corridors. In the EBF Province, MHn and MHc communities are visibly differentiated from MHs communities by the presence of at least some northeastern plants. Where

saturation of peat substrates in OP communities creates anaerobic conditions that prevent establishment of trees and tall shrubs. As a result, OP communities lack the shaded habitats and shade-tolerant plant species characteristic in the understories of FP communities. OP communities have much smaller seasonal water-level oscillations than WM communities, providing conditions more favorable for formation and accumulation of peat. WM communities can be present on relatively deep sedimentary peat deposits or on deep peat on sites previously occupied by peat-forming communities. Differences in species composition and vegetation, however, distinguish OP and WM communities even when deep peat is present in WM communities. OP communities (with the exception of Northern Shrub Shore Fens [OPn81]) are usually dominated by fine-leaved graminoids, mosses, or ericaceous shrubs such as leatherleaf, while WM communities are dominated by broad-leaved graminoids, lack significant moss cover, and lack ericaceous shrubs.

Plant Adaptations

The plants characteristic of OP communities are adapted to full sunlight, sustained water levels, low nutrient levels, and high mineral levels. This environment is well suited to dominance by sun-loving herbaceous species, brown mosses, and minerotrophic *Sphagnum* species. The lack of shade from trees and shrubs favors dominance in the ground layer by shade-intolerant species, especially graminoids (in comparison with FP communities, which have more abundant forbs and shrubs in the understory). Like many wetland plants, the characteristic species in OP communities, such as sedges *(Carex* spp.) and buckbean *(Menyanthes trifoliata)*, have stems, leaves, and roots with intercellular air spaces (aerenchyma) that store oxygen and transport it from above-water structures to roots during waterlogged periods. Other plants, such as bog birch, grow on aerated hummocks, or in the case of species such as tufted bulrush *(Scirpus cespitosus)*, sterile sedge *(Carex sterilis)*, and prairie sedge *(Carex prairea)*, form hummocks that elevate the plant above persistently anaerobic peat surfaces. Generally, desiccation is not a problem for plants in OP communities because the plant-rooting zone is almost always wet and remains moist even during periods of drought when the water table drops below the peat surface.

As in other peatland systems, plants in OP communities are visibly affected by low-nutrient conditions and often have adaptations enabling them to exist on the limited nutrients in substrates and surface water. Particularly evident are reduced growth forms. Many of the characteristic shrubs and graminoids are very short. The dominant graminoids tend to have very narrow leaves (typically < 1/3 inch [3mm] wide), with species such as fen wire grass *(Carex lasiocarpa),* candle-lantern sedge *(C. limosa),* creeping sedge *(C. chordorrhiza),* and white beak rush *(Rhynchospora alba)* most common. OP communities are also characterized by insectivorous plants, including pitcher plant *(Sarracenia purpurea),* sundews *(Drosera* spp.), and bladderworts *(Utricularia* spp.), which supplement their intake of both nitrogen and phosphorus by capturing and digesting insects. Although nutrients are low in OP communities, concentrations of minerals such as calcium can be very high near groundwater discharge points, particularly where peatlands are underlain by calcareous glacial deposits. Plants that thrive in areas of calcareous groundwater discharge include tufted bulrush *(Scirpus cespitosus)*, Kalm's lobelia *(Lobelia kalmii),* marsh arrowgrass *(Triglochin palustris)*, and grass of Parnassus *(Parnassia* spp.), along with the rare species twig rush *(Cladium mariscoides).*

Floristic Regions

Based on geographic variation in species composition, OP communities in Minnesota are grouped into two floristic regions: the Northern Floristic (OPn) Region and the Prairie Floristic (OPp) Region (Fig. OP-1). Communities from both floristic regions are present in the EBF Province, although OPn communities are more prevalent. Communities in the OPp Region are at the western climatic limit in Minnesota of peatland formation

OP Open Rich Peatland System


photo by F.S. Harris MN DNR

Ottertail County, MN

General Description

Open Rich Peatland (OP) communities are graminoid- or low-shrub-dominated wetlands on actively forming deep (> 16in [40cm]) peat. The dominant graminoids most often are fine-leaved sedges *(Carex* spp.); shrubs, when present, typically include ericaceous species such as leatherleaf *(Chamaedaphne calyculata)* and bog rosemary *(Andromeda glaucophylla)* along with bog birch *(Betula pumila)*. Mosses are common in OP communities, particularly brown mosses in wet hollows. OP communities are widespread in the Laurentian Mixed Forest Province, where a cool climate, abundant precipitation, and the presence of poorly drained basins and glacial lake plains provide suitable conditions for peat development. OP communities also occur throughout much of the Eastern Broadleaf Forest (EBF) Province and into the Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces. In the EBF, PPA, and TAP provinces, OP communities are near the southern and western limits of the range of peatland development in Minnesota and are generally confined to floating mats or settings where groundwater discharge is sufficient to offset higher rates of evapotranspiration caused by warmer temperatures.

Peat Characteristics and Hydrology

(For a discussion of general peatland formation in Minnesota, see Peatland Formation under the Forested Rich Peatland System on page EBF-FP1.) The peat in OP communities is moderately decomposed (hemic) and formed predominantly from graminoids and brown mosses. OP communities occur in peatland settings influenced by inputs of groundwater. Concentrations of minerals such as calcium are often abundant in groundwater that has percolated through till and can reach very high levels in areas with calcareous till deposits. Therefore, OP communities often have high concentrations of minerals (and high species diversity) in comparison with Acid Peatland (AP) communities. OP communities, however, are not rich in nutrients, especially nitrogen and phosphorus.

The water inputs to OP communities come primarily from regional or local groundwater. These supplies are steady and maintain fairly constant water levels near the peat surface, in contrast to Forested Rich Peatland (FP) and Wet Meadow/Carr (WM) communities, in which the peat surface is not continuously saturated. The continuous

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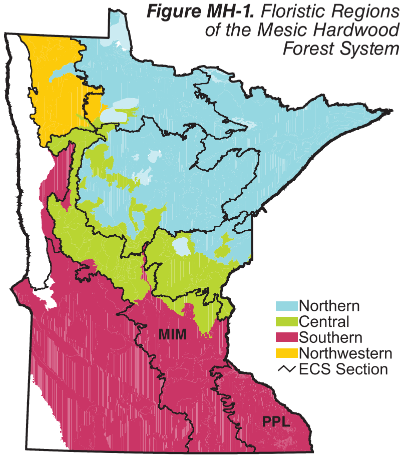

Figure MH-1. *Floristic Regions of the Mesic Hardwood Forest System*

MHn and MHc communities co-occur, they are separated locally by habitat: MHn communities usually are present on wet-mesic sites, while MHc communities occur on dry-mesic and mesic sites.

MHc communities are transitional between MHn and MHs communities. There are large regions of northern and northeastern Minnesota where only MHn communities occur, while the southeastern corner of the state has almost entirely MHs communities. MHc communities, in contrast, are most common in the central and eastern portion of the state in a zone of overlap between MHn and MHs communities. Several observations suggest that the distribution of MHc and MHs communities in the EBF Province is correlated with elevation and local climatic conditions. MHc communities are most prevalent on high (usually between 1,300 and 1,650 feet in elevation), rugged terrain in the Hardwood Hills Subsection, where the duration of snow cover is usually greater than 105 days, and mean annual soil temperatures are below 8°C. MHc communities can also occur at lower elevations in the province in settings where local site conditions promote cooler soil temperatures. These settings include the Anoka Sand Plain, where the presence of extensive peatlands and high water tables leads to locally cooler soil temperatures. MHc communities also occur at low elevations in deep ravines in the blufflands of southeastern Minnesota and along the St. Croix and Mississippi rivers. The valley floors and lower slopes of these ravines are generally protected from direct sunlight and are cooled by cold-air drainage and sometimes by cool air from persistent ice in fissures in rocky substrates. MHs communities, although widespread in the province, are present almost entirely on sites below 1,100 feet in elevation, where snow cover usually lasts less than 100 days, and mean annual soil temperatures are higher than 8°C.

Plant Indicators of MHn, MHc, and MHs Communities

Plant species with high fidelity for MHn relative to MHc and MHs communities are listed in Table MH-1. In general, nearly all of the species that differentiate the MHn Region are more common in Minnesota in WF communities than in MH communities. Especially well represented are ferns and fern allies such as common oak fern *(Gymnocarpium dryopteris)*, long beech fern *(Phegopteris connectilis)*, and groundpines *(Lycopodium dendroideum* or *L. hickeyi)*. Common also are evergreens such as balsam fir, shining firmoss *(Huperzia lucidula)*, and even some herbaceous species that have overwintering leaves such as bunchberry *(Cornus canadensis)*, naked miterwort *(Mitella nuda)*, and drooping wood sedge *(Carex arctata)*.

MHc communities tend to occur on sites that were occupied by northern FD communities (especially jack pine woodlands or forests) in the early Holocene Epoch (10,000 to 8,000 years ago) and by southern FD communities or UP communities during the mid-Holocene Epoch (about 8,000 years ago and continuing until rather recent times). Therefore, MHc communities are much more likely than MHs communities to have plants characteristic of FD communities, including bracken *(Pteridium aquilinum)*, pale vetchling *(Lathyrus ochroleucus)*, Lindley's aster *(Aster ciliolatus)*, and round-leaved dogwood *(Cornus rugosa)* (Table MH-2).

Table MH-1. *Plants useful for differentiating the Northern from the Central and Southern Floristic Regions of the Mesic Hardwood Forest System.*

		Common Name	Scientific Name	frequency (%) MHc	MHn	MHs
Northern Floristic Region	Ferns & Fern Allies	Groundpines	*Lycopodium dendroideum* or *L. hickeyi*	1	32	-
		Common oak-fern	*Gymnocarpium dryopteris*	-	24	-
		Wood horsetail	*Equisetum sylvaticum*	1	13	-
		Shining firmoss	*Huperzia lucidula*	1	12	-
		Long beech-fern	*Thelypteris phegopteris*	-	12	-
	Evergreen*	Balsam fir (U)	*Abies balsamea*	7	55	-
		Bunchberry	*Cornus canadensis*	2	25	-
		Drooping wood-sedge	*Carex arctata*	5	23	-
		Naked miterwort	*Mitella nuda*	1	23	-
	Other	Bluebead lily	*Clintonia borealis*	15	69	-
		White spruce (U)	*Picea glauca*	1	25	-
		Swamp red currant	*Ribes triste*	1	20	-
		Palmate sweet coltsfoot	*Petasites frigidus*	-	17	-
		Yellow birch (U)	*Betula alleghaniensis*	1	15	1
		Small enchanter's nightshade	*Circaea alpina*	2	15	-
		Drooping woodreed	*Cinna latifolia*	2	13	-
		Mountain-ashes (U)	*Sorbus* spp.	-	11	-

* includes species with over-wintering leaves (U) = understory tree

Table MH-2. *Plants useful for differentiating the Central from the Northern and Southern Floristic Regions of the Mesic Hardwood Forest System.*

		Common Name	Scientific Name	frequency (%) MHc	MHn	MHs
Central Floristic Region	Fire-Dependent Forest Affinity	Bracken	*Pteridium aquilinum*	54	38	8
		Pale vetchling	*Lathyrus ochroleucus*	31	26	2
		Lindley's aster	*Aster ciliolatus*	25	22	1
		Round-leaved dogwood	*Cornus rugosa*	23	13	8
		Spreading dogbane	*Apocynum androsaemifolium*	19	13	4
		Veiny pea	*Lathyrus venosus*	18	15	-
		Lowbush blueberry	*Vaccinium angustifolium*	17	8	-
		Wild honeysuckle	*Lonicera dioica*	15	6	4
		Big-toothed aspen (U)	*Populus grandidentata*	14	6	3
	Other	Hog-peanut	*Amphicarpaea bracteata*	64	20	32
		Downy arrow-wood	*Viburnum rafinesquianum*	60	33	14
		Round-lobed hepatica	*Anemone americana*	53	43	4
		Pale bellwort	*Uvularia sessilifolia*	51	39	4
		Pointed-leaved tick-trefoil	*Desmodium glutinosum*	45	3	33
		Leatherwood	*Dirca palustris*	35	24	5
		Large-flowered trillium	*Trillium grandiflorum*	32	7	5
		Nodding fescue	*Festuca obtusa*	24	7	13
		Blue beech (U)	*Carpinus caroliniana*	24	3	19
		Side-flowering aster	*Aster lateriflorus*	18	15	2
		Yellow lady-slipper	*Cypripedium calceolus*	12	4	7
		Tall blackberries	*Rubus allegheniensis* and similar *Rubus* spp.	11	3	5

(U) = understory tree

In the EBF Province, MHs communities occur in the habitats most protected from fire. Generally these areas have rugged terrain and a well-developed system of drains, streams, and rivers. For this reason, the ground layer of MHs communities contains many species that are also common in the riparian communities of the Floodplain Forest (FF) System (Table MH-3). Among these species are trees such as hackberry and box

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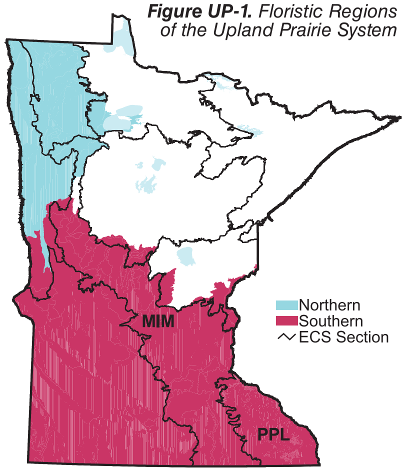

Figure UP-1. *Floristic Regions of the Upland Prairie System*

Not all of the species diagnostic for UPs communities occur throughout the UPs Region. Several of these species are restricted to the southeastern part of the state, a few are limited to the southwestern part, and a few occur in the full latitudinal extent of the UPs Region but only along the eastern side. Table UP-1 lists the most geographically widespread species with high fidelity for one or the other of the floristic regions. None of these species has high frequency within either floristic region, because they occur preferentially or exclusively in either dry or mesic classes within the UP System in addition to being geographically restricted as described above.

These facts raise questions about the legitimacy of recognizing southern versus northern floristic regions. Additional data and analysis may support moving the boundary or creating different floristic regions. Another possibility is the elimination of floristic regions in the UP System. Rather than being an indication of ecologically coherent regions, the geographic variation in species composition of UP communities may be best interpreted as simply the result of independently determined range limits of some of the component species. In fact, the differences between dry and mesic classes within each region are greater than floristic region differences between dry community classes or between mesic community classes.

Table UP-1 *Plants useful for differentiating the Northern and Southern Floristic Regions of the Upland Prairie System.*

	Common Name	Scientific Name	frequency (%) UPn	UPs
Northern Floristic Region	Tufted hair grass	*Deschampsia cespitosa*	24	-
	Glaucous false dandelion	*Agoseris glauca*	20	1
	Blanketflower	*Gaillardia aristata*	8	1
	Spike oat	*Helictotrichon hookeri*	7	-
Southern Floristic Region	Bird's foot coreopsis	*Coreopsis palmata*	-	29
	Gray-headed coneflower	*Ratibida pinnata*	-	25
	Skyblue aster	*Aster oolentangiensis*	-	23
	Scribner's panic grass	*Panicum oligosanthes*	2	22
	Clammy ground cherry	*Physalis heterophylla*	-	16
	Hoary vervain	*Verbena stricta*	-	16
	Whorled milkweed	*Asclepias verticillata*	-	16
	False gromwell	*Onosmodium molle*	1	15
	False boneset	*Kuhnia eupatorioides*	-	13
	Round-headed bush clover	*Lespedeza capitata*	-	12
	Butterflyweed	*Asclepias tuberosa*	-	10

Plant Adaptations

Adaptations to frequent fire are prominent in the flora of the UP System. First, of course, is the overwhelming predominance of herbaceous life-forms. The only generally common woody plants are semi-shrub species that do not form substantial aboveground woody structures. Stems of these plants deteriorate in a few years and the plants rely on new stems from the base—such as those produced following fire—to maintain vigor. These shrubs also share the adaptation of producing flowers and fruit in the first year on new stems arising from the base of the plant after fire. Taller shrubs are common only where fire frequency or intensity is reduced, as in savanna and brush-prairie communities. The oaks that occur in savanna and brush-prairie communities all resprout from stumps when top-killed and can flower and fruit even when reduced to shrub size by repeated fires. One of these species, bur oak, has thickened, corky bark that affords some protection from fire damage to the underlying cambial tissue. Quaking aspen, a tree species typical in brush-prairie communities, suckers copiously from an extensive network of horizontal roots when the aboveground stems are killed, and it can persist indefinitely if fire intervals are long enough to allow the suckers to replenish the root system.

Another obvious adaptation of plants to the fire environment of the UP System is that the perennating organs—buds, tubers, root collars, and other tissue from which new growth originates—are generally deep enough below the soil surface to escape damage in prairie fires. In general, plants of the UP System invest heavily in belowground growth, with biomass below ground in tallgrass prairies estimated to be two to four times that above ground. There are several selective forces that produce this result, but sequestering nitrogen—a limiting nutrient in tallgrass prairies—from loss in fire is probably one. Related to this is sequestration of nutrient and energy reserves to support rapid regrowth following grazing. The graminoid life-form is itself an adaptation to grazing, as the meristematic tissue from which new growth arises is at the base of the plant where it is inaccessible to grazers, which consume only easily replaceable leaf tissue.

The other major selective pressure to which plants of the UP System are adapted is water limitation. The large amount of root biomass characteristic of prairie plants enables them to capture whatever soil moisture is available. In addition to a dense web of roots in the upper soil layer, most species have some roots that extend into the subsoil to tap deep moisture reserves. There are also a variety of morphological adaptations to reduce water loss from leaves. Leaf and stem pubescence and finely divided or dissected leaves are examples and are most common in species characteristic of the dry communities in the UP System. The ability of grasses to fold or roll leaf blades is another example. The dominant grasses of the UP System also utilize the C_4 metabolic pathway in photosynthetic carbon fixation, a physiological mechanism that makes photosynthesis in the high light and temperature and often water-limited summer prairie environment more efficient with respect to water use (and also nitrogen use).

Floristic Regions

UP communities in Minnesota are grouped into two floristic regions based on differences in species composition, the Southern Floristic (UPs) Region and the Northern Floristic (UPn) Region (Figure UP-1). Only the UPs Region is well represented in the EBF Province. Communities of the UPn Region are present in the northern end of the EBF Province, but they are rare enough that they are not described in this guide. Differences in species composition between UPs and UPn communities are subtle. The composition of the dominant graminoids is remarkably constant throughout the UP System, but there are some differences in the composition of forbs and less important graminoids. These differences mainly involve species that are present in UPs but rarely or never present in UPn communities; there are only a few species in UPn communities that are not also present in UPs communities.

Table MH-3. *Plants useful for differentiating the Southern from the Central and Northern Floristic Regions of the Mesic Hardwood Forest System.*

				frequency (%)		
		Common Name	**Scientific Name**	**MHc**	**MHn**	**MHs**
Southern Floristic Region	**Floodplain Forest Affinity**	Virginia waterleaf	*Hydrophyllum virginianum*	10	1	69
		Cleavers	*Galium aparine*	2	1	53
		Honewort	*Cryptotaenia canadensis*	11	-	51
		Wood-nettle	*Laportea canadensis*	4	4	46
		White avens	*Geum canadense*	7	2	45
		Hackberry (U)	*Celtis occidentalis*	1	-	38
		Missouri gooseberry	*Ribes missouriense*	1	2	38
		Box elder (U)	*Acer negundo*	2	1	37
		Kidney-leaf buttercup	*Ranunculus abortivus*	4	4	37
		Wild grape	*Vitis riparia*	7	-	33
		Charming sedge	*Carex blanda*	4	1	29
		Moonseed	*Menispermum canadense*	-	-	20
		Stinging nettle	*Urtica dioica*	1	-	17
	Spring Ephemerals	Dutchman's breeches	*Dicentra cucullaria*	-	3	22
		Cut-leaved toothwort	*Dentaria laciniata*	-	-	17
		False rue-anemone	*Isopyrum biternatum*	-	-	17
		White trout-lily	*Erythronium albidum*	1	-	16
		Mayapple	*Podophyllum peltatum*	-	-	16
		Virginia spring-beauty	*Claytonia virginica*	-	1	12
	Other	Sharp-lobed hepatica	*Anemone acutiloba*	6	-	36
		Gregarious black snakeroot	*Sanicula gregaria*	5	-	26
		Spreading Jacob's-ladder	*Polemonium reptans*	-	-	24
		Blue phlox	*Phlox divaricata*	-	-	23
		Elegant bedstraw	*Galium concinnum*	-	-	21
		Heart-leaved aster	*Aster cordifolius*	1	-	20
		Sprengel's sedge	*Carex sprengelii*	-	-	17
		Common snakeroot	*Eupatorium rugosum*	-	-	17
		Drooping trillium	*Trillium flexipes*	-	-	16
		White bear-sedge	*Carex albursina*	-	-	15
		Hairy-leaved sedge	*Carex hirtifolia*	-	-	14
		Bladdernut	*Staphylea trifolia*	-	-	14
		Bulblet bladder-fern	*Cystopteris bulbifera*	1	-	12
		Showy orchis	*Galearis spectabilis*	-	-	12
		American ginseng	*Panax quinquefolium*	1	-	12
		Stickseeds	*Hackelia spp.*	-	-	11
		Rue-anemone	*Anemonella thalictroides*	-	-	10

(U) = understory tree

elder, climbing plants such as wild grape *(Vitis riparia)* and moonseed *(Menispermum canadense)*, and herbaceous species such as blue phlox *(Phlox divaricata)*, Dutchman's breeches *(Dicentra cucullaria)*, and heart-leaved aster *(Aster cordifolius)*. Incidentally, many of the characteristically FF plants listed in Table MH-3 occur widely in southern deciduous forests in the EBF Province but also extend their ranges into the LMF Province in limited habitats along major rivers or large lakes such as Upper and Lower Red Lake, Leech Lake, Lake Winnibigoshish, Mille Lacs Lake, and Lake Superior. It is possible that rivers and large lakes afford some protection from frost and provide an extended growing season that allows southern plants to grow far to the north in Minnesota. It is also possible that the historically higher levels of human activity and disturbance associated with large rivers and lakes may have contributed to the presence of characteristic MHs plants along water bodies far north of the typical range of MHs communities. MHs communities typically have higher levels of disturbance (especially from wind; see below) than either MHn or MHc communities and have species adapted to at least moderate levels of disturbance.

Disturbance Regimes of MHn, MHc, and MHs Communities

MH communities historically had low rates of catastrophic disturbance from fires and windstorms. Along with WF communities, they are the least disturbed forest communities in the state. Rotation periods for catastrophic fire and wind are in excess of 370 and 360 years, respectively, and often greater than 1,000 years. Disturbances that result in the partial loss of canopy trees, such as light surface fires and moderate windthrow, were far more frequent. MHn communities tended to have the lowest rates of partial canopy disturbance, with rotation periods of 130 to 160 years for moderate surface fire and patchy windthrow. MHc communities were somewhat more disturbed, with rotation periods for partial canopy disturbances of 40 to 140 years. MHs communities had the highest rates of moderate disturbance, with rotation periods of 20 to 160 years (Table MH-4). For MHn and MHc communities there are more explicit references to fire than wind in the Public Land Survey notes, suggesting that surface fires played a more important role than wind. For MHs communities, wind is explicitly referenced more than fire, suggesting that wind played a greater role than fire. This is in spite of the fact that MHs communities were embedded in a matrix of FD and UP communities, which burned frequently. Climatic data for the past 50 years are consistent with the notion that MHs forests are more frequently damaged by wind (probably including ice-laden trees) than are deciduous forests in the MHc and MHn Floristic regions. About three to four times as many damaging windstorms per acre are reported for the MHs Region than for the MHc Region and MHn Region, respectively.

Table MH-4. *Historic tree species composition & disturbance regimes in Mesic Hardwood Forest Classes.*

	Historic Tree Species Frequency by Class and Stand Age						Historic Disturbance Rotation Periods by Class (in years)		
	young forest age	young forest species	mature forest age	mature forest species	old forest age	old forest species	Stand-Regenerating Fire	Moderate Surface Fire + Patchy Windthrow	Catastrophic Windthrow
Northern Floristic Region						**ranges ⟶**	430-970	130-160	800-1000+
MHn35	0 - 55 yrs	paper birch *(quaking aspen)* *(sugar maple)* *(northern red oak)*	95 - 205 yrs	paper birch *(sugar maple)* *(white spruce)*	> 295 yrs	white pine sugar maple *(paper birch)*	970	130	>1000
MHn44	0 -35 yrs	**quaking aspen**	95 - 195 yrs	white spruce *(quaking aspen)* *(paper birch)* *(balsam fir)*	> 195 yrs	white spruce quaking aspen *(paper birch)* *(balsam fir)*	430	160	960
MHn46	0 - 35 yrs	**quaking aspen**	> 95 yrs	quaking aspen *(white spruce)* *(American Elm)****	--	--	600	160	800

***Table MH-4** continued on next page.*

topography, make this subsection an environment favorable for fire. However, the predominant UP communities here are savannas, probably reflecting this subsection's isolation by surrounding forests from more extensive prairie regions and consequently from fires originating in the prairies. All fires in this subsection had to originate within its relatively small area. In contrast, there was no significant barrier to the spread of fires into the Oak Savanna Subsection of the MIM from the prairie-dominated region to the west and south in the PPA Province, increasing the frequency of fires in this part of the EBF Province sufficiently that open prairies rather than savannas predominated.

The interplay of landscape properties and soils with fire in shaping vegetation is sensitive to climate. During the drier, warmer conditions of the middle Holocene Epoch, beginning about 8,000 years ago, the landscape features in the EBF Province were not enough of an impediment to fire to protect forest vegetation, and prairies and savannas occupied most of the province during that time. Return of cooler, moister conditions beginning about 4,000 years ago tipped the balance and allowed woodlands and forests to expand out of stream bottoms and other refugia to reclaim all but the most fire-prone parts of the province.

Grazing and browsing by large mammals including bison, elk, and deer were major processes in presettlement prairies, but it is not clear that these played as significant a role as fire in the formation and maintenance of prairie. The activities of these animals clearly were important for the movement of seeds and other plant propagules and for the persistence in prairies of many short-lived species associated with mechanical disturbance. It is probable that grazing activity also stimulated recruitment in longer-lived species and probably affected competitive interactions among them. Reduction in the height and density of the canopy of tall grasses effected by grazing prevented competitive exclusion of smaller-stature plant species. These influences affect relative abundances of species, but it is not known whether the long-term absence of large grazers will result in the disappearance of species from upland prairie communities.

Soil moisture is the strongest determinant of variation among plant communities in the UP System. Although the soil-moisture gradient in upland prairies is more or less continuous from dry to wet-mesic, plant community classes in the UP System are grouped into two segments, dry and mesic, with the mesic segment spanning dry-mesic to wet-mesic conditions. Classes in the dry segment are characterized by much greater abundance of midheight and short grasses relative to tall grass species, as well as sparser vegetation cover. Classes in the mesic segment are dominated by tall grass species and have dense vegetation cover. Substrate properties are a second determinant of community variation in the system, with community classes in the dry segment of the gradient divided into plant community types based on substrate properties. The categories of substrate are sand (often aeolian deposits but also lacustrine, fluvial, and colluvial deposits), sand-gravel (outwash and ice contact deposits), thin soils (loess and residuum) on steeply sloping bedrock formations, and steeply sloping unsorted glacial till. The moisture-retaining capacity of these substrates varies from least in the sand category to intermediate in the sand-gravel to most in the thin soil over bedrock and unsorted till; in the last there can be considerable variation depending on relative amounts of fine- and coarse-textured material in the till. Although the thin soils on steep bedrock slopes in the PPL Section have a high moisture-retaining capacity, their thinness severely limits their storage capacity. Nutrient availability also varies among these categories in the same order as moisture-retention capacity. There is no substrate-based division of the mesic segment of UP communities at this time, but additional data collection and analysis may support recognition of a mesic sand soil community type. Soils that support communities in the UP System are classified as mollisols (very dark, base-rich mineral soils), except the sand substrates of dry communities, in which very high permeability and susceptibility to wind disturbance limit soil formation.

savanna. Today, most brush-prairies occur in the Tallgrass Aspen Parklands Province of northwestern Minnesota.

Historically, UP communities dominated the landscape in the southern end of the Eastern Broadleaf Forest (EBF) Province, in the Oak Savanna Subsection of the MIM and the Rochester Plateau Subsection of the PPL. In the deeply dissected Blufflands Subsection of the PPL, UP communities were confined to steep south- and west-facing slopes and to occasional large deposits of sand in valleys. UP communities also dominated the Anoka Sand Plain Subsection of the MIM. In the Big Woods and Hardwood Hills subsections of the MIM, UP communities were mostly confined to the western edge adjacent to the continuous prairie of the Prairie Parkland (PPA) Province. However, at several places in the north half of the Hardwood Hills Subsection, UP communities extended more deeply into the province. Very little native upland prairie of any kind remains today; conversion to cropland, succession to woodland and forest, and urban and suburban development have destroyed more than 99 percent of the presettlement upland prairie and savanna communities in the EBF Province.

Natural History

Frequent fire (with return intervals of less than 10 years) is critical for the occurrence of upland prairies in Minnesota. Fire frequency is responsive to climate and to landscape properties. The most important factors are the frequency and intensity of drying events that create flammable conditions, and the absence of topographic and water features that impede the spread of fire. Average annual precipitation declines from east to west across the state, with corresponding increases in length of time between rains and frequency of drought events. Even the driest parts of western Minnesota, however, support tree growth. The principal contribution of drier climate in Minnesota to prairie establishment is to increase the likelihood of ignition and spread of fire. Drier conditions also slow the growth of shrubs and trees, increasing the time it takes for them to become large enough to resist being killed by fire or to produce seeds before being killed. Landscape properties that affect the spread of fire also have a large influence on fire return intervals. For a given ignition rate, the larger the proportion of a landscape that burns in an average fire, the shorter the fire return interval in that landscape. Rivers and lakes interfere with the spread of fires, as does steep topography. Conversely, large expanses of gentle relief without water barriers tend to burn in extensive patches. Vegetation itself may facilitate or impede the spread of fire: deciduous forests are much more resistant to fire than grasslands, which burn readily.

The distribution of upland prairies in the EBF Province before Euro-American settlement reflected these climatic and landscape influences. UP communities predominated in large, continuous areas of subdued relief; in most of the province, hilly topography and abundant lakes and rivers—combined with a slightly cooler and wetter climate than that in the PPA Province—impeded the spread of fire enough to allow woodlands and forests to dominate. The most extensive areas of open prairie communities in the EBF Province were on the level to gently rolling and well-drained landscape of the Oak Savanna Subsection of the MIM. Oak savanna communities dominated the west side of the subsection on a band of end moraines of the Des Moines Lobe that created sufficient relief to favor savannas over open prairies. Similarly, oak savanna was the predominant UP community in the Rochester Plateau Subsection of the PPL east of the prairies of the Oak Savanna Subsection. The Rochester Plateau Subsection is somewhat dissected by deep valleys of streams draining to the Mississippi River, and expanses of open prairie communities were confined to the largest remnants of the plateau between valleys. Smaller prairies occurred on very steep, south- and west-facing slopes on the sides of the valleys; these occurred also in the more deeply dissected Blufflands Subsection of the PPL where none of the original plateau surface remains. The Anoka Sand Plain Subsection of the MIM was the other large non-forested region in the EBF Province. Droughty soils formed in outwash and lacustrine sands, together with very low-relief

Table MH-4. continued

Central Floristic Region						ranges →	370-1000+	40 -140	380-1000+
MHc26	0-35 yrs	**quaking aspen** *(paper birch)* *(American elm)**** *(basswood)*	55 - 135 yrs	paper birch *(quaking aspen)** *(northern red oak)*	> 135 yrs	quaking aspen* *(paper birch)* *(white spruce)* *(northern red oak)* *(white pine)*	370	75	910
MHc36	0-35 yrs	**northern red oak** *(basswood)* *(quaking aspen)**	> 95 yrs	sugar maple *(basswood)* *(American elm)****	--	--	>1000	40	380
MHc38	--	(insufficient data)	--	(insufficient data)	--	(insufficient data)	--	--	--
MHc37	0-55 yrs	**quaking aspen** *(paper birch)*	55 - 135 yrs	sugar maple *(basswood)* *(American elm)**** *(northern red oak)* *(paper birch)*	> 135 yrs	*(quaking aspen)* *(American elm)**** *(sugar maple)* *(white spruce)*	515	70	>1000
MHc47	0-55 yrs	*(basswood)* *(bur oak)* *(quaking aspen)* *(paper birch)* *(sugar maple)*	55 - 155 yrs	*(basswood)* *(bur oak)* *(sugar maple)* *(paper birch*	> 155 yrs	basswood *(bur oak)* *(white pine)* *(sugar maple)*	>1000	140	>1000
Southern Floristic Region						**ranges →**	**1000+**	**20 -160**	**360-1000+**
MHs37	0-55 yrs	**northern red oak** *(white oak)*** *(basswood)*	>95 yrs	white oak** basswood *(northern red oak)* *(American elm)****	--	--	>1000	20	390
MHs38	0-35 yrs	**northern red oak** *(basswood)*	> 75 yrs	sugar maple *(basswood)* *(American elm)**** *(ironwood)* *(northern red oak)* *(white oak)*	--	--	>1000	35	360
MHs39	0-35 yrs	northern red oak *(basswood)* *(quaking aspen)*	> 75 yrs	sugar maple *(basswood)* *(American elm)**** *(northern red oak)*	--	--	>1000	50	680
MHs49	0+ years	American elm**** basswood *(sugar maple)*	--	--	--	--	--	160	>1000

bold = >50% normal = 25-50% *(italics)* = 10-25%

*includes big-toothed aspen **includes bur oak ***includes red elm ****includes red and rock elm

FF Floodplain Forest System

photo by D.S. Wovcha MN DNR

Sherburne County, MN

General Description

Floodplain Forest (FF) communities are present on occasionally or annually flooded sites along streams and rivers. FF communities are dominated by deciduous trees tolerant of saturated soils, prolonged inundation, and frequent erosion and deposition of sediment. Active floodplains, which are inundated most years, have forests dominated by silver maple mixed with green ash and some American elm, cottonwood, hackberry, black willow, peach-leaved willow, red willow, and river birch. Sites such as river or stream terraces that flood less frequently or severely support mixed stands of American elm, box elder, silver maple, green ash, hackberry, cottonwood, basswood, black ash, red elm, and swamp white oak. The understories of FF communities characteristically are open, with few shrubs or saplings. Ground-layer cover is highly variable, ranging from areas of bare silt or sand to dense patches of wood nettle *(Laportea canadensis)* or impatiens *(Impatiens capensis* or *I. pallida).* Woody vines are important in FF communities in the Eastern Broadleaf Forest (EBF) Province, with wild grape (*Vitis riparia*), Virginia creeper *(Parthenocissus* spp.), moonseed (*Menispermum canadense*), and greenbrier (*Smilax tamnoides*) the most common species. Pools or mucky depressions in old channels are often present on actively flooded sites. FF communities are associated with streams and rivers throughout the EBF Province and are extensive along the Mississippi, Minnesota, and St. Croix rivers, contributing significantly to the native habitat available to plants and animals in the province.

In general, the flooding that occurs along streams and rivers is fed by water flowing over the ground surface (surface flow) as well as by water that enters stream and river beds as groundwater (base flow). Much of the surface flow reaches streams or rivers over frozen or saturated ground in the spring, initiating flooding in the lower reaches of watersheds. After spring flooding, base flow maintains river levels as well as stable, high water tables on river terraces and floodplains. Flooding imposes several physical challenges on plants in FF communities, including inundation, erosion, sedimentation, and severe scarring of tree trunks by flood-transported ice and debris. Flooding also results in chemical and physiological stresses, especially lack of the oxygen necessary for plant metabolism and for decomposition of litter. Although the annual pattern of flooding is predictable, the timing, duration, and energy vary from year to year. Flooding

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UP Upland Prairie System

photo by D.S. Wovcha MN DNR

Weaver Dunes Scientific and Natural Area, Wabasha County, MN

General Description

Upland Prairie (UP) communities are herbaceous plant communities dominated by graminoid species, with a species-rich forb component that can approach codominance with the graminoids. The tall grass big bluestem *(Andropogon gerardii)* and the mid-height grasses prairie dropseed *(Sporobolus heterolepis)* and little bluestem *(Schizachyrium scoparium)* are the most important graminoids. Indian grass *(Sorghastrum nutans)*, a tall grass, and porcupine grass *(Stipa spartea)* and side-oats grama *(Bouteloua curtipendula)*, mid-height grasses, are the most important associated graminoids. Sedges *(Carex* spp.), another graminoid group, are sometimes common in UP communities but are typically a minor component. The most common woody species are low, semi-shrubs; leadplant *(Amorpha canescens)* and prairie rose *(Rosa arkansana)* are the most common and widespread of these. Taller typical shrubs such as American hazelnut (*Corylus americana*) and smooth sumac (*Rhus glabra*) occur primarily in the savanna communities that are part of the UP System. The main vegetation layer in prairie communities is usually less than 40in (1m) high, although some forbs and the flowering stalks of the tall grasses elongate above this height as the season progresses. In savannas there is usually also a patchy shrub layer up to 6ft (2m) tall and a patchy tree canopy up to 33ft (10m) tall.

The herbaceous dominance of prairie communities in Minnesota is closely tied to the frequent occurrence of fire. In circumstances where fire frequency or intensity is reduced, more fire-tolerant shrubs and trees can persist, forming brush-prairie and savanna communities that are considered members of the UP System. Savannas typically have scattered trees, sometimes clumps of trees, growing in a prairie matrix. Bur oak is the most common and widespread tree, but northern pin oak and, in the extreme southeastern part of the state, black oak are also typical. Small, open-grown, often gnarled bur oaks are most distinctive. Jack pine is occasionally important on deep sand substrates. Brush-prairies are characterized by an abundance of taller shrubs, oak “grubs” and sprouts, and quaking aspen suckers that alter the aspect from that of grassland to shrubland or brushland even though the herbaceous prairie plants are still a major component of the vegetation. Savanna and brush-prairie communities intergrade. In the absence of fire, they rapidly succeed to woodland, brush-prairie even more so than can lead to greatly increased erosion of riverbanks. The roots of perennial species, especially trees and shrubs, stabilize and protect substrates along rivers much more effectively than annual species such as those commonly planted as crops.

Natural disturbance regimes are often altered significantly along rivers that have been dammed. Downstream from dams, flooding can be markedly reduced, especially the flooding that typically follows heavy summer rains. Upstream from dams, shoreline communities often have disturbance regimes more similar in many respects to communities of the Lakeshore (LK) System, with less fluctuation in water level and increased wave action. Dammed rivers can be managed to restore some of the natural flooding regime through timed releases of water that mimic normal flood cycles downstream. RV communities along major rivers have been increasingly exposed to wave action over the past few decades, a new phenomenon that has come with the onset of major recreational and commercial boat traffic. Boat waves, especially from large and fast boats, have caused rapidly accelerating erosion of many riverbanks. This is especially evident along the largest and busiest rivers, such as the Mississippi and St. Croix, where entire islands have been eroded away by boat waves.

Plant Adaptations

Plant species in RV communities are adapted to annual cycles of major natural disturbance. Characteristic species include perennial forbs and graminoids tolerant of erosion and inundation, annual herbaceous species that germinate on exposed sediments, emergent aquatic plants, and floating-leaved or submerged aquatic plants tolerant of stranding. Perennial plants are generally limited to a few species extremely tolerant of inundation and physical fragmentation. These species tend to have well-developed root systems that help to anchor plants during physical stress from strong currents or erosion. They also may have adaptations that allow them to survive long periods of low oxygen during inundation. A number of perennial species are capable of generating roots from fragments of vegetative tissue that break off from the plant and are dispersed to new habitats by floodwater. Vegetative reproduction through adaptations like adventitious rooting is exemplified by species such as glade mallow *(Napaea dioica)*, sandbar willow *(Salix exigua)*, and other willow species, which seem especially well adapted to river-shore settings. Annual plant species such as creeping lovegrass *(Eragrostis hypnoides)* and awned umbrella sedge *(Cyperus squarrosus)* are common and often abundant in river shore habitats. These species tend to be good at colonizing newly exposed sediments along river shorelines. Many produce seeds that can remain viable buried in sediments for long periods until conditions are suitable for germination and growth. These include species such as beggarticks *(Bidens* spp.) and smartweeds *(Polygonum* spp.) that germinate rapidly and profusely on recently exposed substrates. Others produce floating seeds that are transported by floodwater to other sites favorable for growth of the plant. In addition to various adaptations for surviving inundation, many plants in RV communities must withstand the droughty conditions common on coarse sandy or gravelly substrates after water levels drop over the course of the growing season. As in LK communities, the repeated cycles of natural disturbance in RV communities allow establishment of many invasive plants, and aggressive invaders such as reed canary grass *(Phalaris arundinacea)* are now abundant along shorelines of many rivers.

Floristic Regions

The floristic composition of RV communities has not been systematically surveyed in Minnesota, and there are no recognized floristic regions within the RV System. Additional surveys will likely result in changes in classification within the RV System.

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during the growing season due to unusually heavy rains is highly unpredictable and the most destructive to plants, which are far less tolerant of inundation when leafed out than when dormant or not fully developed. Flooding causes fairly constant shifting of sediment and features such as point-bars, meander scrolls, levees, and backwaters that influence the distribution of understory plants in FF communities.

Plant Adaptations

Among forested native plant community systems, the FF System is unique in its development around an annual disturbance regime. Each episode of flooding causes the death of many understory plants and leaves behind exposed mineral substrates with abundant moisture and nutrients for plant regeneration. The characteristic plants of FF communities have various adaptations and strategies for withstanding inundation and sedimentation. Because new habitat is created after each flood event, floodplain plants tend to be good at colonizing new or recently exposed habitats. Most are extremely mobile during some part of their life cycle, often using flowing water to disperse to new sites. Many are capable of extreme dominance, creating nearly pure colonies to the exclusion of other plants. The characteristic woody species of FF communities have morphological or physiological adaptations for supplying oxygen to tissues below the water or to roots in saturated soils. Some species simply avoid damage from inundation by being dormant or present as seeds or propagules during seasonal flood periods.

The dominant trees on regularly and severely flooded sites—including silver maple, American elm, cottonwood, green ash, and black ash—are among the most flood-tolerant tree species in Minnesota. Numerous indices and rankings have been published concerning the relative and absolute ability of trees to survive flooding. Such rankings vary regionally across North America and are confounded by dormancy and age of individual trees, with all trees surviving better when dormant, and middle-aged trees more resistant than younger or older trees. Among species in Minnesota, silver maple, green ash, cottonwood, and black willow appear to be tolerant even of the prolonged flooding that occurs annually in the bottomlands of large rivers in southern Minnesota, such as the Mississippi and the Minnesota. Hackberry, bur oak, swamp white oak, American elm, river birch, and box elder are tolerant of moderate flooding. The tolerance of black ash is less understood. Black ash occurs commonly with flood-tolerant trees on regularly flooded stretches of rivers in northern Minnesota but rarely occurs on such sites in southern Minnesota (see ***Floristic Regions***, below).

In addition to surviving inundation, floodplain trees share other characteristics that are presumed adaptive for life along rivers. All are capable of rapid growth, and most are adept colonizers of newly exposed or deposited sediments. All of the typical tree species of FF communities can replace damaged stems by sprouting from the base of the stem, and some are capable of sending up new suckers from rootlike rhizomes. Multiple-stemmed old trees are common in FF communities as a result of resprouting from repeatedly damaged main trunks. In addition, all species are extremely resistant to the physical battering caused by spring ice floes and other flood-carried debris. Ice-scarred or beaver-chewed trunks are sometimes present in FF communities with little more than a few inches of intact cambium supporting a full, live crown, indicating the degree to which these species have adapted to physical disturbances associated with floodplain sites.

Trees limited to upland habitats generally have seeds with mechanisms that delay germination until the next advantageous growing period, usually the spring following the development of the seed. In floodplain settings, the dominant species tend to have seeds that can germinate immediately when shed from the tree. Most often, germination occurs early in the growing season after floodwaters have receded, leaving exposed mineral-soil seedbeds. The contrast in seed germination patterns of characteristically floodplain versus characteristically upland species of the maple, oak, birch, and ash genera is illustrative. The floodplain species, such as silver maple, swamp white oak, bur oak, river birch, and green ash, have little or no dormancy. The upland species, such as sugar maple, northern red oak, paper birch, yellow birch, and black ash, exhibit strong seed dormancy. Presumably these differences are an adaptation involving the synchronization of seed dispersal and germination with the different annual periods during which seedbeds are exposed in floodplain and upland sites. In general, the seeds of floodplain tree species tend to survive well in pools but can die within hours if desiccated. This is true of seeds of silver maple, cottonwood, American elm, black willow, and river birch. Carpets of germinating tree seedlings of up to a million per acre are a common feature of floodplains by late summer and fall where these species are dominant in the tree canopy. Interestingly, this strategy of immediate seed germination is not reflected in the herbaceous species characteristic of FF communities, which include many short-lived plants that successfully regenerate from banks of dormant seeds.

In spite of the large number of new seedlings that can be present, saplings are uncommon in the understory in most floodplain forests. The cover of saplings and older seedlings in FF communities is the lowest of the forested plant community systems in Minnesota. Within the FF System, the cover of saplings and older seedlings is lower in FF communities on active floodplain sites than in those on higher terraces or less actively flooded sites. On active floodplains, extensive recruitment of silver maple saplings into the tree canopy seems to occur most often when silver maple has become established within thickets of sandbar willow *(Salix exigua)* or cottonwood. This may be because these stands of silver maple are established as initial components of willow thickets on aggrading floodplain sites and never relinquish dominance to other tree species. Silver maple, green ash, black ash, and American elm are typically present at low abundance at all heights beneath the canopy of mature silver maple–dominated floodplain forests, yet less than 5% of the FF samples on active floodplain sites (i.e., Northern Floodplain Forests or Southern Floodplain Forests) used in developing this classification have structure and composition that suggests the replacement of a silver maple canopy by any of these tree species, including silver maple itself. This contrasts with FF communities on terraces and other infrequently flooded sites (i.e., Northern Terrace Forests or Southern Terrace Forests), where replacement of silver maple by more shade-tolerant trees such as green ash, black ash, and American elm seems common. Better drainage and less intense flooding appear to favor these species over silver maple in the long term on such sites.

The herbaceous plants characteristic of FF communities have a wide variety of strategies for dealing with inundation and sedimentation. Perennial herbs, especially grasses, sedges, nettles, and some ferns, often form much larger monotypic colonies on floodplains than observed in other habitats. Their roots and rhizomes form dense, thick mats that presumably confer some protection from erosion. Other herbaceous plants can survive floods as seeds or vegetative propagules. Nearly 10% of the plants recorded in FF plots in Minnesota are annuals or biennials, the highest proportion recorded for any system with persistent vegetation in this classification. Beggarticks *(Bidens* spp.), cleavers *(Galium aparine),* clearweeds *(Pilea* spp.), kidney-leaved buttercup *(Ranunculus abortivus),* stickseeds *(Hackelia* spp.), and dotted smartweed *(Polygonum punctatum)* are the most frequent annual or biennial plants in FF communities. Some herbs, including bulb-bearing water hemlock (*Cicuta bulbifera),* knotty rush *(Juncus nodosus),* and river bulrush *(Scirpus fluviatilis)*, are capable of vegetative reproduction via bulblets, tubers, or corms that detach from the parent plant, float downstream, and root when they become stranded on land. Yet other species, such as creeping lovegrass (*Eragrostis hypnoides),* grow prostrate on mudflats, rooting at every node and producing small plants that if detached, are capable of colonizing new sites. Others, such as dark green bulrush *(Scirpus atrovirens),* are capable of producing roots and leafy tufts when their stems bend and touch the water. Still others,

RV River Shore System


MN DNR

Washington County, MN

General Description

River Shore (RV) communities occur along the shorelines of rivers and streams throughout Minnesota in the zone between the annual low-water level and the upper limit of impacts from currents and ice scouring. RV communities are inundated during annual spring flooding and sporadically following heavy rains at other times during the year. Most RV communities are sparsely vegetated, at least seasonally, because of absence of well-developed soils and frequent disturbance from flooding, ice scouring, and strong currents. River shores are often narrow, not more than a few yards wide, but can be wider along large rivers with distinct floodplains. Substrates range from silt to loose sand, gravel, cobbles, and bedrock. In addition to plant communities on river shorelines, the RV System includes communities on slumping river embankments well above high-water levels and on dry streambeds of intermittent streams. RV communities are common throughout the Eastern Broadleaf Forest Province.

Structure and Disturbance Regime

The vegetation of RV communities is zonal, usually with distinct upper and lower zones. These zones are produced by differences in severity of erosion and by differences in timing of exposure of sediments as river levels drop during the growing season. The upper zone is often severely eroded by ice scouring and strong currents during spring breakup and flooding. As a result, perennial plant species cover is typically sparse in upper zones, consisting of only a few species tolerant of inundation and physical fragmentation. Annual species, however, can become common on exposed sediments in upper zones after floodwaters recede. The lower beach zone, which is exposed later in the growing season, supports terrestrial forms of perennial aquatic species and other species, especially annuals, that can survive long periods of inundation or have seeds that remain viable buried in river sediments.

The most common pattern of natural disturbance in RV communities is repeated erosion and deposition of materials by currents. This process generally results in removal of organic matter and nutrients from substrates along river shores, or burial of organic matter by new deposits of silt or sand. Normal erosion also commonly removes existing shoreline vegetation, leaving bare sediments for recolonization by plants. Clearing or replacement of native vegetation on uplands adjacent to river shore communities each containing a different assortment of species and each resulting from a different storm earlier in the growing season. On bedrock shores, plants are largely restricted to crevices in the rock or depressions with shallow soil deposits. Lower zones are constantly washed by waves and generally lack plants; however, in small, shallow lakes subject to drawdown, a series of lower zones are often present on exposed sediments and populated by plants that disperse quickly to the site or germinate from seeds buried in sediments. Zonation is especially pronounced on sand shores along the largest lakes, which may have lower, middle, and upper zones. The lower zone, as in smaller lakes, is constantly influenced by waves and has few vascular plants. The middle zone is wave washed mainly during storms and is sparsely vegetated; its upper boundary is marked by a line of driftwood and other flotsam. The upper zone experiences wave action only during the most severe storms; it is more often exposed to spray and blowing sand. Grass- and shrub-dominated dune areas may be present beyond the upper zone on some large lakes.

LK communities tend to be dynamic; they grow, shrink, shift, or even disappear as water levels change seasonally and over years and decades. These dynamics complicate the delineation of the upper and lower boundaries of LK communities, particularly their interface with aquatic communities dominated by emergent, submergent, and floating-leaved aquatic plants. The position of shoreline communities along small, shallow ponds varies annually with seasonal fluctuations in water. Spring-fed lakes on outwash plains in Minnesota experienced low water levels in the 1930s, producing broad sand beaches that were inundated again in the 1950s as water levels rose to more typical levels. Even large lakes, especially those that are part of river systems, may experience significant changes in water level, both seasonally and over periods of several years.

Disturbances from waves, wind, ice, and fluctuation in water level cause dynamic changes in vegetation composition. Species common one year may be uncommon or absent the next, and sites that are rich in species one year may be barren the next. Such unpredictable and harsh disturbance regimes favor annual plants and perennials that develop from detached and floating parts, including rhizomes and tubers. Because of frequent erosion and alternating inundation and exposure of sediments, many characteristic lakeshore species are opportunistic, and adapted to colonizing recently exposed sites. LK communities share many species with communities of the River Shore (RV) System. Despite the rather different natural disturbance regimes responsible for shaping LK and RV communities, they produce habitats with a number of similarities.

Floristic Regions

The structure and floristic composition of LK communities vary according to geographic location as well as substrate. In this classification, LK communities are grouped into two floristic regions: the Inland Lake Floristic (LKi) Region and the Lake Superior Floristic (LKu) Region, with only the LKi Floristic Region present in the EBF Province. The floristic composition of LKi communities has not been systematically surveyed in much of Minnesota. There are several vascular plant groups that appear to be well represented in LKi communities, including members of the mint family and of the *Cyperus, Eleocharis, Juncus, Polygonum, Bidens, Sagittaria,* and *Mimulus* genera. Surveys are in progress to identify and better understand the characteristic plant species and patterns of variation in species composition in LKi communities across Minnesota and will likely lead to revision in classification of these communities.

including water parsnip *(Sium suave)* and water smartweed *(Polygonum amphibium),* produce aquatic leaves when submerged and normal leaves upon emergence, with some individuals having both leaf types. Many herbaceous species, as well as some trees, can develop adventitious roots, which form when the plant is in standing water or its stem is partially buried by sediment. Individuals with this adaptation, when present on sites where sediment has accumulated over several years, often have successive whorls of adventitious roots that correspond to successive soil-surface levels.

The most prominent stress on plants in FF communities is lack of oxygen needed for respiration. During the flood stage, anoxia affects the portions of woody plants that are normally aboveground, in addition to plant roots, and flooding severely constrains the connections of cells in plant stems and roots with the atmosphere. Within hours of the onset of flooding, actively growing tissues can deplete their supply of oxygen, while concentrations of the gaseous by-products of respiration begin to increase. The buildup of ethylene, in particular, provides a chemical signal that alters hormone levels and causes plants to respond to the stress of flooding. Numerous physiological and morphological changes happen in flood-stressed plants, but in general activities associated with photosynthesis and resource acquisition shut down. Wilted leaves, yellow leaves, and leaf fall are obvious symptoms of flood-stressed trees. Less obvious are the construction of special gas-conducting cells (or aerenchyma), the production of lenticels on stems, and the formation of adventitious roots that can serve to reconnect submerged tissues with the atmosphere. Trees that survive floods and subsequently maintain these gas-conducting tissues are in a sense pre-adapted to flooding in the future, a strategy not available to herbaceous plants. Another strategy for woody plants is dormancy during the typical period of annual flooding. Woody vegetation is less susceptible to death from anoxia when plants are dormant because of low respiration rates in inactive tissues. This may be one reason why leaves are slow to emerge in the spring in characteristic FF species, and why the perennial understory vegetation in FF communities develops much later than in surrounding terrestrial forests.

Floodplains and river terraces have persistently high water tables. This property is shared with Wet Forest (WF) and Wet Meadow/Carr (WM) communities, which commonly have some surface drainage features (such as rivulets) that are smaller or more intermittent than those characteristic of streams or rivers. High water tables cause deep soil layers to be continuously saturated, anaerobic, and chemically reducing, presenting many of the same obstacles for plant growth as flooding. Rooting in these layers is limited to plants that can supply oxygen to their roots through specialized gas-conducting cells. In addition, saturated soil conditions cause the mobilization of ions such as manganese and formation of by-products from anaerobic decomposition that can be toxic to plants. Roots in this environment often exude oxygen into the soil to create a small but effective oxidized zone (called a rhizosphere) that diminishes the uptake of toxic ions or compounds.

Nutrient Cycling

The processing of organic matter and release of essential nutrients is quite different in FF communities than in upland forests and in peatlands. In comparison with other forest systems, the plants of FF communities produce much more organic matter, which is augmented by deposition of organic litter washed from uplands into streams and rivers. The residence time of organic matter on floodplains is exceedingly short in comparison with that of peat in wetland forests or leaf litter in upland forests. The bulk of the fine organic matter deposited on floodplains is processed by invertebrates and other decomposers in a single season. A substantial amount of processing happens in backwaters and pools, where aquatic invertebrates reduce leaves to particles that can remain in suspension or to compounds soluble in water. Another fraction is incorporated into the mineral soil, mostly by earthworms. The soils of floodplains have about twice the incorporated organic matter (2-6%) of upland forest soils, while unprocessed organic material on the soil surface is likely to be washed away by subsequent floods. At the same time, substantial amounts of organic matter can be deposited by floodwater on sites that previously had none. Therefore, FF communities, unlike upland forests or peatlands, have no persistent bank or reserve of dead organic matter.

The mineralization of nitrogen—that is, the process by which microorganisms convert nitrogen-containing organic matter to inorganic compounds and simple organic compounds that plants can use—is of particular interest to forest ecologists because plant growth in most temperate forests is limited by the availability of nitrogen. Knowledge of nitrogen mineralization rates is also important for commercial forest management because mineralization rates are predictive of yield and can be reduced without proper management practices. In the FF System, the rate at which nitrogen mineralization occurs, the seasonal timing of mineralization, and the prevalent form of nitrogen available to plants are all quite specific compared with other forested ecological systems described in this field guide. Because FF communities are open systems at the scale normally used in studying forest dynamics, the common notion of nutrient cycling in forests is not completely applicable. Rather, it is more useful to think about fluxes and seasonal pulses of water, organic matter, and nutrients in FF communities. Instead of cycling within the community, the organic matter mineralized in floodplain forests may well have been produced elsewhere, while the nitrogen released may be taken up by plants at other sites. In all other forested systems in Minnesota, the primary pool of nitrogen is organic matter, living and dead. In FF communities, the primary pool is nitrates dissolved in water and in the tissues of live trees. Unfortunately, both the runoff and groundwater affecting FF communities in Minnesota has been greatly enriched in nitrates over the past 100 to 150 years from human activities, especially the burning of fossil fuels and use of industrial fertilizers. In watersheds with extensive human development, the natural behavior of nitrogen is unknown as is the effect of nitrogen enrichment on floodplain plant communities. It is known that contemporary FF communities serve the important role of nitrogen sinks by helping to immobilize nitrogen or return it to the atmosphere. In specific, when nitrate-laden groundwater enters organic-rich river backwaters, under the anaerobic conditions present in the backwaters the nitrates are converted by microbes to gaseous nitrogen or nitrous oxides that reenter the atmosphere. This process of denitrification is much more prevalent in FF communities than in other forested wetland systems in Minnesota. In addition, some floodplain trees are known to sequester large amounts of nitrogen, often far more than needed for growth and survival. If these trees remain intact after death, either submerged in the river (where they can remain for hundreds of years) or buried in sediments (for up to thousands of years), the nitrogen taken up by the living tree is effectively immobilized. This immobilization can help to lessen the effects of nitrates as pollutants downstream and ultimately in oceans (such as the Gulf of Mexico).

Floristic Regions

Based on geographic variation in species composition or flora, FF communities in Minnesota are divided into two floristic regions: the Northern Floristic (FFn) Region and the Southern Floristic (FFs) Region (Fig. FF-1). Both of these floristic regions are represented in the EBF Province. The FFn Region is present from Todd County to the north and west; the FFs Region is present south and east from Todd County. Because the land in the northern and western part of the EBF Province is rugged and forms the topographic high point of the region, catchments of rivers in the FFn Region are small, and few rivers become large enough to form extensive terraces or floodplains. Therefore, FFn communities are rare in the province. In contrast, in the FFs Region there are many large rivers with extensive bottomland forests that provide large areas of natural habitat in a landscape that is mostly farmland and urban land.

The boundary between the floristic regions depicted in Fig. FF-1 is based on regional differences in the assemblages of plants that occur on floodplains and river terraces.

LK Lakeshore System

photo by B.C. Delaney

Cedar Creek Natural History Area, Anoka County, MN

General Description

Lakeshore (LK) communities occur along the shorelines of lakes and ponds throughout Minnesota in the zone between the annual low-water level and the upper limit of storm waves and spring ice scouring. Most LK communities are sparsely vegetated because of absence of well-developed soils and frequent disturbance by waves, ice, and wind. LK communities are usually narrow, sometimes not more than a few yards wide, although width varies considerably depending on the nature of the water body and its basin. Small ponds in shallow basins where the water level declines greatly during the summer months have broad lakeshore zones. Along larger lakes, powerful storm waves and ice scouring produce relatively broad beaches and occasionally associated dune areas. Small lakes with relatively stable water levels have narrow shoreline communities, as do bays and other sheltered areas in large lakes. Within the Eastern Broadleaf Forest (EBF) Province, LK communities are most common in the MIM, where geologic processes during the last glaciation created numerous basins in pitted glacial moraines, outwash plains, and other glacial landforms. LK communities are uncommon in the PPL, which was not as widely affected by glacial processes during the last glaciation and has few natural lake basins.

Substrates in LK communities range from organic mucks and silt to loose sand, gravel, and bare rock. Storm waves and lake currents, especially along larger lakes, reshape deposits of substrate particles such as silt, sand, gravel, and even cobbles. Scouring by large pieces of ice pushed ashore during spring breakup can remove existing vegetation and bulldoze sand, gravel, and cobbles into beach ridges. When present, these ice-thrust ridges occur in ecotones between LK communities and adjacent terrestrial communities. In forested landscapes, they are often covered by trees and forest shrubs, herbs, and graminoids.

Patterns of Vegetation and Dynamics

The strong influences of waves, ice, and wind produce characteristic zonal patterns in LK communities. Many LK communities have well-defined upper and lower zones. Upper zones are affected by waves or ice scouring only during storms. On broad sand or gravel beaches, plants in the upper zone tend to grow in a series of linear aggregations, just a portion of a typical community occurrence, with individual exposures rarely larger than 2 acres (1ha) and usually much smaller (often ¼ acre or less) and embedded in a matrix of prairie, woodland, or forest vegetation. In the EBF Province, RO communities occur most often in wooded, fire-prone landscapes dominated by communities of the Fire-Dependent Forest/Woodland (FD) System, and less often in landscapes dominated by Upland Prairie (UP) or Mesic Hardwood (MH) Forest communities. Because of their small size, RO communities are often mapped as complexes with or inclusions within prairie, savanna, woodland, forest, or, occasionally, cliff and talus communities. Complexes of RO communities with prairie, savanna, woodland, or forest communities can be larger than 10 acres but are rarely more than 25 acres (10ha).

Because of their small size, RO communities are frequently affected by disturbances in surrounding woodlands, prairies, and forests. Removal of adjacent forest canopies by fire or windstorm results in warmer and drier local microclimates on adjacent outcrops, which further favors drought-tolerant RO species. Fires, as evidenced by the presence of charcoal on some rock outcrops, also can burn through RO communities, reducing woody cover and removing organic matter from the soil. Severe fires can effectively remove most vascular plants from an outcrop. The patchy distribution of fuels on outcrops, however, typically causes great spatial variability in fire intensity. As a result, the specialized plants characteristic of outcrops—which are typically present on microsites with very low levels of fuel within the community—often escape combustion. Major fires may result in expansion of RO communities into adjacent forests and can create new outcrop openings in woodlands with shallow soils over bedrock. In general, under a regime of periodic natural disturbance such as fire, RO communities are resistant to successional change because of limited habitat for root establishment and prevalence of species that persist from year to year. In the absence of fire and other succession-suppressing disturbances, RO communities will succeed over centuries to woodland or forest.

Floristic Regions

Communities in the RO System are divided into two floristic regions based on geographic variation in climate and plant species composition (Fig. RO-1). One of these regions, the Southern Floristic (ROs) Region, is present in both the EBF and Prairie Parkland provinces. The other, the Northern Floristic (ROn) Region, is present to the north in the Laurentian Mixed Forest Province. Vascular plants with high fidelity for RO communities in the ROs Region include brittle prickly pear *(Opuntia fragilis)*, small-seeded fameflower, rusty woodsia, false pennyroyal *(Isanthus brachiatus)*, pale corydalis *(Corydalis sempervirens)*, bulbostylis *(Bulbostylis capillaris)*, slender knotweed *(Polygonum tenue)*, bearberry *(Arctostaphylos uva-ursi)*, Carolina foxtail *(Alopecurus carolinianus)*, disk hyssop *(Gratiola neglecta)*, mousetail *(Myosurus minimus)*, common ragweed *(Ambrosia artemisiifolia)*, rock spikemoss *(Selaginella rupestris)*, and rock sandwort *(Arenaria stricta)*. Only one native plant community class is recognized in the ROs Region; additional sampling, especially of lichens and mosses, may result in changes in the classification of ROs communities.

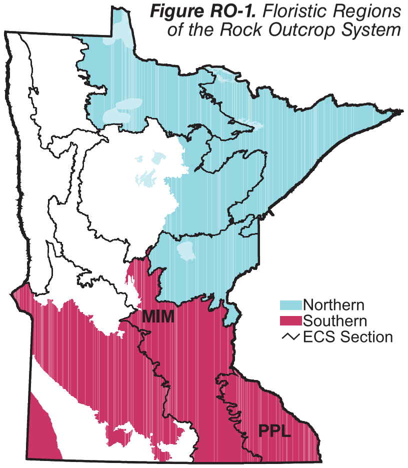

Figure RO-1. *Floristic Regions of the Rock Outcrop System*

There are several physical differences between river valleys in the FFn and FFs regions that may act independently or in concert to account for variation in species composition. These include differences in physiography, landscape maturity, bedrock geology, and flooding regime. The physiographic differences between river valleys in the FFn and FFs regions are marked. In general, the major river valleys in the FFs Region are wide (up to several miles), deep (with local relief of 100 to 600 feet), rock walled, and have broad alluvial bottoms made up of diverse alluvial landforms such as fans, deltas, meander scrolls, levees, backwater lakes, and terraces. River valleys in the FFn Region are narrow (only hundreds of feet wide), shallow (less than 100 feet deep), cut in glacial drift, and have minimal deposits of alluvium and variation in landform. These valleys tend to lie on extremely flat glacial lake plains and outwash trains; because these settings are so flat, rivers in the FFn Region have little fall or erosive power, causing them to wind and to have poorly developed alluvial features and tributaries. This is especially true of northern rivers within the Mississippi and Red River drainages. River valleys in the FFn Region that are within the Lake Superior drainage, however, share some features with rivers in the FFs Region.

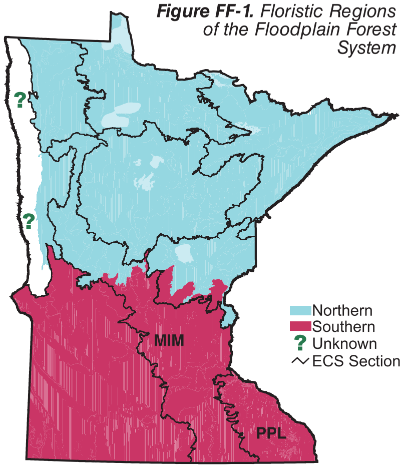

Figure FF-1. *Floristic Regions of the Floodplain Forest System*

Differences in the maturity of landscapes in the FFs and FFn regions are related to differences between the two regions in history of deglaciation. The rivers in the FFs Region have been developing drainages and eroding lands within their watersheds for a much longer period than rivers in the FFn Region. This is particularly true of the Cannon, Zumbro, Whitewater, and Root rivers in the PPL but applies also to tributaries of the lower St. Croix and Minnesota rivers as they traverse the MIM. When the glaciers were melting most rapidly in Minnesota about 12,000–15,000 years ago, vast amounts of meltwater were coursing through the largely ice-free FFs Region, cutting deeply into the bedrock that now forms the valley walls of the Minnesota, lower St. Croix, and lower Mississippi rivers. From these deep gorges, high-gradient streams eroded headward into the adjacent lands, creating a geologically mature and dissected landscape with many streams, innumerable drains, and steep side-slopes. Later, when the volume and energy of glacial meltwater feeding rivers in the FFs Region waned, the lower energy streams deposited large quantities of suspended particles, filling their valleys with alluvium. Eventually, deposition of glacial sediment subsided and rivers and streams in the FFs Region began incising the alluvium in their valleys, often leaving several sets of abandoned terraces along valley walls as the streams eroded downward toward the major rivers. Ongoing sheet erosion of the steep side-slopes typical in the FFs Region has delivered fine soil particles (especially silt) to the terraces and active floodplains of streams and rivers, so bottomlands in the region tend to be composed of fine-textured alluvial deposits that retain nutrients more effectively than coarse-textured deposits such as sand or gravel. The mature, deeply incised drainages of the FFs Region also are characterized by relatively high inputs of organic matter and nutrients from terrestrial sources to river bottomlands.

At the time the river valleys of the FFs Region were being incised by glacial meltwater, most of the FFn Region was covered by glacial ice or glacial lakes and the general courses of the rivers that now drain the FFn Region had not been established. Even after the ice covering the surface of the FFn Region melted, large areas of ice remained buried beneath glacial deposits. This led to repeated abandonment of newly forming river channels as ice-cored lands collapsed to reveal new, lower river outlets. Overall, therefore, the channels of rivers in the FFn Region became established much more recently than those in the FFs Region and their drainages have developed over a much shorter period. The northern rivers and their tributaries are more likely than rivers in the FFs Region to have sandy, rather than silty, alluvial bottomlands. They are also much less incised in the landscape than rivers in the FFs Region and tend to have lower inputs of organic matter and nutrients from surrounding uplands.

Because of differences in sediment texture and inputs of nutrients to the bottomlands of rivers in the FFs and FFn regions, FFs communities are characterized by plants more demanding of nutrients. Natural differences in nutrient richness between FFs and FFn communities have been clouded, however, by changes in the landscape caused by agricultural activity. The climate of the FFs Region is more suitable for agriculture than that of the FFn Region. As a result, agricultural activity is more widespread in the FFs Region and in particular, poor agricultural practices (combined with logging) at the height of Euro-American settlement caused massive erosion and delivery of fine sediments to stream and river bottomlands. Widespread use of commercial fertilizers has also contributed to nutrient loading of FFs communities, possibly to the point of nitrogen satiation (see above).

Another obvious difference between the FFs and FFn regions is in their bedrock geology. The FFs Region is underlain by sedimentary rocks largely deposited during the Paleozoic Era. These rocks form the valley walls of the larger rivers and the lower stretches of their tributaries. Aquifers in this bedrock contribute significantly to the base flow of rivers in the FFs Region and contribute groundwater that is often saturated in bicarbonates. Springs, spring runs, and seeps are common along the lower valley slopes and can provide impressive amounts of cold groundwater to bottomland forests (WF communities, in particular). The alluvial soils present in FFs communities commonly have free carbonates within the rooting zone and may have free carbonates present up to the surface in areas of upwelling groundwater. In contrast, the FFn Region is underlain by some of the oldest rocks on earth, deposited in early Precambrian times, when the core of North America was being formed largely through volcanism. These rocks may be igneous, metamorphic, or sedimentary, but all tend to be noncalcareous. Where these rocks form river valley walls, the alluvial sediments are noncalcareous. This is also true within the area of glacial drift derived from these rocks, which includes the NSU, WSU, and SSU. Elsewhere in the FFn Region, the glacial drift is thick, and the underlying bedrock has no direct influence on the chemistry of base flow waters or on the mineralogy of the alluvium.

A final generalization is that rivers within the FFs Region flood more frequently and for longer periods than rivers in the FFn Region. Several features of the landscape contribute to this. First, unlike rivers in the FFs Region, rivers in the FFn Region are at the headwaters of (three) continental drainages and therefore do not receive water from as broad an area as the rivers that pass through the FFs Region. Second, while peatlands are generally small and uncommon in the FFs Region, the catchments of FFn rivers contain many large peatlands with the capacity to store significant amounts of surface water, thereby dampening increases in river flow following periods of heavy rain. Third, much of the native vegetation in the FFs Region has been cleared for agriculture and residential and urban development, while the FFn Region has large areas of intact forest vegetation, which helps to slow runoff and remove soil water through transpiration.

Plant Indicators of FFn and FFs Communities

Plant species with high fidelity for FFn relative to FFs communities are listed in Table FF-1. The valleys of rivers in the FFn Region are narrow and shallow compared to river valleys in the FFs Region and have small and often discontinuous alluvial deposits.

southern MIM. These are predominantly layers of sandstone, limestone, and dolomite of various thicknesses. Even with the amount of exposed bedrock in the PPL and parts of the southern MIM, the conditions suitable for development of bedrock outcrop plant communities are limited. Many bedrock exposures are cliffs rather than horizontal or sloping bedrock. Many others have no (or few) diagnostic outcrop plants, especially smaller exposures, which are best treated as inclusions in the larger forest, woodland, savanna, or prairie communities in which they are typically embedded.

Vegetation Structure and Composition

The vegetation of RO communities is variable, although they are usually sparsely vegetated because of scarcity of soil. RO communities can be dominated by lichens, graminoids, or shrubs. In this classification, RO communities are classified by bedrock type and geography, which are major determinants of plant community composition.

Lichens are the dominant life forms on most outcrops. Crustose and foliose lichens cover exposed rock surfaces. Fruticose species are also common, especially in undisturbed sites. Mosses can be codominant with lichens along crevices and on bedrock margins. Vascular plant cover is sparse to patchy, limited mostly by the amount of soil present. On many outcrops, the amount of soil is closely tied to bedrock fragmentation, with soil accumulating in cracks and crevices and providing rooting areas for plants. Shrub-dominated outcrops often have greater soil buildup than open outcrops but less than surrounding forested communities. With fire suppression since Euro-American settlement, woody plant cover is increasing in many RO communities.

RO communities are perhaps more accurately treated as heterogeneous assemblages of different plant communities rather than as a single vegetation type. A typical example may include a bare rock community mostly composed of lichens, a crevice and thin soil community with specialized vascular plants, a deeper soil community with prairie or woodland species, and a shallow pool community supporting aquatic plants.

Plant Adaptations

Species in RO communities are subjected to greater environmental extremes than species in surrounding terrestrial communities. Many plants that grow on bedrock outcrops have adaptations to withstand frequent desiccation resulting from full exposure to direct sun and to wind, combined with limited moisture reserves in thin pockets of soil. Fleshy water-storing tissues are present in such vascular plant outcrop specialists as prickly pear cactuses *(Opuntia* spp.) and small-seeded fameflower *(Talinum parviflorum)*. During periods of drought some species, such as rusty woodsia *(Woodsia ilvensis),* die back to their roots and then resprout when rains return. Plants must also withstand rapid fluctuations in substrate temperatures, which are significantly colder at night than in surrounding forests and much warmer during midafternoon on sunny days. Limited nutrient availability also influences community composition by preventing more nutrient-demanding species characteristic of other systems from competitively excluding characteristic RO species. Species in RO communities commonly reproduce by vegetative structures such as rhizomes, runners, or stolons and tend to persist from year to year once established at a site; species that disperse and reproduce by seed alone are much less common. The annual species present in RO communities germinate only if ample moisture is available; they mature rapidly to produce seeds before moisture is depleted and the seeds remain dormant until the next wet period. Some of the long-lived species flower and produce seeds only during periods of above-average rainfall. Because of similarity in several environmental conditions, RO communities often share a number of plants with communities in the CT system.

Landscape Setting and Disturbance Regime

In the broader landscape, RO communities are small features, rarely covering more than 10 acres (4ha) and most often less than 5 acres (2ha). Exposed rock often makes up

RO Rock Outcrop System

photo by M.D. Lee MN DNR

Stearns County, MN

General Description

Rock Outcrop (RO) communities are open or shrub-dominated plant communities on horizontal or sloping bedrock exposures. They occur in landscapes with thin soils over bedrock. Crustose and foliose lichens typically cover exposed rock surfaces, with fruticose lichens also often present. Vascular plant cover is sparse to patchy, depending on the amount of fracturing of bedrock surfaces and accumulation of soil in cracks, crevices, and shallow depressions. RO communities are uncommon over most of the Eastern Broadleaf Forest (EBF) Province because exposed bedrock is rare, except in the Blufflands Subsection in the PPL where depth to bedrock is generally less than 50 feet (15 meters) and often much shallower. Outside of the PPL, bedrock is mostly buried beneath glacial sediments generally greater than 50 feet deep.

In the central MIM, RO communities occur locally in the Anoka Sand Plain and Hardwood Hills subsections near the Mississippi and Sauk rivers in the vicinity of St. Cloud, and very locally in the Big Woods Subsection along the Minnesota River between Mankato and Shakopee. Here, the bedrock is mostly granitic and occasionally gabbro and gneiss; all are Precambrian in origin. These outcrops are present in level to gently rolling outwash and glacial till landscapes. Most RO communities in the central MIM date from the most recent glaciation, when the bedrock was exposed by the scouring action of ice and meltwater. Over the past 10,000 years, further erosion has exposed some additional bedrock, especially along streams.

In the southern MIM and in the PPL, the bedrock is sedimentary and of Cambrian and Ordovician (Paleozoic) origin. Bedrock exposures are abundant in the rugged, stream-dissected bedrock terrain of the Blufflands Subsection. Here, exposures typically occur on steep slopes and ridgetops and along streams. There are also sporadic exposures of Paleozoic rocks in the Rochester Plateau, Oak Savanna, St. Paul–Baldwin Plains and Moraines, and Big Woods subsections. These outcrops are largely restricted to major river valleys including the lower Minnesota River downstream from Mankato, the lower St. Croix River downstream from Taylors Falls, the Mississippi River in and south of the Twin Cities metropolitan area, and the Cannon River downstream from Owatonna. Exposures from multiple bedrock formations are represented in both the PPL and the

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Table FF-1. *Plants useful for differentiating the Northern from the Southern Floristic Region of the Floodplain Forest System.*

				frequency (%)	
		Common Name	**Scientific Name**	**FFn**	**FFs**
Northern Floristic Region	Wet Forest Affinity	Sensitive fern	*Onoclea sensibilis*	64	11
		Sweet-scented bedstraw	*Galium triflorum*	52	11
		Bladder sedge	*Carex intumescens*	39	7
		Graceful sedge	*Carex gracillima*	33	-
		Projecting sedge	*Carex projecta*	29	-
		Field horsetail	*Equisetum arvense*	29	1
		Spinulose shield fern	*Dryopteris carthusiana*	23	1
		Meadow horsetail	*Equisetum pratense*	21	-
		Dwarf Raspberry	*Rubus pubescens*	21	-
		Lady-fern	*Athyrium angustum*	21	1
		Nodding trillium	*Trillium cernuum*	21	1
		Virgin's bower	*Clematis virginiana*	19	-
		Retrorse sedge	*Carex retrorsa*	17	-
		Brome-like sedge	*Carex bromoides*	15	-
		Lettuces	*Lactuca* spp.	15	-
		High-bush cranberry	*Viburnum trilobum*	15	-
		Winterberry	*Ilex verticillata*	13	1
		Balsam fir (U)	*Abies balsamea*	11	-
		Fringed brome	*Bromus ciliatus*	11	-
	Open Wetland Affinity	Tall meadow-rue	*Thalictrum dasycarpum*	52	3
		Northern blue Flag	*Iris versicolor*	37	1
		Spotted water-hemlock	*Cicuta maculata*	35	-
		Giant goldenrod	*Solidago gigantea*	31	1
		Canada anemone	*Anemone canadensis*	29	-
		Bluejoint	*Calamagrostis canadensis*	23	1
		Fowl bluegrass	*Poa palustris*	17	-
		Three-cleft bedstraw	*Galium trifidum*	17	-
		Spotted Joe-pye weed	*Eupatorium maculatum*	13	-
		Yellow loosestrife	*Lysimachia terrestris*	11	-
		Water-parsnip	*Sium suave*	11	-
		Dotted smartweed	*Polygonum punctatum*	11	1
	FF Affinity	Ostrich-fern	*Matteuccia struthiopteris*	58	5
		Fringed loosestrife	*Lysimachia ciliata*	39	1
		Tuckerman's sedge	*Carex tuckermanii*	27	-
		Virginia bugleweed	*Lycopus virginicus*	13	-
	Other	Canada Mayflower	*Maianthemum canadense*	41	1
		Bur oak (U)	*Quercus macrocarpa*	41	1
		Early meadow-rue	*Thalictrum dioicum*	37	5
		Nanyberry	*Viburnum lentago*	33	7
		Fringe sedge	*Carex crinita*	29	-
		Pale bellwort	*Uvularia sessifolia*	29	1
		Prickly or Smooth wild rose	*Rosa acicularis or R. blanda*	23	-
		Amercian hazelnut	*Corylus americana*	19	-
		Dewey's sedge	*Carex deweyana*	19	-
		Red baneberry	*Actea rubra*	19	1
		Hawthorn	*Crataegus spp.*	17	3
		Common strawberry	*Fragaria virginiana*	15	-
		Wood-anemone	*Anemone quinquefolia*	15	1
		Beaked hazelnut	*Corylus cornuta*	13	-
		Speckled alder	*Alnus incana*	13	-
		Red raspberry	*Rubus strigosus*	11	-
		Pennsylvania sedge	*Carex pensylvanica*	11	-
		Downy arrowwood	*Viburnum rafinesquianum*	11	-

(U) = understory tree

Because of this, FFn communities are more likely than FFs communities to be adjacent to plant communities from a variety of other systems and consequently are more likely to contain plant species characteristic of other systems. Plants characteristic of WF communities are especially common in FFn communities because WF communities are often present on river terraces cut into fresh glacial drift. Among these species are sensitive fern *(Onoclea sensibilis)*, sweet-scented bedstraw *(Galium triflorum)*, bladder sedge *(Carex intumescens)*, and graceful sedge *(Carex gracillima)* (Table FF-1). Open grassy riparian wetland areas are also much more common along rivers in the FFn Region than in the FFs Region. Therefore, plants of open wetland systems such as Open Rich Peatlands (OP), Wet Meadows/Carrs (WM), and Wet Prairies (WP) are occasional in FFn communities (Table FF-1). This is especially true where northern rivers traverse paludified lake plains and have tributaries that are lengthening headward into peatlands. Often, the lands adjacent to the tributaries and along segments of the main channels are peaty at the surface and too wet to support the growth of trees. Plants like northern blue flag *(Iris versicolor)*, fowl bluegrass *(Poa palustris)*, and yellow loosestrife *(Lysimachia terrestris)* are common in OP communities along these peaty shores as well as in nearby FFn communities. Where northern rivers and streams moderately overflow their main channel in spring, they are often bordered by WM communities. In the FFn Region such flooding is commonly caused by beavers. In modern times, dams constructed for waterfowl and wild rice management also often lead to the development of WM communities along rivers in the FFn Region. Plants such as bluejoint *(Calamagrostis canadensis)*, three-cleft bedstraw *(Galium trifidum)*, and spotted Joe pye weed *(Eupatorium maculatum)* are characteristic in both the forested and wet meadow–lined stretches of northern rivers.

Of the northern plants in Table FF-1, only ostrich fern *(Matteuccia struthiopteris)*, fringed loosestrife *(Lysimachia ciliata)*, nannyberry *(Viburnum lentago)*, fringe sedge *(Carex crinita)*, Tuckerman's sedge *(Carex tuckermanii)*, and Virginia bugleweed *(Lycopus virginicus)* have their peak presence in FF communities. None of these plants is restricted to FFn communities, having fairly high presence in WF communities as well. Tuckerman's sedge is the best indicator of FFn communities, but it also occurs fairly often in vernal pools present within WF and MH communities. Very few of the plants listed in Table FF-1 have ranges restricted to the FFn Region. Most are widespread in both the Laurentian Mixed Forest and EBF provinces, but for some reason (probably related to duration of flooding) they do not occur on floodplains in the southern part of the state. Although balsam fir rarely occurs in the FFs Region, it is abundant only in the FFn Region and occurs infrequently along rivers there. Just five other plants listed in Table FF-1 have ranges restricted to the FFn Region. Curiously, they are all sedges and include fringe sedge, projecting sedge *(Carex projecta)*, Tuckerman's sedge, retrorse sedge *(Carex retrorsa)*, and brome-like sedge *(Carex bromoides)*.

Plant species with high fidelity for FFs relative to FFn communities are listed in Table FF-2. FFs communities have a rather large group of species that reach their peak presence in FF communities and are limited to the FFs Region, including plants such as wild grape *(Vitis riparia)*, hackberry, greenbrier *(Smilax tamnoides)*, and Virginia knotweed *(Polygonum virginianum)*. All of these plants have much higher presence in FF communities than in other systems, making them rather good indicators of the FF System as well as indicators of FFs relative to FFn communities.

The list of species that are diagnostic for FFs communities (Table FF-2) is substantially shorter than the list for FFn communities (Table FF-1). The primary reason appears to be that contemporary FFs communities occur almost exclusively next to MH communities rather than communities from a variety of systems, as is the case for FFn communities. Therefore, FFs communities tend to pick up very few species from adjacent ecological systems other than MH forests. Red elm, gregarious black snakeroot *(Sanicula gregaria)*, and bitternut hickory are among the species indicative of FFs communities

destroyed or altered by quarrying for building stone, construction aggregate, agricultural lime, or rip-rap material. In recent years, increased human foot traffic along trails and near scenic vistas and campsites, especially in popular areas such as state parks, has become a threat to some cliff communities. Other threats include rock climbing, erosion from upslope areas that have been developed or otherwise cleared, and pollution of the groundwater that sustains some of the rarer cliff and talus communities.

Floristic Regions

Communities in the CT System are divided into three floristic regions based on geographic variation in climate, bedrock type, and plant species composition (Fig. CT-1). The Southern Floristic (CTs) Region occurs in the EBF and Prairie Parkland Provinces. The other two floristic regions, the Northern Floristic (CTn) Region and the Lake Superior Floristic (CTu) Region, occur entirely within the Laurentian Mixed Forest Province.

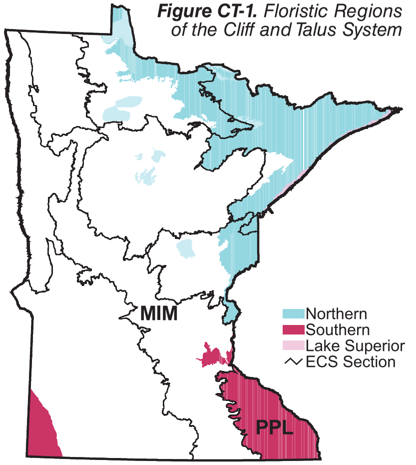

Figure CT-1. *Floristic Regions of the Cliff and Talus System*

Plants with high fidelity for the CTs Region relative to the CTn and CTu regions include cliff goldenrod *(Solidago sciaphila)*, smooth cliff brake *(Pellaea glabella)*, slender lip fern *(Cheilanthes feei)*, bulblet fern *(Cystopteris bulbifera)*, walking fern *(Asplenium rhizophyllum)*, jeweled shooting star *(Dodecatheon radicatum)*, northern bedstraw *(Galium boreale)*, reniform sullivantia *(Sullivantia renifolia)*, plains muhly *(Muhlenbergia cuspidata)*, alumroot *(Heuchera richardsonii)*, miterwort *(Mitella diphylla)*, sharp-lobed hepatica *(Hepatica acutiloba)*, zigzag goldenrod *(Solidago flexicaulis)*, and wild ginger *(Asarum canadense)*.

woody plant cover is variable. On talus slopes, vascular plant cover is influenced by the stability of talus and the amount of soil accumulated between talus blocks. Because of shifting substrates, woody cover is usually less than 50%, and many talus slopes have no trees or shrubs.

Plant Adaptations

Plants in CT communities are generally tolerant of greater environmental extremes than species in surrounding terrestrial communities. Many plants on cliffs and talus slopes are well adapted to desiccation because of low moisture-holding capacities of substrates and exposure to direct sunlight and strong winds. They must also withstand rapid fluctuations in substrate temperatures, which are significantly colder at night than in surrounding forests and, in some settings, much warmer during midafternoon on sunny days. Limited availability of nutrients on many cliffs and talus slopes strongly influences community composition and growth rates of plants. Wind and gravitational stresses have a visible impact on the growth forms of trees and shrubs, causing stunting, stem dieback, and misshapen trunks. Vascular plant species in CT communities commonly reproduce by vegetative structures such as rhizomes, runners, or stolons and tend to persist from year to year once established at a site; species that disperse and propagate primarily by seed are less common.

CT communities in the EBF Province provide habitat for several rare vascular plant species, some of which are boreal species with disjunct populations in Minnesota. On shaded moist cliffs with cool microclimates in the PPL these species include Leedy's roseroot *(Sedum rosea* var. *integrifolium)*, montia *(Montia chamissoi)*, and Arabian whitlow grass *(Draba arabisans).* Cool, moist talus slopes in the PPL support rare cold-loving plants such as Iowa golden saxifrage *(Chrysosplenium iowense)* and moschatel *(Adoxa moschatellina).* These talus slopes also support populations of plants that, although common in northern Minnesota, are generally uncommon in the EBF Province, including naked miterwort *(Mitella nuda)*, panicled bluebells *(Mertensia paniculata),* northern oak fern *(Gymnocarpium robertianum),* northern black currant *(Ribes hudsonianum),* dwarf alder *(Rhamnus alnifolia),* and balsam fir. Other rare plants have been documented on shaded mesic cliffs and on sunny dry cliff and talus communities throughout the southern portions of the EBF Province. Many CT communities, especially the drier ones, have plant species that occur also in Rock Outcrop and Upland Prairie (UP) communities. Moister cliffs often have species that are common in Mesic Hardwood (MH) Forest communities.

Landscape Setting and Disturbance Regime

In the broader landscape, CT communities are small features, rarely covering more than 5 acres (2ha). In the EBF Province, they are commonly surrounded by upland forests, especially Fire-Dependent Forest/Woodland and MH communities, and occasionally by UP communities. The disturbance regimes that shape these forests, woodlands, and prairies often affect CT communities. Fires that originate in forests, woodlands, or prairies may scorch cliff vegetation. Removal of forest canopies by fire often leaves cliffs or talus slopes more exposed to sunlight, causing warmer and drier conditions. Major windstorms or logging in forests adjacent to CT communities causes similar warming and drying effects. Fracturing of large pieces of rock from cliff faces are major, although rare, events that disrupt community equilibrium. Cliffs along streams may have higher rates of erosion, especially those that experience periodic high-water events. In general, cliff communities are fairly stable over time as a result of fairly low rates of natural disturbances, combined with limited habitat for plant establishment and growth and prevalence of species that persist once established.

Cliff and talus communities are some of the least human-disturbed habitats in Minnesota and are likely present today in most of the locations where they have existed over the past 10,000 years. Since the late 1800s, some cliff and talus communities have been

Table FF-2. *Plants useful for differentiating the Southern from the Northern Floristic Region of the Floodplain Forest System.*

				frequency (%)	
		Common Name	Scientific Name	FFn	FFs
Southern Floristic Region	Mesic Hardwood Forest Affinity	Red elm (U)	*Ulmus rubra*	3	23
		Gregarious black snakeroot	*Sanicula gregaria*	-	17
		Bitternut hickory (U)	*Carya cordiformis*	-	15
		Blue phlox	*Phlox divaricata*	-	13
	Floodplain Forest Affinity	Wild grape	*Vitis riparia*	15	66
		Hackberry (U)	*Celtis occidentalis*	7	58
		Green-briar	*Smilax tamnoides*	5	45
		Virginia knotweed	*Polygonum virginianum*	3	31
		Cleavers	*Galium aparine*	1	29
		Moneywort	*Lysimachia nummularia*	-	27
		Missouri gooseberry	*Ribes missouriense*	1	25
		Ambiguous sedge	*Carex amphibola*	3	21
		Swamp white oak (U)	*Quercus bicolor*	-	19
		Common Elder	*Sambucus canadensis*	-	19
		Anise-root	*Osmorhiza longistylis*	1	17
		Gray's sedge	*Carex grayi*	-	15
		Stickseeds	*Hackelia* spp.	-	15
		Green dragon	*Arisaema dracontium*	-	13
		Tall bellflower	*Campanula americana*	-	11
		Cattail sedge	*Carex typhina*	-	11
		Black willow	*Salix nigra*	1	11
		Virginia bluebells	*Mertensia virginica*	-	10
		Woodmint	*Blephilia hirsuta*	1	10
	Other	Rice cut grass	*Leersia oryzoides*	-	15

(U) = understory tree

with peak presence in forests of the MH System. Historic descriptions of the bottomlands of the Mississippi River mention marshes, meadows, and prairies being intermingled with floodplain forest communities. Records also indicate that historic floodplain forests were substantially more open than today's closed-canopy stands. Plants characteristic of marshes, meadows, and prairies are now essentially gone from river bottomlands in the FFs Region, in part because these open areas have been converted to fields, in part because the low meadows and prairies were flooded as a result of the lock and dam system on the Mississippi River, and in part because FF communities now have denser tree canopies than historic FF communities.

WF Wet Forest System

photo by M.D. Lee MN DNR

Wabasha County, MN

General Description

Wet Forest (WF) communities occur commonly in narrow zones along the margins of lakes, rivers, and peatlands; they also occur in shallow depressions or other settings where the groundwater table is almost always within reach of plant roots but does not remain above the mineral soil surface for long periods during the growing season. Because of the relatively warm and dry climate in the Eastern Broadleaf Forest (EBF) Province, WF communities are uncommon, occurring mainly in areas fed by upwelling groundwater from deep aquifers. Black ash is the most common dominant canopy tree in WF communities in the EBF Province and is usually mixed with other species, especially basswood, American elm, red elm, paper birch, yellow birch, and tamarack. American elm was historically more important, but elm populations have declined dramatically due to Dutch elm disease. WF communities dominated by white cedar are infrequent in the province. Understories are characterized by patches of shrubs, including dogwoods *(Cornus* spp.) and gooseberries or currants *(Ribes* spp.), along with speckled alder *(Alnus incana),* nannyberry *(Viburnum lentago)*, winterberry *(Ilex verticillata)*, and poison sumac *(Rhus vernix)*. Wet mucky hollows are common on the forest floor; downed logs and tip-up mounds are the primary substrate for grasses, sedges, and wetland forbs.

WF communities are strongly shaped by steady fluxes of water and nutrients supplied to deep soil layers by moving groundwater. In basins or depressions connected to annually recharged shallow aquifers, the supply of groundwater peaks early in the growing season but persists at some level through much of the summer. In settings connected to deeper aquifers that discharge groundwater throughout the year, the supply of water and nutrients is steady through the growing season. The groundwater moves laterally below the surface but often upwells to create springs, seeps, or spring runs within and adjacent to WF communities. Varied microtopography and variation in groundwater supply on sites fed by shallow aquifers result in the alternating presence of water-logged and dry conditions in upper soil layers. This variability in soil moisture in both space and time is a hallmark of the WF System and controls the availability of the oxygen needed for roots to respire, for decomposition of organic litter, and for release of nutrients in forms usable by plants.

CT Cliff/Talus System

photo by F.S. Harris MN DNR

Olmsted County, MN

General Description

Communities in the Cliff/Talus (CT) System are present on cliffs and talus slopes on steep-sided bluffs, along streams, on margins of bedrock ridges, and in other settings with sheer bedrock exposures. Often, cliffs and talus slopes are associated with one another because talus slopes are composed of rock fractured from either cliffs or smaller areas of exposed bedrock on steep hillsides. The vegetation of CT communities is generally open. Lichens and mosses are often the dominant life-forms, with vascular plants sparse or patchy because of scarcity of soil. In this classification, cliff communities are grouped by moisture and light regimes and by bedrock type, which are major determinants of species composition. Cliff habitats range from warm and dry to cold and wet depending on cliff aspect, proximity to streams or lakeshores, and presence of groundwater or cold air seepage on the cliff face; in the Eastern Broadleaf Forest (EBF) Province, cliffs are formed most commonly of sedimentary bedrock. Talus habitats vary from rather warm and very dry to cold and moist.

In the EBF Province, CT communities are abundant in the Blufflands Subsection in the PPL, where bedrock is typically at or near the surface, and topography is rugged. The bedrock is sedimentary, of Cambrian and Ordovician (Paleozoic) origin. Exposures of limestone, dolomite, and sandstone are all common. Scattered cliffs are present on similar bedrock formations in the Rochester Plateau Subsection in the PPL, the St. Paul–Baldwin Plains and Moraines Subsection in the MIM, and very locally in the Oak Savanna Subsection in the MIM, primarily along streams where water has exposed the underlying bedrock.

Vegetation Structure and Composition

Lichens, mosses, and liverworts cover rock surfaces in CT communities and colonize areas exposed by erosion. On cliffs, vascular plant cover is strongly correlated with the amount of fracturing of bedrock, with plants generally limited to crevices and ledges where soil has accumulated and roots can take hold. As a result, cliffs composed of highly fractured bedrock tend to have higher plant cover than those with few fractures. On wet cliffs, vascular plants may also root in thick mats of mosses and liverworts that cover the bedrock. Most cliffs have less than 25% cover of trees or shrubs, although

Non-Mineotrophic Peatland Species

Because only those species listed below can persist in the ombrotrophic conditions of bogs, the occurrence of any other species can be considered an indicator of minerotrophic conditions. However, some seedlings, particularly of tree species, can germinate in bogs but are short-lived and should not be considered as minerotrophic indicators.

	Common Name	Scientific Name
Tree	Tamarack	*Larix laricina*
	Black spruce	*Picea mariana*
	Jack pine	*Pinus banksiana*
Low Shrub	Bog rosemary	*Andromeda glaucophylla*
	Leatherleaf	*Chamaedaphne calyculata*
	Creeping snowberry	*Gaultheria hispidula*
	Bog laurel	*Kalmia polifolia*
	Labrador tea	*Ledum groenlandicum*
	Lowbush blueberry	*Vaccinium angustifolium*
	Velvet-leaved blueberry	*Vaccinium myrtilloides*
	Small cranberry	*Vaccinium oxycoccus*
	Lingonberry	*Vaccinium vitis-idaea*
	Dwarf misletoe	*Arceuthobium pusillum*
Forb	Stemless lady's slipper	*Cypripedium acaule*
	Round-leaved sundew	*Drosera rotundifolia*
	Heart-leaved twayblade	*Listera cordata*
	Indian pipe	*Monotropa uniflora*
	Pitcher plant	*Sarracenia purpurea*
	Three-leaved false Solomon's seal	*Smilacina trifolia*
Graminoid	Bog wiregrass sedge	*Carex oligosperma*
	Few-flowered sedge	*Carex pauciflora*
	Poor sedge	*Carex paupercula*
	Three-seeded bog sedge	*Carex trisperma*
	Tussock cottongrass	*Eriophorum spissum*
	Tawny cottongrass	*Eriophorum virginicum*

Plant Adaptations

As in other wetland systems, deep soil layers in WF communities are continuously saturated, anaerobic, and chemically reducing. Although a potential source of water for plants, deep soil layers have few roots other than those of species that can supply oxygen to roots through specialized gas-conducting cells (aerenchyma). As a consequence, rooting is shallow in WF communities. Roots are concentrated above or near the top of the water table, and canopy trees are susceptible to windthrow. In response to water-table fluctuations, trees, shrubs, and other perennial plants must tolerate root loss from anoxia because of prolonged water-table elevation and must be able to develop and extend roots more deeply again as water levels fall. Some characteristic WF plants have adapted to this problem by producing both normal roots and adventitious roots with gas-conducting cells.

Soils & Nutrients

Soil surfaces in WF communities are saturated in the spring but dry out later in the growing season. This pattern of alternately wet and dry soil surfaces has two important consequences. First, it creates a thin surface layer of highly decomposed organic matter, or muck. Muck is physically and chemically distinct from the peat present in peatland communities and from the humus of upland forest communities (such as Mesic Hardwood Forest [MH] communities) in its ability to absorb water, adsorb metals toxic to plants, and release nutrients. Second, the soils are not saturated continuously enough to build up thick layers of peat as in Acid Peatland (AP), Forested Rich Peatland (FP), and Open Rich Peatland (OP) communities. In instances where WF communities occur on thick layers of organic matter, they have usually replaced a peatland community (because of human-caused changes in hydrology), and the production of organic matter in the WF community is roughly in equilibrium with decomposition.

The rate and pattern of release of nutrients—especially nitrogen—from mucky soils in WF communities strongly influence plant species composition and growth. Nitrogen is mineralized in mucky soils at annual rates that are only about one-half to one-tenth of rates in upland forest soils. In addition, although WF and MH communities commonly occur within feet of each other, availability of nitrogen is seasonally reversed in the two systems. In upland forests, nitrogen is mineralized to produce ammonium (NH_4^+) immediately in spring, and most of the ammonium is quickly converted by nitrification to nitrates (NO_3^-). Therefore, about half of the annual supply of nitrogen is available in late May and early June in MH forests. Because of waterlogged and cold soils, very little nitrogen is mineralized in WF forests in spring. After soils have warmed in early summer, available nitrogen is produced at a steady but slow rate during the growing season, almost completely in the form of ammonium. Nitrification is an aerobic process, so significant production of nitrate does not begin in WF communities until the surface dries, usually in mid-August or September. Therefore, in contrast to MH communities, nitrogen available for plant uptake does not reach peak levels in WF communities until late summer. Furthermore, WF communities tend to lose more nitrogen than MH communities, with as much as 10% of annually mineralized nitrogen converted to nitrogen gas that is released to the atmosphere.

Floristic Regions

There are three floristically distinct groups of WF communities. These groups have strong geographic affinities and are recognized as separate floristic regions within the WF System: the Northern Floristic (WFn) Region, the Southern Floristic (WFs) Region, and the Northwestern Floristic (WFw) Region (Fig. WF-1). The WFn Region covers nearly all of the LMF Province and extends into the EBF Province in the Hardwood Hills and Anoka Sand Plain subsections. The WFs Region lies mostly within the EBF Province but extends into the southeastern quarter of the LMF Province and into the Prairie Parkland (PPA) Province. The WFw Region is mostly within the Tallgrass Aspen

Parklands Province, extending into the extreme western part of the LMF Province and possibly the northernmost part of the EBF Provoince. The WFw Region is not treated in detail in this field guide.

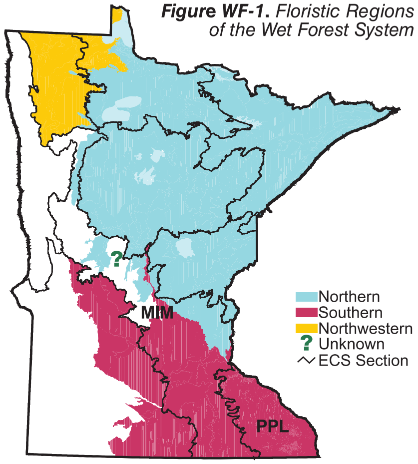

Figure WF-1. *Floristic Regions of the Wet Forest System*

Differences in species composition among the WFn, WFs, and WFw Regions appear to be strongly influenced by regional floristic variation in surrounding landscapes. This may be because WF communities are often present in narrow, linear ecotonal zones between uplands and adjacent lakes, rivers, and peatlands and so are regularly exposed to colonization by plants from adjacent, more extensive communities. Regional floristic variation in the WF System also appears to be related to regional differences in groundwater hydrology, especially differences in local relief and groundwater head, depth and conductivity of regional aquifers, and groundwater temperature and chemistry. The influence of groundwater hydrology on variation in species composition among WF communities is especially evident in the response of plants to patterns of water flow, mineral content, and temperature.

Groundwater Hydrology and Plant Indicators of WFn Communities

Communities of the WFn Region exhibit greater variation in vegetation and in landscape setting than WFs or WFw communities. WFn communities occur most often in settings that are transitional between upland forests (MH and FD communities) and northern peatlands (AP, FP, OP, and WM communities) and have many plants that are characteristic of these adjacent, more extensive communities. WFn communities are hydrologically very distinct from WFw and WFs communities. The WFn Region lies in an area that receives more precipitation (especially as snow) and has more runoff than either the WFs or WFw regions. WFn communities are highly influenced by the groundwater component of this runoff, which moves annually through shallow, local aquifers into streams, lakes, and peatlands. In comparison with groundwater in the WFw and WFs regions, this groundwater is substantially more dilute, has lower, nearly neutral pH, is warmer, and is more seasonal in its abundance. Because the WFs and WFw regions are significantly warmer and drier than the WFn Region, WFs and WFw communities are largely restricted to settings where deep aquifers deliver steady supplies of groundwater through the growing season, independently of the annual hydrologic cycle.

Selected plants with high fidelity for the WFn Region in comparison with the WFs and WFw regions are presented in Table WF-1. The only plant species with high affinity for WFn communities that also have higher affinity for the WF System than any other system are balsam fir, common oak fern *(Gymnocarpium dryopteris)*, long beech fern *(Phegopteris connectilis)*, brownish sedge *(Carex brunnescens)*, shining firmoss *(Huperzia lucidula)*, fine-nerved sedge *(Carex leptonervia),* and panicled bluebells *(Mertensia paniculata)*. These species all have affinity for WF communities that are transitional to MH forests. Many of the plants with high fidelity for the WFn Region are equally at home in mossy habitats in upland communities in the FD System and in peatland communities in the FP and AP systems. Among these plants are several evergreen species such as balsam fir, white cedar, goldthread *(Coptis trifolia)*, and twinflower *(Linnaea borealis),* and herbaceous and deciduous species such as bristle-

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Variation Among Acid Peatland Classes

Only two of the four plant community classes in the AP system occur in the EBF Province, Northern Poor Conifer Swamp (APn81) and Northern Poor Fen (APn91). Northern Poor Conifer Swamps and Poor Fens have pH greater than 4.2 and receive some minerotrophic groundwater or surface water. The other two classes, which are true bogs and have pH less than 4.2 and are totally dependent on precipitation for minerals, do not extend south into the EBF Province. The small basins characteristic of the province do not develop peat surfaces that are sufficiently raised above the water table to prevent plant root contact with underlying minerotrophic water, a precursor for formation of bogs.

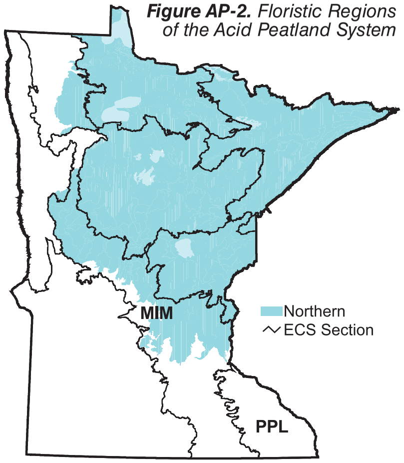

Figure AP-2. *Floristic Regions of the Acid Peatland System*

The two AP Classes that occur in the EBF Province are distinguished from one another by water-table level. Northern Poor Conifer Swamps develop on drier sites and are characterized by the presence of a tree canopy and associated shade-tolerant understory species. Northern Poor Fens occur on sites with water tables high enough to prevent survival of trees, which favors the presence of shade-intolerant species not common in forested swamps. Because the AP System is climatically at the edge of its range in the EBF Province, these two classes are not as well developed as they are in the LMF Province, and distinctions between the classes are not as clear.

Succession

In the absence of external influences, such as flooding by beaver activity or changes in hydrology, succession in peatlands moves in the direction of conversion of rich peatlands (OP or FP communities) to acid peatlands (AP communities) and from open to forested peatlands; this is driven by accumulation of *Sphagnum* peat, which leads to acidification of surface waters and development of aerated hummocks on which trees can become established. Succession to more acidic conditions, however, can be stopped (or even reversed) by mineral inputs from outside sources that offset depletion of calcium by *Sphagnum*. Even groundwater inputs of less than 5% of the total water budget (i.e., relative to inputs from precipitation) can neutralize the acids produced by *Sphagnum* and raise pH above 5.0. The predominance of calcareous till and the marginal climatic conditions in the EBF Province prevent succession of poor fens or poor conifer swamps to true bogs.

concentrations of minerals such as calcium and magnesium. Most woody plants in AP communities are evergreen, an adaptation that enables plants to retain scarce nutrients. Deciduous woody plants, which lose nutrients every year when leaves are shed, are uncommon in AP communities. Many plants in AP communities have thickened outer leaf membranes and alkaloids in leaf tissues that help to reduce herbivory. The low palatability of leaves also retards breakdown of litter by decomposing organisms and contributes to peat accumulation. Graminoids, which are the most abundant herbaceous plants in AP communities, are limited to short, fine-leaved sedges and cottongrasses. Although most species in AP communities are physiologically adapted to extract nutrients from substrates with very low nutrient concentrations, a few characteristic peatland species, such as pitcher plant *(Sarracenia purpurea),* sundews *(Drosera* spp.), and intermediate bladderwort *(Utricularia intermedia)*, have developed means of supplementing their intake of nitrogen and phosphorus by capturing and digesting insects.

In addition to physiological adaptations for obtaining or conserving scarce nutrients and minerals, it appears that vascular plant survival in AP communities is strongly linked to associations with mycorrhizal fungi. As a result, AP communities are among the most diverse communities in Minnesota in species of ectomycorrhizal fungi. Many of the plants in AP communities, including conifers, ericaceous shrubs, and orchids, depend on mycorrhizal associations to obtain minerals and nutrients and even to prevent uptake of toxic heavy metals that are soluble in waters with extremely low pH. It is possible that most, if not all, vascular plants in the AP System have symbiotic associations with mycorrhizal fungi.

Even with the adaptations mentioned above, the effect of nutrient-poor conditions is evident in reduced growth of woody plants. Trees are usually stunted and have small crowns. They are often only a few feet tall and rarely more than 33 feet (10m) tall, even when over 100 years old. The predominant shrub species are low ericaceous shrubs, such as bog rosemary *(Andromeda glaucophylla),* Labrador tea *(Ledum groenlandicum),* and bog laurel *(Kalmia polifolia).* When characteristically tall shrubs such as speckled alder *(Alnus incana)* and willows *(Salix* spp.) are present in AP communities, they are sparse and diminished in size.

Like most wetland species, plants in the AP system have adaptations that allow them to survive waterlogged, anoxic conditions. Many plants in AP communities are also adapted to survive desiccation because acid peatlands are highly dependent on precipitation, and summer drought can cause drastic lowering of local water tables. Some species, such as *Sphagnum angustifolium,* have xerophytic structural and physiological adaptations that enable them to regenerate from dried tissue after desiccation. Other species, such as the ericaceous shrubs, have thick, hirsute leaves with thick cuticles that retard moisture loss. The extremes of summer drawdown are also modified in peatland environments by the wicking capability of *Sphagnum*, which draws water from the water table by capillary action and can hold up to 25 times its weight in water. Because of the characteristically rapid growth of *Sphagnum*, other acid peatland plants have adaptations to prevent being over-topped by accumulating peat. Black spruce, for example, is able to layer, or reproduce vegetatively, from branches that become covered by moss.

Floristic Regions

Only one floristic region is recognized in the AP system in Minnesota, the Northern Floristic (APn) Region (Fig. AP-2). APn communities are similar to the continental bogs north of Minnesota in Ontario. They differ from the maritime bogs characteristic of Maine and eastern Canada, which receive significantly more precipitation and are not subjected to severe drought and low water tables during the summer. In comparison with maritime bogs, continental bogs have developed more recently, have rapidly accumulating peat, are wooded, lack surface pools, and have a crested profile in cross section rather than a convex or plateau shape.

Table WF-1. *Plants useful for differentiating the Northern from the Southern and Northwestern Floristic Regions of the Wet Forest System.*

		Common Name	Scientific Name	frequency (%) WFn	WFs	WFw
Northern Floristic Region	Moss Substrate Affinity: Deciduous	Bristle-stalked sedge	*Carex leptalea*	37	6	-
		Three-fruited bog sedge	*Carex trisperma*	23	-	-
		Big-leaf white or northern white violet	*Viola blanda* or *V. macloskeyi*	17	3	-
		Brownish sedge	*Carex brunnescens*	15	3	-
		Lowbush blueberry	*Vaccinium angustifolium*	10	-	-
	Moss Substrate Affinity: Evergreen	Balsam fir (U)	*Abies balsamea*	63	3	11
		White cedar (U)	*Thuja occidentalis*	43	-	-
		Goldthread	*Coptis trifolia*	41	-	-
		Twinflower	*Linnaea borealis*	20	-	-
		Three-leaved false Solomon's seal	*Smilacina trifolia*	18	-	3
		Black spruce (U)	*Picea mariana*	15	-	-
		Shining firmoss	*Huperzia lucidula*	14	-	-
		Creeping snowberry	*Gaultheria hispidula*	12	-	-
		One-sided pyrola	*Pyrola secunda*	10	-	-
	Other	Common oak fern	*Gymnocarpium dryopteris*	53	3	-
		Bluebead lily	*Clintonia borealis*	46	3	3
		Fly honeysuckle	*Lonicera canadensis*	35	-	7
		Large-leaved aster	*Aster macrophyllus*	33	6	-
		Long beech fern	*Phegopteris connectilis*	23	-	-
		Mountain ashes (U)	*Sorbus* spp.	18	-	-
		Drooping wood sedge	*Carex arctata*	13	-	-
		Hairy honeysuckle	*Lonicera hirsuta*	13	-	-
		Fine-nerved sedge	*Carex leptonervia*	10	-	-
		Panicled bluebells	*Mertensia paniculata*	10	-	-

(U) = understory tree

stalked sedge *(Carex leptalea),* three-fruited bog sedge *(Carex trisperma)*, three-leaved false Solomon's seal *(Smilacina trifolia)*, and big-leaf white or northern white violet *(Viola blanda* or *V. macloskeyi)*. There are no evergreen plants that have their highest fidelity in the WF System for WFs communities, and only one evergreen plant (pink shinleaf *[Pyrola asarifolia]*) that has highest fidelity within the system for WFw communities. Mosses themselves are rather diagnostic of WFn communities. The most important high-affinity moss species in WFn communities are *Plagiomnium ellipticum, Calliergon cordifolium, Hypnum lindbergii, Climacium dendroides, Thuidium delicatulum,* and *Thuidium recognitum*.

Groundwater Hydrology and Plant Indicators of WFs Communities

Communities of the WFs Region have been documented most commonly at contacts between steep, high bedrock walls and alluvial bottomlands of the St. Croix, Minnesota, and Mississippi rivers and their tributaries. WFs communities are also present in deep valleys and at bases of slopes adjacent to highlands composed of glacial drift. In either case, local relief is often high, resulting in substantial vertical head in aquifers and the presence of active springs and spring runs in many WFs communities. The primary aquifers are relatively conductive bedrock layers or basal layers of till over bedrock. Secondary aquifers may consist of confined layers of sand and gravel (called stringers) that hydrologically connect the sites where WFs communities occur to highlands composed of glacial till. These highlands can be many miles away from the zones of discharge. The groundwater is typically cold, and its chemistry somewhat alkaline, reflecting the composition of the sedimentary bedrock and calcareous drift.

Selected plants with high fidelity for WFs communities in comparison with WFn and WFw communities are listed in Table WF-2. Plants with high affinity for WFs

Table WF-2. *Plants useful for differentiating the Southern from the Northern and Northwestern Floristic Regions of the Wet Forest System.*

		Common Name	Scientific Name	frequency (%)		
				WFn	WFs	WFw
Southern Floristic Region	Disjunct Populations	Bulblet fern	*Cystopteris bulbifera*	1	36	-
		Virginia spring beauty	*Claytonia virginica*	-	23	-
		Cut-leaved toothwort	*Cardamine concatenata*	-	23	-
		False rue anemone	*Enemion biternatum*	-	20	-
		Goldie's fern	*Dryopteris goldiana*	-	13	-
	Associated with Springs	Skunk cabbage	*Symplocarpus foetidus*	2	36	-
		False mermaid	*Floerkea proserpinacoides*	-	20	-
		Spring cress	*Cardamine bulbosa*	-	16	-
		Pensylvania bitter cress	*Cardamine pensylvanica*	2	13	-
		Bog bluegrass	*Poa paludigena*	-	13	-
		American water pennywort	*Hydrocotyle americana*	-	10	-
		True forget-me-not	*Myosotis scorpioides*	-	10	-
		Icelandic yellow cress	*Rorippa palustris*	-	10	-
	Floodplain Forest Affinity	Wood nettle	*Laportea canadensis*	10	80	-
		Tall coneflower	*Rudbeckia laciniata*	3	60	7
		White avens	*Geum canadense*	9	53	-
		Cleavers	*Galium aparine*	2	43	-
		Honewort	*Cryptotaenia canadensis*	1	43	-
		Virginia waterleaf	*Hydrophyllum virginianum*	1	36	-
		Bland sedge	*Carex blanda*	3	33	-
		Brome-like sedge	*Carex bromoides*	3	23	-
		Hawthorn	*Crataegus* spp.	1	23	3
		Tall scouring rush	*Equisetum hyemale*	-	23	-
		Missouri gooseberry	*Ribes missouriense*	-	23	-
		Prickly ash	*Zanthoxylum americanum*	2	20	-
		Blue phlox	*Phlox divaricata*	-	20	-
		Gregarious black snakeroot	*Sanicula gregaria*	-	20	-
		Appendaged waterleaf	*Hydrophyllum appendiculatum*	-	16	-
		Virginia knotweed	*Polygonum virginianum*	-	16	-
		False nettle	*Boehmeria cylindrica*	1	13	-
		Common elder	*Sambucus canadensis*	-	13	-
	Mesic Hardwood Forest Affinity	Wild geranium	*Geranium maculatum*	1	66	-
		Common enchanter's nightshade	*Circaea lutetiana*	5	60	3
		Two-leaved miterwort	*Mitella diphylla*	6	50	-
		Zigzag goldenrod	*Solidago flexicaulis*	8	40	-
		Common false Solomon's seal	*Smilacina racemosa*	2	36	3
		Ironwood (U)	*Ostrya virginiana*	3	33	-
		Blue cohosh	*Caulophyllum thalictroides*	1	30	-
		Maidenhair fern	*Adiantum pedatum*	-	30	-
		Bloodroot	*Sanguinaria canadensis*	3	26	-
		Blue beech (U)	*Carpinus caroliniana*	1	26	-
		Hairy-leaved sedge	*Carex hirtifolia*	-	26	3
		Red-berried elder	*Sambucus pubens*	3	16	-
		Shining bedstraw	*Galium concinnum*	-	16	-
		Large-flowered trillium	*Trillium grandiflorum*	2	13	-
		White bear sedge	*Carex albursina*	-	13	-
		Mayapple	*Podophyllum peltatum*	-	13	-
		Giant Solomon's seal	*Polygonatum commutatum*	-	13	-
		Drooping trillium	*Trillium flexipes*	-	13	-
		Sharp-lobed hepatica	*Hepatica acutiloba*	-	13	-

Table WF-2. *continued on next page*

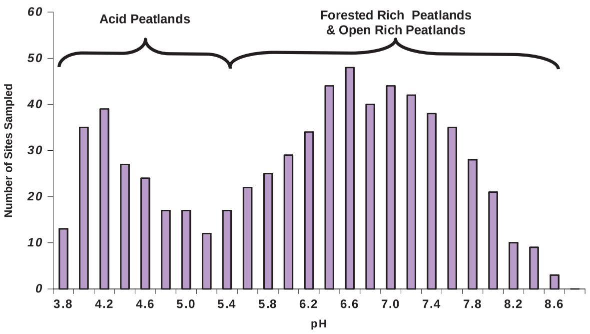

Figure AP-1.
Histogram of surface water pH from wetland sites in Minnesota. The natural bimodal distribution corresponds to separation of Acid Peatlands from Rich Peatlands.

the pH to 5.0. Humic acid–buffered peatlands are transitional and relatively short-lived, quickly succeeding to poor fens or poor swamp forests, and therefore are uncommon. This results in a natural bimodal distribution of pH in peatland communities (Fig. AP-1) that coincides with floristic differences in vascular plants and changes in dominance in the moss layer from brown mosses to *Sphagnum*. These distinctions among peatlands are the basis for differentiating the AP System from rich peatland (FP and OP) systems. At pH of 5.0, the acidification process slows, but the peat surface continues to build up until it is no longer in contact with groundwater and becomes dependent solely on precipitation. At this point, the pH of surface water is generally about 4.2. In the best-developed examples of raised peatlands, a crest with a radiating pattern of black spruce forms, which is visible on aerial photos.

It is possible to have features of AP and OP or FP communities within the same peatland because of the differing water chemistry characteristic of hummocks and hollows. In OP and FP communities, hummocks and hollows have similar water chemistry. If peat accumulates, however, and the peat surface becomes isolated from mineral-rich water, the hummocks change more quickly to acidic conditions than hollows. The peatland then becomes a mosaic of patches of AP communities within larger areas of OP or FP communities until acidic species of *Sphagnum* invade the hollows. Even when the hollows have acidified to the point where the water chemistry is characteristic of AP communities (i.e., pH < 5.5), deeply rooted minerotrophic plants such as aquatic sedge *(Carex aquatilis)* and beaked sedge *(C. utriculata)* can persist in the hollows for some time. Mosaics of AP with OP or FP communities occur most commonly in peatland systems where woody plants (shrubs and trees) are abundant, creating varied microtopography with hummocks developing initially over woody debris or around tree bases. These peatlands are most likely to develop in settings with water-table drawdowns large enough to provide the aerated microhabitats necessary for establishment of trees. Where the water table does not fluctuate significantly and woody plants are not common, more uniform peatlands develop that are dominated by OP or FP communities and lack small inclusions of AP communities.

Plant Adaptations

With decline in pH and nutrients, the number of vascular plant species that can survive in peatland communities drops significantly. The vascular plants in AP communities consist mainly of a subset of the species present in FP and OP communities; only tussock cottongrass *(Eriophorum vaginatum),* tawny cottongrass *(E. virginicum),* few-fruited sedge *(Carex pauciflora),* and bog wiregrass sedge *(C. oligosperma)* are unique to the AP System. Within the AP System, bogs, which have the most acidic and nutrient-poor conditions, are inhabited by a set of only 25 species (see page EBF-AP5). Species in AP communities have many of the physiological and structural adaptations to low pH and low-nutrient environments present in plants in rich peatland communities. In addition, species in AP communities are adapted to survive in environments with very low

AP Acid Peatland System

photo by M.D. Lee MN DNR

Todd County, MN

General Description

The Acid Peatland (AP) System is characterized by conifer-, low-shrub-, or graminoid-dominated communities that develop in association with peat-forming *Sphagnum*. AP communities are acidic (pH < 5.5), extremely low in nutrients, and have hydrological inputs dominated by precipitation rather than groundwater. These communities are floristically depauperate, with the flora composed primarily of a small subset of species characteristic of rich peatlands that are able to survive in the harsh, low-nutrient environments typical in AP communities. The floristic differences between forested and open, low-shrub- or graminoid-dominated AP communities are subtle because of low species diversity in the AP System as a whole and because trees, when present, are usually sparse, making the boundary between forested and open AP communities diffuse. Therefore, this classification places all acid peatland communities into one system, unlike the rich peatland communities, which are divided into forested and open systems (i.e., Forested Rich Peatland [FP] and Open Rich Peatland [OP] Systems).

AP communities are widespread in the Laurentian Mixed Forest (LMF) Province but are present only in the northern half of the Eastern Broadleaf (EBF) Province. The warmer climate of the EBF Province, less abundant precipitation, and absence of poorly drained glacial lake plains limit peat development relative to the northern part of Minnesota, making AP communities much less common and not as well developed. AP communities in the EBF Province occur in small peatland basins with small watersheds and are often present on floating mats adjacent to open water.

Peatland Development

AP communities develop from FP or OP communities in areas where there is sufficient rainfall and low enough evapotranspiration to enable *Sphagnum* peat to accumulate to levels above the groundwater table. Once the peat surface is above the water table, surface water flows away from or around the elevated peat surface, reducing inputs of minerals and nutrients. *Sphagnum* absorbs dissolved mineral cations, particularly calcium, and exchanges them for hydrogen ions, releasing organic acids and lowering the pH of stagnant surface waters. This conversion proceeds slowly until the pH falls to 5.5, below which the water chemistry switches from a bicarbonate- to a humic acid–buffered system. In humic acid–buffered peatlands, slight additions of acids rapidly decrease

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Table WF-2. *continued*

Southern Floristic Region	Other	Michigan lily	*Lilium michiganense*	3	40	-
		Crooked aster	*Aster prenanthoides*	-	30	-
		Golden ragwort*	*Senecio* spp.	5	30	-
		Reed canary grass	*Phalaris arundinacea*	3	20	-
		Smooth-sheathed sedge	*Carex laevivaginata*	-	16	-
		Wood's sedge	*Carex woodii*	-	16	-
		Silvery spleenwort	*Deparia acrostichoides*	-	13	-
		Duckweed	*Lemna* spp.	1	13	-
		Porcupine sedge	*Carex hystericina*	2	13	-

*Golden ragwort or Western heart-leaved groundsel *(Senecio aureus* or *S. pseudaureus)*

communities that are also more frequent in the WF System than any other system include Michigan lily *(Lilium michiganense)*, bulblet fern *(Cystopteris bulbifera)*, skunk cabbage *(Symplocarpus foetidus)*, crooked aster *(Aster prenanthoides)*, Wood's sedge *(Carex woodii)*, spring cress *(Cardamine bulbosa)*, silvery spleenwort *(Deparia acrostichoides)*, Pennsylvania bitter cress *(Cardamine pensylvanica)*, Goldie's fern *(Dryopteris goldiana)*, bog bluegrass *(Poa paludigena)*, true forget-me-not *(Myosotis scorpioides)*, Icelandic yellow cress *(Rorippa palustris)*, and American water pennywort *(Hydrocotyle americana)*. A few WFs plants, including bulblet fern, Virginia spring beauty *(Claytonia virginica)*, cut-leaved toothwort *(Cardamine concatenata)*, false rue anemone *(Enemion biternatum)*, and Goldie's fern, have disjunct populations in northern riparian habitats along the Mississippi River and around large lakes such as Lake Mille Lacs, Winnibigoshish Lake, Leech Lake, and Lake Superior. Presumably, large water bodies and river valleys have an ameliorating effect on local climate that allows plants typical of WFs communities to occur well into the WFn Region. Several plants with highest affinity for WFs communities are intimately associated with springheads and cold-water runs. These plants include skunk cabbage, false mermaid *(Floerkea proserpinacoides)*, and spring cress. The majority of the plants with high fidelity for WFs relative to WFn and WFw communities are actually more frequent in MH communities and Floodplain Forest (FF) communities, most likely because WFs communities often occur at bases of steep valley walls in zones of transition between upland and floodplain forests.

Disturbance Regimes of WFn, WFs, and WFw Communities

The most frequent natural disturbance in WF communities is flooding, typically caused by cyclical increases in precipitation or by beaver activity. If flooding is severe enough, it can kill canopy trees and bring about conversion to WM or Marsh communities. Other potential disturbances include fire and windthrow. Historically, WFn and WFs communities were affected by catastrophic fires very infrequently, with rotations of 800 to more than 1,000 years (Table WF-3). WFw communities were affected by catastrophic fires about twice as often as WFn and WFs communities, a result of being surrounded by fire-prone woodlands, prairies, and open wetlands that burned severely during drought periods. Relative to WFn and WFs communities, WFw communities also had much greater frequencies of moderate disturbances such as light surface fires and patchy windthrow of canopy trees.

Table WF-3. *Historic tree species composition and disturbance regimes in Wet Forest Classes.*

	Historic Tree Species Frequency by Class and Stand Age						Historic Disturbance Rotation Periods by Class (in years)		
	young forest age	young forest species	mature forest age	mature forest species	old forest age	old forest species	Stand-Regenerating Fire	Moderate Surface Fire + Patchy Windthrow	Catastrophic Windthrow
Northern Floristic Region						ranges ⟶	800-1000+	110-340	365-480
WFn55	0 - 75 yrs	**black ash**	75 - 195 yrs	**black ash**	> 195 yrs	black ash *(tamarack)* *(white spruce)*	>1000	140	370
WFn64	0 - 75 yrs	**black ash**	75 - 135 yrs	**black ash**	> 135 yrs	**black ash** *(tamarack)* *(white spruce)*	>1000	110	480
WFn53	0 - 55 yrs	**balsam fir** *(white cedar)*	75 - 105 yrs	**white cedar**	> 155 yrs	white cedar *(white spruce)* *(balsam fir)* *(tamarack)*	800	340	365
Southern Floristic Region									
WFs57	0-35 yrs	(insufficient data)	55 - 135 yrs	(insufficient data)	> 135 yrs	(insufficient data)	none	140	630
Northwestern Floristic Region									
WFw54	0 - 55 yrs	**quaking aspen** *(balsam poplar)* *(black ash)* *(tamarack)*	55 - 105 yrs	tamarack quaking aspen black ash	> 105 yrs	tamarack quaking aspen	490	20	250

bold = >50% normal = 25-50% *(italics)* = 10-25%

Table FP-2 *Plants useful for differentiating the Southern from the Northern Floristic Region of the Forested Rich Peatland System.*

	Layer	Common Name	Scientific Name	frequency (%) FPn	FPs
Southern Floristic Region	Tree	American elm (C,U)	*Ulmus americana*	4	57
		Box elder (U)	*Acer negundo*	-	27
		Red elm (U)	*Ulmus rubra*	1	20
		Black cherry (U)	*Prunus serotina*	-	7
	Shrub	Poison ivy	*Toxicodendron rydbergii*	4	57
		Poison sumac	*Toxicodendron vernix*	2	13
		Bush juniper	*Juniperus communis*	1	13
		Nannyberry	*Viburnum lentago*	1	10
	Vine	Virginia creeper	*Parthenocissus* spp.	5	60
		Wild grape	*Vitis riparia*	1	40
		Wild honeysuckle	*Lonicera dioica*	-	37
	Forb	Clearweed	*Pilea* spp.	3	33
		Swamp thistle	*Cirsium muticum*	2	20
		Purple avens	*Geum rivale*	1	20
		Loesel's twayblade	*Liparis loeselii*	-	17
		Cut-leaved bugleweed	*Lycopus americanus*	1	13
		Jack-in-the-pulpit	*Arisaema triphyllum*	1	10
		Elliptic shinleaf	*Pyrola elliptica*	1	10
		Spring cress	*Cardamine bulbosa*	-	10
		American spikenard	*Aralia racemosa*	-	10
		Skunk cabbage	*Symplocarpus foetidus*	-	10
		Swamp lousewort	*Pedicularis lanceolata*	-	7
		Dotted smartweed	*Polygonum punctatum*	-	7
	Graminoid	Fringed brome	*Bromus ciliatus*	6	33
		Bristly sedge	*Carex comosa*	4	30
		Porcupine sedge	*Carex hystericina*	3	27
		Prairie sedge	*Carex prairea*	3	20
		Golden fruited sedge	*Carex aurea*	2	20

(C) = canopy tree (U) = understory tree

roots, and fallen trees. Although initially formed over woody debris or tree bases, the hummocks become amplified by growth and accumulation of moss. The settings most likely to have abundant trees and shrubs are also those with slightly larger water-table drawdowns, making the establishment of woody plants possible.

Table FP-1. *Plants useful for differentiating the Northern from the Southern Floristic Region of the Forested Rich Peatland System.*

	Layer	Common Name	Scientific Name	frequency (%)	
				FPn	FPs
Northern Floristic Region	Tree	White cedar (C,U)	*Thuja Occidentalis*	48	-
		White pine (U)	*Pinus strobus*	6	-
	Tall Shrub	Mountain maple	*Acer spicatum*	11	-
		Beaked hazelnut	*Corylus cornuta*	11	-
		Balsam willow	*Salix pyrifolia*	7	-
		Black chokeberry	*Aronia melanocarpa*	6	-
	Low Shrub	Creeping snowberry	*Gaultheria hispidula*	54	-
		Velvet-leaved blueberry	*Vaccinium myrtilloides*	33	3
		Leatherleaf	*Chamaedaphne calyculata*	31	3
		Bog rosemary	*Andromeda glaucophylla*	26	7
		Bog laurel	*Kalmia polifolia*	12	-
		Lingonberry	*Vaccinium vitis-idaea*	9	-
	Forb	Goldthread	*Coptis trifolia*	57	10
		Bluebead lily	*Clintonia borealis*	34	7
		Northern blue flag	*Iris versicolor*	28	7
		Pitcher plant	*Sarracenia purpurea*	17	-
		Heart-leaved twayblade	*Listera cordata*	12	-
		Large-leaved aster	*Aster macrophyllus*	11	-
		Lesser rattlesnake plantain	*Goodyera repens*	10	-
		Arctic raspberry	*Rubus acaulis*	10	-
		Indian pipe	*Monotropa uniflora*	9	-
		Gaywings	*Polygala paucifolia*	7	-
		Palmate sweet coltsfoot	*Petasites frigidus*	7	-
		Green-flowered pyrola	*Pyrola chlorantha*	7	-
		Rose twistedstalk	*Streptopus roseus*	6	-
	Fern	Common oak fern	*Gymnocarpium dryopteris*	18	-
		Woodland horsetail	*Equisetum sylvaticum*	17	3
		Lady fern	*Athyrium filix-femina*	16	3
		Bristly clubmoss	*Lycopodium annotinum*	10	-
		Meadow horsetail	*Equisetum pratense*	8	-
		Marsh horsetail	*Equisetum palustre*	7	-
		Dwarf scouring rush	*Equisetum scirpoides*	6	-
	Graminoid	Three-fruited bog sedge	*Carex trisperma*	47	7
		Drooping woodreed	*Cinna latifolia*	14	-
		Sparse-fruited sedge	*Carex tenuiflora*	12	-

(C) = canopy tree (U) = understory tree

hummocks change more quickly in water chemistry than hollows. The hummocks, which are elevated above the water table, often become lower in minerals and more acidic and support species characteristic of AP communities. The hollows, which remain in contact with mineral-rich water, have water chemistry and flora typical of FP communities. The site then is characterized by a mosaic of patches of AP and FP communities until the hollows also become dominated by acidic species of *Sphagnum*. Mosaics of FP and AP communities occur most commonly in settings where woody plants (shrubs and trees) are abundant, because these sites often are hummocky from presence of stumps,

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FP Forested Rich Peatland System

photo by E.R. Rowe MN DNR

Becker County, MN

General Description

Forested Rich Peatland (FP) communities are conifer- or tall shrub–dominated wetlands on deep (>15in [40cm]), actively forming peat. They are characterized by mossy ground layers, often with abundant shrubs and forbs. FP communities are widespread in the Laurentian Mixed Forest Province but extend only into the northern half of the Eastern Broadleaf (EBF) Province. The warmer climate of the EBF Province, less abundant precipitation, and absence of poorly drained glacial lake plains limit peat development relative to the northern part of Minnesota, making FP communities much less common.

Peatland Formation

Most of Minnesota's peatlands began to form following climate cooling and increased precipitation about 5,000 to 6,000 years ago. Change in climate stabilized seasonal water levels in many basins and on large, flat, poorly drained landscapes such as glacial lake plains, causing saturation of soils and oxygen deficiency (anaerobic conditions). The anaerobic conditions, along with lower temperatures, inhibit plant decomposition and result in accumulation of peat. Peat accumulation rates in Minnesota are variable but generally range from 0.4 to 0.8mm per year (or 1.5–3in [4–8cm] per century). Once peat accumulates to a depth of 12–15in (30–40cm), the nutrients available to plants fall sharply because plants are no longer rooted in mineral soil. In addition to isolating plants from mineral soil, peat adsorbs and holds nutrients, which combined with low levels of microbial activity in anaerobic environments, limits nutrient recycling. With accumulation of peat, plants become dependent on inputs of essential nutrients from hydrologic processes such as precipitation, surface runoff from adjacent uplands, and groundwater-derived subsurface flow. (In some instances, low-nutrient environments can develop on thinner peat deposits, either in shallow basins with small watersheds or in landscapes with nutrient-poor sandy soils.) These sources usually supply very low concentrations of the essential nutrients nitrogen and phosphorus. However, concentrations of minerals are often high in groundwater that has percolated through till. Therefore, peatlands influenced by inputs of groundwater (including FP and Open Rich Peatland [OP] communities) can have relatively high concentrations of minerals such as calcium and magnesium.

The peat in FP communities is moderately decomposed (hemic) and formed from woody plant debris. The water table is typically below the peat surface and drops regularly and predictably during the summer. At high water levels, pools may form on the peat surface, but undulating microtopography and low hummocks at the bases of trees provide substrates that remain dry and aerated enough to support trees and shrubs. The presence of trees and shrubs in turn favors herbaceous species in the ground layer that are tolerant of at least moderate levels of shade. In contrast, OP communities have water-table levels that remain near the surface throughout the growing season, preventing establishment of significant tree cover and leaving the ground exposed to full sunlight. As a result, FP communities typically are richer in forb species than OP communities because forbs tend to be more competitive than graminoids in low-light environments. Another prominent feature of FP communities is the presence of feathermosses and other brown mosses, which are adapted to high mineral content, low nutrients, and sustained moisture. Brown mosses typically dominate the moss layer, with patches of minerotrophic *Sphagnum.*

Plant Adaptations

The environment in FP communities is well suited to dominance by herbaceous vascular plants, brown mosses, minerotrophic *Sphagnum*, and tree and shrub species that can survive periods of inundation or saturated substrates. Many of the plant species in FP communities have structures that allow them to survive waterlogged conditions for short periods. For example, speckled alder (*Alnus incana*) has adventitious roots that provide access to oxygen during high water levels. Other plants grow on aerated substrates on tree bases and moss hummocks elevated above the water table.

As in other peatland systems, plants of FP communities are adapted to low-nutrient environments. Evergreen species, including black spruce and ericaceous shrubs such as bog rosemary *(Andromeda glaucophylla)*, Labrador tea *(Ledum groenlandicum)*, and bog laurel *(Kalmia polifolia)*, conserve nutrients by retaining their leaves from year to year. Deciduous tree species, which lose nutrients when leaves are shed each year, are nearly absent from FP communities. The thickened outer leaf membranes characteristic of ericaceous shrubs and other species such as bog birch *(Betula pumila)* and the presence of chemical compounds in leaves help to reduce herbivory. The low palatability of leaves also retards breakdown of litter by decomposing organisms and contributes to peat accumulation. Some species in the community, such as pitcher plant *(Sarracenia purpurea)* and sundews *(Drosera* spp.), supplement their intake of the important nutrients, nitrogen and phosphorus, with structures that trap and digest insects.

Floristic Regions

Based on general differences in species composition, FP communities in Minnesota are grouped into three floristic regions: the Northern Floristic (FPn) Region, the Southern Floristic (FPs) Region, and the Northwestern Floristic (FPw) Region (Fig. FP-1). Two of these floristic regions, the FPn Region and the FPs Region, are represented in the EBF Province. Differences in species composition between FPn and FPs communities are presented in Tables FP-1 and FP-2.

In plant community composition and ecosystem function, the FPn Region is the most varied of the three floristic regions in the FP System. It is represented by seven native plant community classes, although only two occur in the EBF Province. These two classes, Northern Rich Tamarack Swamp (Western Basin) (FPn82) and Northern Rich Alder Swamp (FPn73), form in basins underlain by fine-textured substrates with relatively low hydraulic conductivity. These communities are influenced primarily by stagnant groundwater and are common where irregular topography allows the development of poorly drained, isolated depressions. They form in peat-filled depressions and on floating mats adjacent to lakes, ponds, or rivers. Species characteristic of FPn communities relative to FPs communities include white cedar, three-fruited bog sedge *(Carex trisperma),* and ericaceous shrubs such as creeping snowberry *(Gaultheria hispidula)* and leatherleaf *(Chamaedaphne calyculata).*

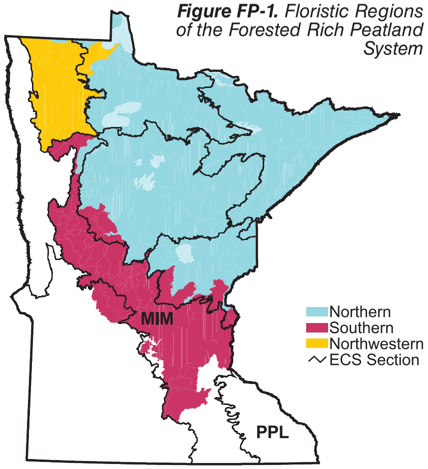

Figure FP-1. *Floristic Regions of the Forested Rich Peatland System*

The FPs Region is represented by one native plant community class, Southern Rich Conifer Swamp (FPs63). FPs communities in Minnesota are at the edge of the range of climate suitable for peat-forming vegetation. Because of a relatively warm climate and severe periodic droughts that cause drawdown of the water table and loss of peat in many basins, FPs communities are restricted to basins fed by groundwater flow that maintains sufficiently saturated conditions to promote peat development. They are most common on glacial moraines and outwash plains and appear to be associated with areas underlain by sandy substrates. It is likely that frequent drought and prolonged drawdown of the water table, along with more frequent fire, reduce the presence in FPs communities of some of the species characteristic in FPn communities. The scarcity or lack of ericaceous shrubs in FPs relative to FPn communities may be related to minimal snow cover in the FPs Region, resulting in desiccation of these plants during winter. Species characteristic of the FPs Region relative to the FPn Region include American and red elm, box elder, poison ivy *(Toxicodendron rydbergii)*, and vines such as Virginia creeper (*Parthenocissus* spp.), wild grape *(Vitis riparia)*, and wild honeysuckle *(Lonicera dioica)*.

Succession

FP communities can develop from Wet Forest communities if conditions become suitable for accumulation of organic matter (peat), and rooting contact with mineral soil is reduced. These conditions typically occur in settings where the water table becomes elevated or stabilized so that the ground surface is continuously saturated. As peat accumulates, and the peat surface and water table rise, rates of water flow and inputs of minerals to the peat surface are gradually reduced, and the community is transformed into a Forested Rich Peatland. Conditions then become suitable for invasion of the site by minerotrophic *Sphagnum* species, which absorb and retain minerals—particularly calcium—and release hydrogen ions, increasing the acidity of surface waters. As acidity increases, more acid-tolerant *Sphagnum* species become established at the site, and pH gradually falls. At pH 5.5 the water chemistry reaches a critical buffering point. It is no longer buffered by bicarbonates but by humic acids, and the community becomes an Acid Peatland (AP). The higher parts of hummocks quickly become more boglike, and minerotrophic *Sphagnum* species in hollows are replaced by oligotrophic species. The transformation of an FP community to an AP community can be stopped or slowed if groundwater or surface water inputs to the site increase and supply enough minerals to compensate their removal by *Sphagnum*.

It is possible to have characteristics of both AP and FP communities in the same peatland when peatlands have well-developed hummock and hollow topography. Originally, both hummocks and hollows in rich peatland communities have similar water chemistry, but as peat accumulates and the surface becomes more isolated from mineral-rich water,