Ecological Land Classification Program
Division of Forestry

Minnesota County Biological Survey
Division of Ecological Resources

Natural Heritage and Nongame Research Program
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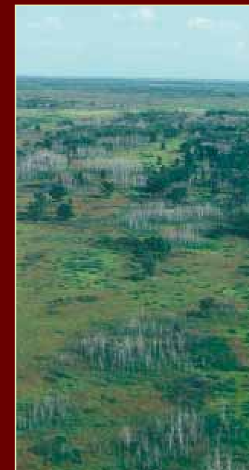


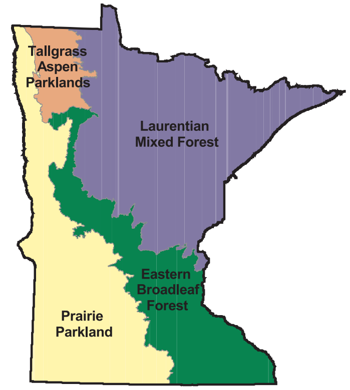
Field Guide to the

NATIVE PLANT COMMUNITIES *of* MINNESOTA

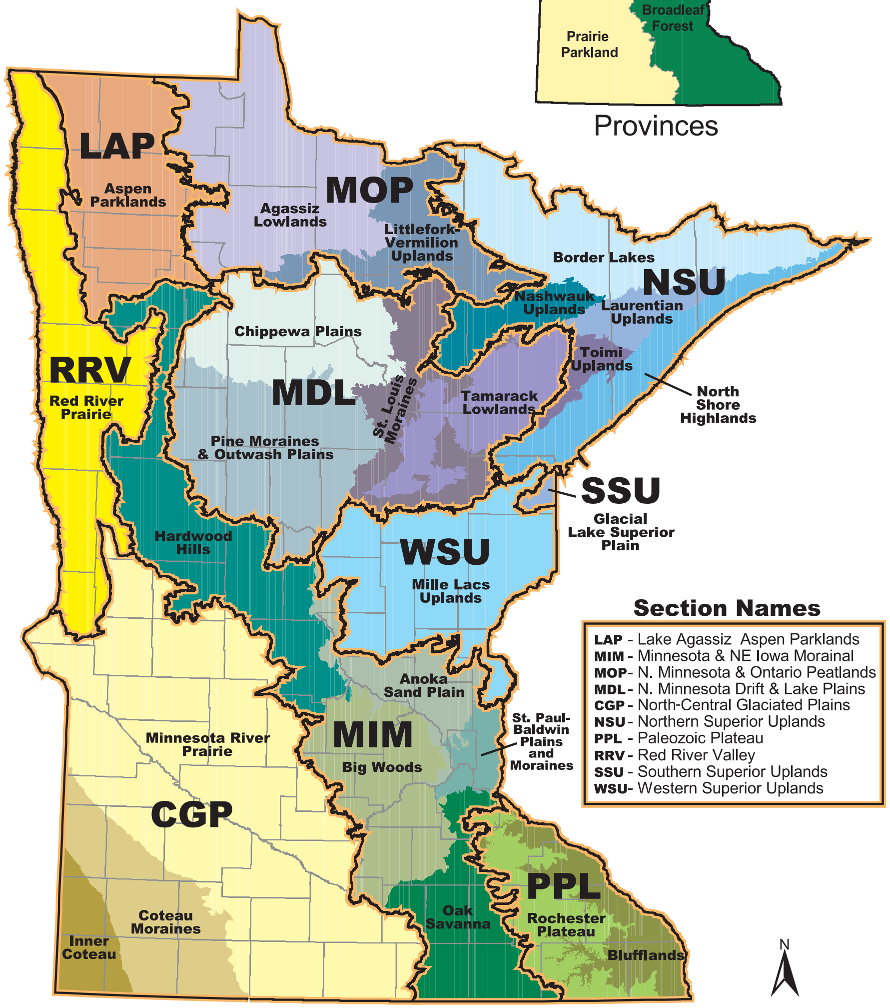
The Prairie Parkland and Tallgrass Aspen Parklands Provinces

ECOLOGICAL SYSTEM SUMMARIES

Ecological Provinces, Sections, & Subsections of Minnesota



Provinces



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.

December 2005

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

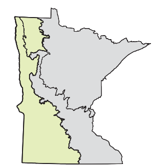
Wetland Prairie System

WPn53 Northern Wet Prairie

WPs54 Southern Wet Prairie

Field Guide to the

NATIVE PLANT COMMUNITIES *of* MINNESOTA



The Prairie Parkland and Tallgrass Aspen Parklands Provinces

Ecological System Summaries

This material is excerpted from: *Field guide to the native plant communities of Minnesota: The Prairie Parkland and Tallgrass Aspen Parklands Provinces.* 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.

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.

Additional data and analysis may support moving the boundary between these two regions 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, it is possible that the geographic variation in species composition of WP communities is the result of independently determined range limits of some of the component species.

Table WP-1. *Plants useful for differentiating the Northern and Southern Floristic Regions of the Wetland Prairie System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

	Common Name	Scientific Name	frequency (%) UPn	frequency (%) UPs
Northern Floristic Region	Tufted hair grass	*Deschampsia cespitosa*	64	-
	Bog birch	*Betula pumila*	43	-
	White aster-like goldenrod	*Solidago ptarmicoides*	20	-
	Kalm's lobelia	*Lobelia kalmii*	20	-
	Slender willow	*Salix petiolaris*	54	10
	Bebb's willow	*Salix bebbiana*	43	10
	Seaside arrowgrass	*Triglochin maritima*	27	6
	Crawe's sedge	*Carex crawei*	12	2
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

photo by D.S. Wovcha, MN DNR

new growth originates—are generally deep enough below the soil surface to escape damage in prairie fires. This is not as true of shrubs, but moist soil conditions in WP communities 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, including WP communities, 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 and can replace lost leaf tissue simply by adding new cells to the leaf base to reelongate the blade.

Because severe water limitation is not frequent in WP communities in the PPA and TAP provinces, 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. The dominant graminoids of the WP System utilize the C_4 metabolic pathway in photosynthetic carbon fixation, a physiological mechanism that makes photosynthesis in the high-light and high-temperature summer prairie environment more efficient with respect to water use (and also nitrogen use). Although water is seldom limiting in WP communities, the dominance of C_4 grasses indicates 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 morphological adaptations to cope with prolonged 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 (WPn) Region (Figure WP-1). All WP communities in the southern part of the PPA Province (from Traverse County south) are recognized as being in the WPs Region, and all WP communities north of this in the PPA Province and the TAP Province are in the WPn Region. 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.

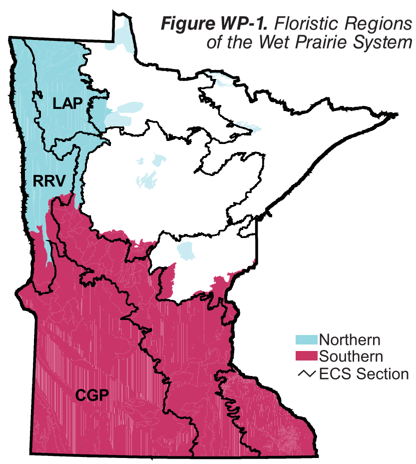


Figure WP-1. *Floristic Regions of the Wet Prairie System*

Table WP-1 lists the most geographically widespread species with at least moderately high fidelity for either the northern or the southern floristic region. 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. None of the indicators for the WPs Region has high frequency for communities in that floristic region, because each of these species occurs in only part of the region, or is uncommon, or both. Low

► 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
CGP – North-Central Glaciated Plains
NSU – Northern Superior Uplands
PPL – Paleozoic Plateau
RRV – Red River Valley
SSU – Southern Superior Uplands
WSU – Western Superior Uplands

photo by R.P. Dana, MN DNR

Kittson County, MN

General Description

The Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces historically were characterized by wide expanses of open prairie and open wetlands. Forests, woodlands, and brushlands were restricted to patches of land that did not burn as frequently as surrounding prairies. In the PPA Province, woody vegetation accounted for just 4% of the landscape and was concentrated around lakes and rivers. In the TAP Province, woody vegetation covered about 36% of the landscape and was concentrated in regions with perennially high water tables and poorly drained soils. The wooded vegetation consisted of patches of true, closed-canopy forests (such as Mesic Hardwood Forest [MH] and Floodplain Forest [FF] communities) on sites well protected from prairie fires. Sites that burned often enough to prevent the formation of closed-canopy forests but not enough to favor development of prairies were characterized by patches of scrubby or brushy Fire-Dependent Forest/Woodland (FD) communities. In the past, when fires were more frequent, landscape context strongly influenced where woody vegetation developed. Areas of greater local relief, presence of lakes and wetlands, and relatively high water tables all potentially interrupted the spread of prairie fires, enabling persistence of trees and brush. Within patches of wooded vegetation, slope, aspect, and soil drainage affected the finer-scale pattern of vegetation types.

In the past, FD communities in the PPA and TAP provinces appear to have consisted predominantly of shrubs and trees resprouting after fire or stunted by fire, with scattered taller trees or groves of trees. The most common tree species in these communities were bur oak and quaking aspen. It is interesting that vast areas of Minnesota were inventoried by public land surveyors in the 1800s with rather casual mention of the upland vegetation, which was simply described as either forest or prairie. In regions of the PPA and TAP provinces where patches of woodland were intermixed with prairie, the surveyors' descriptions were more elaborate as they attempted to describe the greater complexity of vegetation patterns. In parts of the PPA and TAP provinces where oaks were the most common trees in woodlands and brushlands, the public land surveyors described the vegetation as oak barrens, oak savanna, and oak openings. In areas where aspen was more common, the land surveyors described the vegetation as groves, thickets, and parklands of aspen, often with some oak. Natural remnants of this

meters. Mechanical disturbance of the soil by their hooves is critical for the regeneration of many short-lived plant species that are part of WP communities. Reduction in the height and density of the canopy of tall grasses by grazing allows shorter plant species to persist in the community. Grazing also stimulates recruitment of new individuals of longer-lived plant species and affects competitive interactions among them. 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 hand, during drier periods, wetland prairies provided superior forage and were probably preferentially grazed.

Grazing and fire apparently interacted in a way that helped distribute their effects evenly throughout prairies and provided periods of respite from both disturbances. New plant growth following fire is more palatable and nutritious than older growth, so grazing animals tended to follow fires. Areas neglected by grazers accumulated greater fuel loads and therefore burned more readily than grazed areas. Thus, in the past, a cycle of burning, followed by grazing, abandonment by grazers, and, after fuel buildup, burning again, characterized the WP system. WP communities are readily degraded by repeated season-long grazing; conversely, prolonged absence of grazing, even with periodic fire, will probably result in greater dominance by taller species, as described above. Therefore, the movement of herds to new areas seeking the superior forage of recently burned prairie was likely important in maintaining the full component of species in wetland prairie communities. 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 Wet Meadow (WM) communities. WP communities typically receive surface runoff but are subjected to only brief, periodic inundation. Although the water table usually remains in the lower part of the plant rooting zone for much of the growing season, most of the 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 that lack morphological adaptations for 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. Severe moisture stress is an infrequent experience for plants in WP communities in the PPA and TAP provinces. In the far western part of Minnesota, where evapotranspiration regularly exceeds precipitation, translocated salts concentrate at the surface in many low areas, making water uptake by plants difficult. A distinctive variant of wet prairie occupies these saline places. Plants associated with drier conditions, such as little bluestem *(Schizachyrium scoparium)* and western ragweed *(Ambrosia psilostachya)*, are often common in these sites, along with a reduced set of typical species of WP communities and some species restricted to saline conditions. 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. Plants with herbaceous life-forms, unlike woody plants, do not lose much investment when fire destroys their aboveground parts, and strongly dominate WP communities. 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 aboveground parts. The perennating organs of most of the plants—buds, tubers, root collars, or other tissue from which boundaries of the CGP in the Coteau Moraines Subsection, WP communities were irregularly scattered in the prairie landscape. They were similarly scattered in the broad central zone of the Minnesota River Prairie Subsection, but there were also more extensive occurrences in low-relief areas that had been the beds of shallow, short-lived glacial lakes. Shallow stream valleys tributary to the Minnesota River, many of which followed old meltwater channels, were additional sites for WP communities. In the Inner Coteau Subsection, where closed depressions are uncommon, WP communities were concentrated along valleys. The most extensive occurrences of WP communities were probably in the broad, nearly flat lake plain of Glacial Lake Agassiz, which dominates the RRV. WP communities may have comprised more of the prairie landscape here than UP communities. Along the east margin of the lake plain, WP communities dominated long, linear zones behind the beach ridges formed at different stages of the lake's history. The TAP Province, a ground moraine reworked by wave action during a period when it was a shallow-water part of Glacial Lake Agassiz, is almost as topographically smooth as the deep-water lake plain in the RRV, and WP communities were often quite extensive. A broad band of prominent beach ridges arcs through the province, and WP communities were similarly disposed within it as in the interbeach zone on the east side of the RRV. In the TAP Province, communities of the WP System were frequently associated with communities of the Open Rich Peatland (OP) System. Very little native wetland prairie remains today in either province; drainage and cultivation, succession to woodland and forest, and urban and suburban development have destroyed more than 99% of the wetland prairies present in the PPA Province before Euro-American settlement. A greater fraction has been spared from cultivation in the TAP Province, where some substantial areas remain.

Natural History

Frequent fire (with return intervals less than 10 years) is critical for the occurrence of wetland prairies. The association, noted above, of wetland prairies with larger upland prairies is explained by their dependence on 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 reduce 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. In the PPA Province, the combination of a relatively dry climate and a topographically subdued landscape with few lakes resulted in the strong dominance of the entire province by prairie communities. Increasingly moist climatic conditions eastward in Minnesota, together with rougher topography and much higher density of lakes, dramatically altered the fire environment in most of the Eastern Broadleaf Forest Province, resulting in dominance by woodland and forest communities. The importance (noted above) of brush-prairies in the TAP Province probably involves cooler, moister soil conditions in the spring when dead vegetation is most flammable. The longer duration of snow cover and cooler average temperatures presumably afford some protection to the root crowns of woody plants during the spring fire season, and the wet soils might even still be frozen when many fires occur in the province.

WP communities were historically subject to grazing and browsing by large mammals, primarily bison and elk. 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. These animals are major dispersers of seeds and are especially important for dispersals of more than a few

scrubby and brushy vegetation have developed into taller woodlands or forests following the decline in fire frequency that came with Euro-American settlement in the region. The descriptions of FD communities in this guide are based largely on current examples of these previously more fire-prone communities. In the PPA Province, the majority of these examples are on sandy, gravelly, or otherwise droughty sites where succession to closed-canopy MH communities has been slowed by harsh growing conditions. In the TAP Province, most current examples of FD communities are on wet but sandy sites that dry out during severe droughts and burn often enough to prevent succession to closed-canopy MH or Wet Forest (WF) communities.

As the name implies, FD communities are or have been strongly influenced by wildfires. The fires common in the past in the deciduous woodlands of the PPA and TAP provinces were capable of killing stands of trees and other aboveground vegetation under the right combination of climate, fuel supply, and topographic setting. However, even intense fires in these deciduous woodlands did not generate the kinds of conflagrations possible in the closed-canopy coniferous forests of the Laurentian Mixed Forest (LMF) Province, where crown fires produce enough heat to completely consume branches of live trees, coarse woody debris, litter, and even some soil organic matter, resulting in the death of most trees at a site and recolonization of the site through germination of seeds banked in the soil or dispersed from other sites. The less intense fires in the deciduous woodlands of the PPA and TAP provinces generally did not completely kill trees and shrubs on the site, but instead killed aboveground stems, promoting vegetative recovery mainly from existing rootstocks rather than from new seedlings. Any mortality of trees and shrubs that did occur in these deciduous FD communities came primarily from attrition following repeated fires rather than consumption in a single fire. In addition to promoting vegetative sprouting, these fires also enhanced sexual plant reproduction by exposing mineral soil, triggering seed dispersal, breaking seed dormancy, and increasing light and heat conditions on the ground. Fires also prevented accumulation of litter and humus, thus affecting nutrient cycling, nutrient availability, and soil-forming processes linked to humus.

At present, most of the once-extensive prairies and parklands of the PPA and TAP provinces have been converted to agricultural or urban land. Thus, the prairie wildfires that swept across the landscape and maintained the FD communities are gone. The landscape has been changed further by extensive ditching and draining of wetlands, which has altered the high local water tables and distribution of water bodies that influenced the distribution and persistence of woodlands in the fire-prone provinces. Herds of bison and elk, which likely supplemented fire in shaping the composition and structure of FD communities, are also now gone from the landscape.

Plant Adaptations

Plants that occur in FD communities have seeds or vegetative structures that can survive fire; they also tend to be 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 the PPA and TAP provinces of Minnesota is their ability to sprout prolifically. The trees and shrubs, and many of the herbaceous species, 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 PPA and TAP provinces have a mixture of species with life history traits and morphological features that are generally associated with either

Upland Prairie (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 in Minnesota, such as lady fern *(Athyrium filix-femina)*, rattlesnake fern *(Botrychium virginianum)*, and bracken *(Pteridium aquilinum)*. Many additional fern species common in MH communities are absent from FD communities. Several other kinds of species present in 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 in the PPA and TAP provinces are oaks and aspen. Bur oak and quaking aspen are by far the most common trees, but northern pin oak and balsam poplar 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 and balsam poplar survive repeated burning by forming suckers that sprout from an extensive network of roots. This produces a dispersed, thicket-like 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 PPA and TAP provinces land surveyors in the 1800s commonly listed aspen and oak as "underbrush" rather than "timber." Aboveground, the FD communities in the two provinces 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 under natural fire regimes, 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 PPA and TAP provinces: the Northwestern Floristic (FDw) Region and the Southern Floristic (FDs) Region. FDw communities are restricted to the TAP Province, while FDs communities—which are most common in the Eastern Broadleaf Forest Province—are present at scattered sites in the PPA Province.

Floristic differences between the two regions are likely to be related in part to climate. The FDw Region is under the influence of Arctic air masses in the winter much more often than the FDs Region, and is much colder. The FDw Region experiences extreme winter temperatures of -41°F to -45°F (-41°C to -43°C), which exceed the physiological tolerances of species such as northern red oak, ironwood, and black cherry, which are present in the FDs Region but not the FDw Region. The FDw Region also has, on average, about 20 to 70 days more snow cover each year than the FDs Region, which may also lead to differences in presence of species.

WP Wetland Prairie System

photo by R. P. Dana, MN DNR

Ulen Wildlife Management Area, Kittson 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 (*Carex pellita*) and Buxbaum's sedge (*C. buxbaumii*) are 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.). Bog birch (*Betula glandulifera*) and shrubby cinquefoil (*Potentilla fruticosa*) are common in the far north. The main vegetation layer is usually less than 40in (1m) high, although some forbs and the flowering stalks of many of the grasses rise well above this height as the season progresses.

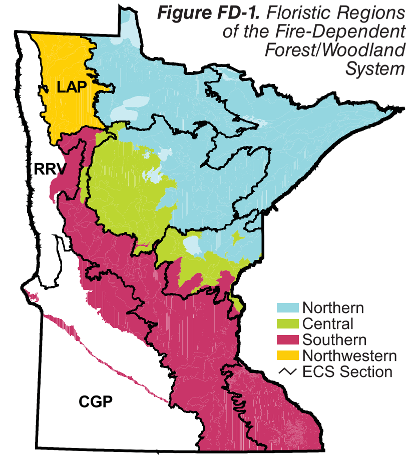
The herbaceous dominance of WP communities is closely tied to the frequent occurrence of fire. In circumstances where fire frequency or intensity is reduced, shrubs and suckers of quaking aspen and balsam poplar can increase in abundance, forming wet brush-prairie communities. These wet brush-prairies may appear more like brushland or shrubland than prairie, but herbaceous prairie plants remain a major component of the vegetation. The shrub layer is patchy and usually less than 5ft (1.5m) tall. In the absence of fire, wet brush-prairies rapidly succeed to woodlands. Today, most wet brush-prairies occur in the Tallgrass Aspen Parklands (TAP) Province of northwestern Minnesota.

WP communities almost always occur in association with Upland Prairie (UP) communities, most frequently as inclusions in landscapes dominated by the latter. Historically, they were common in the Prairie Parkland (PPA) Province, occurring in slight depressions and along drains. Marshes and meadows in the province typically had a fringe of wet prairie. In the hummocky morainic areas along the north and east 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.

Clay County, MN

In addition to differences in climate, the FDw and FDs regions differ strongly in physiography, parent material, and major geologic processes, all of which likely have an effect on species composition. FDw communities are present in flat landscapes with poorly developed surface drainage. In the past, before ditching and draining of wetland basins, the steady accumulation of peat in shallow depressions promoted high water tables in the adjacent uplands on which FDw communities occur. As a result, the soils in most FDw communities are moderately well drained to very poorly drained, and the water table is usually within reach of tree roots if not other plants in the community. Because FDw communities are present on seasonally wet sites and tend to occur next to perennially wet plant communities, they have plant species characteristic of mucky wetland habitats. The occurrence of FDw communities on wet sites is unusual among communities in the FD system. In other parts of Minnesota, these sites typically support WF, MH, or FF communities little affected by fire. The TAP Province, however, experiences prolonged and severe droughts during which fires will burn through almost any site with dry fuels, even sites that soils and plants would suggest are normally quite wet. The floristic composition of FDw communities suggests a successional relationship with both Wetland Prairie (WP) and WF communities. It is likely that sites currently occupied by FDw communities were previously occupied by WP communities in periods following severe fire. In the long-term absence of fire or severe drought, FDw communities may succeed to WF or possibly MH communities. Descriptions of the vegetation of northwestern Minnesota made by public land surveyors in the 1800s and researchers in the early 1900s indicate that WP, FDw, and WF communities were present in a fine-scale mosaic that shifted across the flat landscape in response to drought cycles and fire patterns.

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



In comparison with FDw communities, FDs communities often occur in landscapes with rolling to rugged terrain. The soils are well to excessively well drained, and the water table is beyond the reach of most plant roots. Because peatlands are less prevalent in the FDs Region, FDs communities are less likely than FDw communities to have plants characteristic of mucky wetland communities. On relatively level terrain, FDs communities were often present in the past as a buffer of brush and scattered timber separating riparian MH and FF communities from prairies. In rugged terrain, FDs communities formed larger patches of vegetation, often with inclusions of MH communities in ravines, on north-facing slopes, and around lakes. Because of proximity to MH communities, FDs communities have plant species that, although tolerant of fire, are characteristic of and more common in MH communities. With the reduction in prairie wildfires that has accompanied agricultural development of the region, FDs communities have tended to succeed toward closed-canopy MH communities, promoting occurrence of additional shade-tolerant species from adjacent MH and FF communities.

Plant Indicators of FDw vs. FDs Communities

Plant species with high fidelity for FDw communities relative to FDs communities are listed in Table FD-1. The largest group of diagnostic plants for the FDw Region relative to the FDs Region are species common on peaty or mucky habitats throughout the LMF Province, including Bebb’s willow *(Salix bebbiana)*, bluejoint *(Calamagrostis canadensis)*, fringed brome *(Bromus ciliatus)*, swamp gooseberry *(Ribes hirtellum)*,

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

Region	Group	Common Name	Scientific Name	frequency (%) FDw	FDs
Northwestern Floristic Region	Affinity for Peaty Habitats in Northeastern Minnesota	Bebb's willow	*Salix bebbiana*	49	-
		Bluejoint	*Calamagrostis canadensis*	44	2
		Fringed brome	*Bromus ciliatus*	40	4
		Swamp gooseberry	*Ribes hirtellum*	40	-
		Flat-topped aster	*Aster umbellatus*	40	2
		Red-osier dogwood	*Cornus sericea*	37	2
		Fringed loosestrife	*Lysimachia ciliata*	31	-
		Dwarf alder	*Rhamnus alnifolia*	30	-
		White rattlesnakeroot	*Prenanthes alba*	27	2
		Red-stemmed aster	*Aster puniceus*	26	-
		Swamp thistle	*Cirsium muticum*	22	-
		Giant goldenrod	*Solidago gigantea*	20	-
		Pussy willow	*Salix discolor*	19	-
		Fowl bluegrass	*Poa palustris*	19	-
		Meadow horsetail	*Equisetum pratense*	16	-
		Meadowsweet	*Spiraea alba*	16	-
		Bog birch	*Betula pumila*	16	-
		Marsh straw sedge	*Carex tenera*	16	-
		Bunchberry	*Cornus canadensis*	10	-
		Swamp fly honeysuckle	*Lonicera oblongifolia*	10	-
	Prairie Affinity	Veiny meadow-rue	*Thalictrum venulosum*	66	-
		Bastard toadflax	*Comandra umbellata*	44	-
		Yarrow	*Achillea millefolium*	34	-
		Slender wheatgrass	*Elymus trachycaulus*	25	-
		Woods' rose	*Rosa woodsii*	21	-
		Canada anemone	*Anemone canadensis*	20	2
		Marsh vetchling	*Lathyrus palustris*	19	-
		Wood betony	*Pedicularis canadensis*	18	-
		Mexican muhly grass	*Muhlenbergia mexicana*	16	-
		Nodding wild rye	*Elymus canadensis*	16	-
		White sage	*Artemisia ludoviciana*	12	-
		Gray goldenrod	*Solidago nemoralis*	12	-
		Black-eyed Susan	*Rudbeckia hirta*	10	-
		Prairie cordgrass	*Spartina pectinata*	10	-
		Big bluestem	*Andropogon gerardii*	10	-
		Alumroot	*Heuchera richardsonii*	10	-
		Wood lily	*Lilium philadelphicum*	10	-
		Clustered muhly grass	*Muhlenbergia glomerata*	10	-
		Shrubby cinquefoil	*Potentilla fruticosa*	10	-
	Central Fire-Dependent Forest/Woodland Affinity	American vetch	*Vicia americana*	74	-
		False melic grass	*Schizachne purpurascens*	46	2
		Veiny pea	*Lathyrus venosus*	40	8
		Fireweed	*Epilobium angustifolium*	20	-
		Kalm's hawkweed	*Hieracium kalmii*	18	-
		Balsam poplar (U)	*Populus balsamifera*	14	-
		Blue giant hyssop	*Agastache foeniculum*	14	-
		Harebell	*Campanula rotundifolia*	12	-
		Poverty grass	*Danthonia spicata*	12	-
		Yellow panic grass	*Panicum xanthophysum*	10	-
	*	Interrupted wild rye	*Elymus diversiglumis*	15	-

* **Other** (U) = understory tree

be more restricted to settings with steady inputs of groundwater.

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. At present, by convention the floristic regions in the MR System are delineated using province boundaries; collection of additional data will likely provide a better understanding of the most important factors in regional variation among MR communities and lead to realignment of floristic region boundaries.

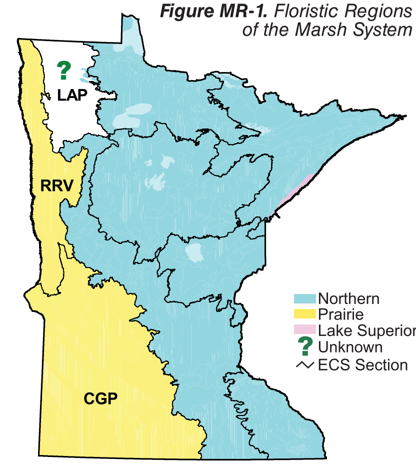


Figure MR-1. *Floristic Regions of the Marsh System*

Plant Community Classes in the PPA and TAP Provinces

Four MR community classes are present in the PPA and TAP provinces: Northern Mixed Cattail Marsh (MRn83), Northern Bulrush-Spikerush Marsh (MRn93), Prairie Mixed Cattail Marsh (MRp83), and Prairie Bulrush-Arrowhead Marsh (MRp93). These classes can be divided into two groups based largely on differences in dominant species, which appear to be correlated with degree of exposure to wave action or differences in water depth, although other factors such as the amplitude of water-level changes may also be important. The classes in the first group—MRn83 and MRp83—are dominated by cattails and sedges *(Carex* spp.) and have forb species such as star-duckweed *(Lemna trisulca),* common bladderwort *(Utricularia vulgaris),* and marsh bellflower (*Campanula aparinoides)*. MRn83 and MRp83 typically occur in shallow basins, ponds, bays of lakes, or sluggish streams where vegetation is at least partially protected from wave action or strong currents. In comparison, MRn93 and MRp93 are dominated by bulrushes *(Scirpus* spp.), spikerushes *(Eleocharis* spp.), broad-leaved arrowhead *(Sagittaria latifolia)*, and grasses such as northern manna grass *(Glyceria borealis)*, and occur in deep wetland basins, in shallow wetlands that are adjacent to large areas of open water and are subject to wave action, along wave-washed lakeshores, on sandbars, and in stream channels.

Succession

Marshes can develop from submerged or floating-leaved aquatic communities if water depth is reduced by deposition of sedimentary peat, siltation, or draining, and persistent emergent plants then become established in the shallower waters that characterize 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, which commonly remove large patches of vegetation in marshes, can also create 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 *(Carex* spp.), and affiliated submerged and floating-leaved species are eliminated, resulting in conversion to WM communities. The creation and eventual draining of beaver ponds

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 species germinate only when seeds buried in sediments are exposed following water-level drawdowns. These include species 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 pondweeds (*Potamogeton* spp.) 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.

Invasion of marshes by the non-native species narrow-leaved cattail *(Typha angustifolia)* and hybrids of narrow-leaved and broad-leaved cattails *(T. angustifolia* x *T. latifolia* = *Typha* x *glauca)* has profoundly altered the species composition of MR communities throughout the prairie and deciduous forest regions of Minnesota. When narrow-leaved and hybrid cattails invade marshes, they typically outcompete and displace the native broad-leaved cattail (and most other native species). Marshes in the PPA and TAP provinces are likely predisposed to invasion by narrow-leaved and hybrid cattails because of the high mineral content of the calcareous substrates typical in these provinces. Invasion is further promoted in many basins by inputs of silt from eroding uplands and by fertilizer- and road salt–laden runoff. Narrow-leaved and hybrid cattails are more tolerant than broad-leaved cattail of water-level changes brought about by ditching and land cover conversion. They also tend to form taller and denser cover than broad-leaved cattail, thereby displacing or eliminating other native understory species from MR communities. Narrow-leaved and hybrid cattails have replaced broad-leaved cattails to such an extent that marshes dominated by native cattails are rare in the prairie regions of Minnesota, as well as in much of the deciduous forest regions to the east. Non-native cattails are also problematic invaders of bulrush-dominated marshes and of WM communities in Minnesota.

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). Communities of the MRn Region have been documented in the TAP Province, but very little data are available for these occurrences; communities of the MRp Region are present in the PPA Province. 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

flat-topped aster *(Aster umbellatus)*, red-osier dogwood *(Cornus sericea)*, fringed loosestrife *(Lysimachia ciliata)*, and dwarf alder *(Rhamnus alnifolia)*. Another group of species diagnostic for FDw communities are plants that have high frequency in Central Floristic (FDc) Region jack pine–dominated communities in the LMF Province. These communities, including Central Poor Dry Pine Woodland (FDc12) and Central Dry Pine Woodland (FDc23), occur on sites that in the past (ca. 1,000 to 2,000 years ago) were occupied by deciduous woodlands that were perhaps similar to FDw communities. In addition, like FDw communities, FDc12 and FDc23 typically occur on sandy lacustrine parent material in proximity to paludified peatlands. Species common in these FDc communities and also present in FDw communities include American vetch *(Vicia americana)*, false melic grass *(Schizachne purpurascens)*, veiny pea *(Lathyrus venosus)*, fireweed *(Epilobium angustifolium)*, Kalm's hawkweed *(Hieracium kalmii)*, and blue giant hyssop *(Agastache foeniculum)*. Other species that help to separate FDw from FDs communities include species most common in UP or WP communities, including veiny meadow-rue *(Thalictrum venulosum)*, bastard toadflax *(Comandra umbellata)*, yarrow *(Achillea millefolium)*, slender wheatgrass *(Elymus trachycaulus)*, Woods' rose *(Rosa woodsii)*, and Canada anemone *(Anemone canadensis).*

Plants with high fidelity for FDs communities relative to FDw communities are listed in Table FD-2. Most of these plants have their peak presence in MH communities, including several of the dominant tree species such as basswood, northern red oak, and ironwood. Also diagnostic are many shade-tolerant herbs such as Clayton's sweet cicely *(Osmorhiza claytonii)*, lopseed *(Phryma leptostachya)*, large-flowered bellwort *(Uvularia*

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

		Common Name	Scientific Name	frequency (%) FDw	FDs
Southern Floristic Region	Mesic Hardwood Forest Affinity	Clayton's sweet cicely	*Osmorhiza claytonii*	7	82
		Lopseed	*Phryma leptostachya*	9	64
		Early meadow-rue	*Thalictrum dioicum*	10	64
		Large-flowered bellwort	*Uvularia grandiflora*	-	57
		Common false Solomon's seal	*Smilacina racemosa*	1	53
		Pointed-leaved tick trefoil	*Desmodium glutinosum*	-	51
		Common enchanter's nightshade	*Circaea lutetiana*	1	44
		Prickly gooseberry	*Ribes cynosbati*	8	44
		Black cherry (U)	*Prunus serotina*	1	42
		Ironwood (U)	*Ostrya virginiana*	-	33
		Basswood (U)	*Tilia americana*	-	28
		Pale bellwort	*Uvularia sessilifolia*	1	26
		Bottlebrush grass	*Elymus hystrix*	-	24
		Zigzag goldenrod	*Solidago flexicaulis*	-	24
		Large-leaved aster	*Aster macrophyllus*	1	22
		Blue cohosh	*Caulophyllum thalictroides*	-	22
		Bloodroot	*Sanguinaria canadensis*	-	22
		Pagoda dogwood	*Cornus alternifolia*	-	17
		Northern red oak (U)	*Quercus rubra*	1	17
		American spikenard	*Aralia racemosa*	-	13
	Floodplain Forest Affinity	Virginia creeper	*Parthenocissus* spp.	8	66
		Prickly ash	*Zanthoxylum americanum*	1	60
		Wild grape	*Vitis riparia*	2	40
		Box elder (U)	*Acer negundo*	7	33
		Honewort	*Cryptotaenia canadensis*	1	20
		Missouri gooseberry	*Ribes missouriense*	-	13
	Other	Bush honeysuckle	*Diervilla lonicera*	3	24
		Round-leaved dogwood	*Cornus rugosa*	-	17
		Lady fern	*Athyrium filix-femina*	1	17

(U) = understory tree

grandiflora), common false Solomon's seal *(Smilacina racemosa)*, pointed-leaved tick trefoil *(Desmodium glutinosum)*, common enchanter's nightshade *(Circaea lutetiana)*, zigzag goldenrod *(Solidago flexicaulis)*, blue cohosh *(Caulophyllum thalictroides)*, and bloodroot *(Sanguinaria canadensis)*. Given the historic description of the structure of FDs communities, which ranged from woodland to brushland with scattered trees, it is difficult to imagine that shade-tolerant species were components of these communities in the past. More likely, increasing closure of the canopy in FDs communities following fire suppression has promoted invasion of these sites by shade-tolerant herbaceous species from nearby MH communities. The FDs Region is also distinguished from the FDw Region by the presence of species that have their highest presence statewide in FF communities, including Virginia creeper *(Parthenocissus* spp.*)*, prickly ash *(Zanthoxylum americanum)*, wild grape *(Vitis riparia)*, box elder, and honewort *(Cryptotaenia canadensis)*. These species are likely present in FDs communities because of the proximity of these communities to rivers and lakes.

Natural History and Fire Regimes of FDw vs. FDs Communities

The natural rotation periods of fires in FDw and FDs communities are fairly similar (Table FD-3). In the past, communities in both floristic regions were far more likely to experience moderate surface fires than catastrophic fires that killed existing trees and caused regeneration of forest stands. In general, FDw communities have rotations of 15 years for surface fires and 90 to 100 years for catastrophic fires. FDs communities have rotations of 10 to 20 years for surface fires and 100 to 110 years for catastrophic fires. The chance of any fire resulting in significant mortality of canopy trees was about one in seven for both FDw and FDs communities.

Table FD-3. *Historic tree species composition and disturbance regimes in FDs and FDw 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
Southern Floristic Region						ranges →	100-110	10-20	9-18	>1000
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 pin oak)*	--	--	110	10	9	>1000
Northwestern Floristic Region						ranges →	90-100	15	13-14	230-290
FDw24	0 - 90+ yrs	**quaking aspen** bur oak	--	--	--	--	100	15	14	260
FDw34	0 - 90+ yrs	**quaking aspen** *bur oak* *balsam poplar*	--	--	--	--	90	15	13	290
FDw44	0 - 90+ yrs	**quaking aspen** *balsam poplar* *tamarack*	--	--	--	--	100	15	14	230

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

photo by R.P. Dana MN DNR

Fuglie Waterfowl Production Area, Clay 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.[1] MR communities occur statewide; the wetland settings that support MR communities are common throughout much of the Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces in wetland basins, along sheltered lakeshores, near stream mouths, and in river backwaters or sluggish streams. However, many of these wetlands have been affected by anthropogenic disturbances such as sediment-, nutrient-, and salt-laden runoff from surrounding uplands and artificial changes in water level. As a result, intact, high-quality MR communities are rare in the two provinces. The maximum water depth in MR communities is typically sustained at 20–40in (50–100cm) 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 calcareous glacial deposits underlie most of the PPA and TAP provinces, the pH of water in MR communities in the provinces 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.

[1]Although floating-leaved and submergent aquatic plants may be present as components of some of the MR communities described in this classification, deeper-water aquatic communities dominated by floating-leaved or submergent plant species have not been included in the classification and are not described in this field guide.

Table WM-1. *continued*

		Common Name	Scientific Name	frequency (%) WMn	Wms	WMp
Prairie Floristic Region	Graminoid	Prairie cordgrass	*Spartina pectinata*	-	21	85
		Narrow reedgrass	*Calamagrostis stricta*	4	14	81
		Woolly sedge	*Carex pellita*	-	22	69
		Sartwell's sedge	*Carex sartwellii*	2	13	69
		Baltic rush	*Juncus arcticus*	-	2	62
		Dark green or Pale bulrush	*Scirpus atrovirens* or *S. pallidus*	1	13	35
		Buxbaum's sedge	*Carex buxbaumii*	3	8	35
		Flattened spikerush	*Eleocharis compressa*	-	-	31
		Foxtail barley	*Hordeum jubatum*	-	-	23
		Rigid sedge	*Carex tetanica*	-	-	15
		Very slender sedge	*Carex praegracilis*	-	-	12
		Sweet grass	*Hierochloe odorata*	-	-	12
		Dudley's rush	*Juncus dudleyi*	-	-	8
		Mat muhly grass	*Muhlenbergia richardsonis*	-	-	8
		Switchgrass	*Panicum virgatum*	-	-	8

communities. WMp communities have species that have affinity for WP communities or very rich fens (i.e., Prairie Extremely Rich Fens [OPp93]) and very few, if any, species typical of forested wetland communities.

Recent plot data collected for WMs and WMp communities show a much greater geographical overlap between the two floristic regions than was previously thought, and future analysis may indicate that they should be combined into a single floristic region.

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) and Southern Basin Wet Meadow/Carr (WMs92). WMs83 develops in settings fed by groundwater and is characterized by a relatively constant water supply. WMs92 occurs in settings where water is supplied by precipitation and surface runoff and is characterized by distinct wet and dry cycles. There is only one class in the WMp floristic region, Prairie Wet Meadow/Carr (WMp73). WMp73 occurs in basins where water is supplied by precipitation or possibly groundwater but the seasonal change in water level is not great.

Succession

WM communities can develop from 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 where siltation, accumulation of sedimentary peat, development of floating root mats, or lowering of water tables—commonly following artificial drainage or 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 bluejoint and sedges *(Carex* spp.) over emergent aquatic plants such as cattails *(Typha* spp.) and bulrushes *(Scirpus* spp.). Lowered water tables in MR communities often result in more rapid invasion by reed canary grass than by native sedges and grasses. In the TAP Province, WM communities can be invaded by peat-producing bryophytes (particularly *Sphagnum*), causing decline in nutrient levels and replacement of the dominant broad-leaved sedge species by fine-leaved sedges, leading to conversion to OP communities. WM communities can also succeed to MR communities following hydrological changes that result in raising of the water table.

FDw and FDs communities are remnants of what the land surveyors described in the late 1800s as "thickets" or "upland brush with scattered timber." At present, their structure is better described as woodland or even forest. Before Euro-American settlement, the number of trees per acre in FDs communities was about one-third that of MH communities in the same general region (i.e., MHs communities). Today, there is no difference in tree density between FDs communities and MHs communities. A clear consequence of fire suppression has been development of tree canopies in FDs communities, filling the gaps created in the past by frequent surface fires. The combined cover of tree species in the canopy and subcanopy of both FDs and MHs communities at present averages about 150%. The tripling of the density of aspen and bur oak and the shadier, more humid understory conditions now present in FDs communities have likely made these communities less flammable than the more open brushlands and scrubby woodlands of the past. FDw communities have not responded to decline in fire frequency in quite the same way as FDs communities. At present, tree densities in FDw communities have about the same ratio to other forest types in the region (such as WFw and MHw communities) as they did historically. Most likely the apparent lack of increase in tree density in FDw communities is a consequence of aspen dominance, in which young, thicketlike stands have high tree densities and succession to other species like oak is uncommon. Managed aspen stands in the FDw Region are clear-cut on short rotations, which results in stand structures not unlike those present under natural fire disturbance regimes.

It appears that the historic fire regimes in brushy FDw and FDs communities were more the product of landscape setting or context rather than of properties of the vegetation itself. For example, in comparison with conifer-dominated woodlands or some shrublands in the western United States, it does not appear that FDw and FDs communities were more likely to burn over time because of changes in the vegetation. The colonies of hazelnuts *(Corylus* spp.), dogwoods *(Cornus* spp.), and other native deciduous woodland shrub species that formed the dominant vegetation layer in these deciduous woodlands do not appear more likely to burn as they age. It is also unlikely that they would burn much hotter as they age 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 shrubs in the western United States. Rather, in the past, brushy deciduous woodlands developed in Minnesota in settings where the fire regime was imposed on the landscape by context more than by site properties or the developmental stage of these brushlands. FDw and FDs communities probably burned frequently because they were next to or surrounded areas of prairie. Where there were extensive areas of FDw communities in the historic landscape, they almost always had inclusions of prairie, brush-prairie, or grassy wetlands. Where there were extensive areas of FDs communities, it appears that almost always they were in areas between prairies and true forests (such as MH communities). Under dry conditions, fires that originated in prairies probably burned through FDw and FDs communities, while under wetter conditions they did not. Humans likely had influence on the past fire regime in FDw and FDs communities. Grasslands and wet hay meadows within short distances of forests and woodlands were of great value to American Indians and European settlers alike. These openings attracted game and provided food for the settlers' horses and livestock. Therefore, in the past, people commonly set fire to maintain grassland and meadow openings within woodland areas, bringing fire to the edge of FDw and FDs communities.

photo by Craig Anderson, MN DNR

Pope County, MN

General Description

Mesic Hardwood Forest (MH) communities are extremely rare in the Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces. Historically, they were limited to small areas of upland that were isolated from prairie wildfires by lakes, rivers, or rough topography. MH communities are characterized by continuous, often dense canopies of trees. Beneath the main canopy are successively shorter strata composed of shade-adapted seedlings (usually including seedlings of canopy trees), shrubs, and herbs. In most of the PPA Province, MH communities are similar to those in the Eastern Broadleaf Forest (EBF) and Laurentian Mixed Forest (LMF) provinces, with mixed canopies of basswood, ironwood, and sugar maple. Bur oak, American elm, box-elder, and green ash, however, have greater importance in MH communities in the PPA Province than in eastern parts of Minnesota, replacing northern red oak, black ash, red maple, and paper birch as common co-dominants. In the TAP Province, MH communities consist of mixed stands of quaking aspen, paper birch, black ash, bur oak, American elm, green ash and conifers such as white spruce and balsam fir. Sugar maple, one of the most characteristic trees of MH communities in Minnesota, is absent from the TAP Province, and two others, basswood and ironwood, are rare.

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 waterlogged 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 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

Table WM-1. *continued*

		Common Name	Scientific Name	frequency (%) WMn	Wms	WMp
Northern Floristic Region	Fern	Northern marsh fern	*Thelypteris palustris*	42	22	-
		Crested fern	*Dryopteris cristata*	25	4	-
		Spinulose shield fern	*Dryopteris carthusiana*	6	-	-
	Graminoid	Lake sedge	*Carex lacustris*	72	32	-
		Beaked sedge	*Carex utriculata*	33	11	-
		Woolgrass	*Scirpus cyperinus*	23	2	-
		Silvery sedge	*Carex canescens*	6	-	-
		Creeping sedge	*Carex chordorrhiza*	5	-	-
		Three-way sedge	*Dulichium arundinaceum*	5	-	-
Southern Floristic Region	Tree	Box elder	*Acer negundo*	1	10	-
	Shrub	Poison ivy	*Toxicodendron rydbergii*	-	7	-
		Silky dogwood	*Cornus amomum*	1	5	-
	Vine	Wild grape	*Vitis riparia*	-	5	-
	Forb	Virginia mountain mint	*Pycnanthemum virginianum*	-	21	15
		Swamp thistle	*Cirsium muticum*	4	18	-
		Willow-herbs*	*Epilobium* spp.	9	15	-
		White turtlehead	*Chelone glabra*	4	14	-
		Clearweed	*Pilea* spp.	8	14	-
		Starry false Solomon's seal	*Smilacina stellata*	-	10	4
		Spring cress	*Cardamine bulbosa*	-	9	-
		Swamp saxifrage	*Saxifraga pensylvanica*	1	8	-
		Bottle gentian	*Gentiana andrewsii*	-	5	-
	Graminoid	Whitetop	*Scolochloa festucacea*	-	14	-
		Awl-fruited sedge	*Carex stipata*	6	11	-
		Rice cut grass	*Leersia oryzoides*	4	10	-
		Common reed grass	*Phragmites australis*	6	10	-
		Hairy-fruited sedge	*Carex trichocarpa*	-	5	-
		Crested sedge	*Carex cristatella*	1	5	-
Prairie Floristic Region	Shrub	Shrubby cinquefoil	*Potentilla fruticosa*	-	-	8
		Wood's rose	*Rosa woodsii*	-	-	8
	Forb	Rough bugleweed	*Lycopus asper*	3	24	58
		Sunflowers**	*Helianthus* spp.	-	26	42
		Spotted water hemlock	*Cicuta maculata*	2	18	42
		Stemless blue violets***	*Viola* spp.	2	23	38
		Clasping dogbane	*Apocynum sibiricum*	-	8	38
		Prairie loosestrife	*Lysimachia quadriflora*	-	4	38
		Grass-leaved goldenrod	*Euthamia graminifolia*	2	4	31
		Silverweed	*Potentilla anserina*	-	-	31
		Autumn sneezeweed	*Helenium autumnale*	-	8	19
		Golden & False golden ragwort	*Senecio aureus & S. pseudaureus*	-	5	15
		Golden alexanders	*Zizia aurea*	-	4	15
		Maximilian's sunflower	*Helianthus maximiliani*	-	2	12
		Seaside arrowgrass	*Triglochin maritima*	-	2	12
		Veiny pea	*Lathyrus venosus*	-	-	12
		Kalm's lobelia	*Lobelia kalmii*	-	-	12
		Riddell's goldenrod	*Solidago riddellii*	-	-	8
		Common false Solomon's seal	*Smilacina racemosa*	-	-	8
		Obtuse bedstraw	*Galium obtusum*	-	-	8

*American, Purple-leaved, or Northern willow-herb (*Epilobium ciliatum, E. coloratum,* or *E. glandulosum*)
**Sunflowers (*Helianthus giganteus*, *H. grosseserratus*, or *H. nuttallii*)
***Stemless blue violets (*Viola nephrophylla* and similar *Viola* spp.)

Table WM-1. *continued on next page*

wetland settings, such as the margins of marshes, that rarely experience prolonged dry periods. Because of frequent fire in the PPA Province, shrub cover is typically low or is limited to the most protected sites.

WMp communities are confined to the TAP and PPA provinces and appear to be associated with shallow basins that do not receive large quantities of surface runoff from the surrounding area and are at least somewhat open to down-gradient drainage. The water table remains close to the surface for much of the growing season but drops somewhat by late summer most years. Shrubs are scarce or absent because of frequent fire.

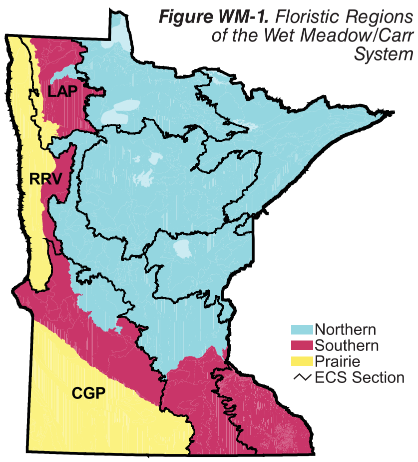


Figure WM-1. *Floristic Regions of the Wet Meadow/Carr System*

Species that help to differentiate the WMn, WMs, and WMp regions are presented in Table WM-1. WMn communities are more likely to have species characteristic of FP and OP communities and species with a distinctly northern geographic distribution. WMs communities can have species of Wet Forest (WF) as well as Wetland Prairie (WP)

Table WM-1. *Plant species useful for differentiating the Northern, Southern, and Prairie Floristic Regions of the Wet Meadow/Carr System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

Region	Group	Common Name	Scientific Name	frequency (%) WMn	WMs	WMp
Northern Floristic Region	Tree	Paper birch	*Betula papyrifera*	8	-	-
		Red maple	*Acer rubrum*	5	-	-
	Shrub	Speckled alder	*Alnus incana*	24	-	-
		Red raspberry	*Rubus idaeus*	13	3	-
		Bog willow	*Salix pedicellaris*	9	-	-
		Balsam willow	*Salix pyrifolia*	7	-	-
		Leatherleaf	*Chamaedaphne calyculata*	7	-	-
		Steeplebush	*Spiraea tomentosa*	5	-	-
	Forb	Marsh skullcap	*Scutellaria galericulata*	53	26	-
		Three-cleft & Small bedstraw	*Galium trifidum & G. tinctorium*	46	9	-
		Bulb-bearing water hemlock	*Cicuta bulbifera*	46	13	-
		Marsh cinquefoil	*Potentilla palustris*	39	3	-
		Arrow-leaved tearthumb	*Polygonum sagittatum*	27	3	-
		Marsh St. John's wort	*Triadenum fraseri*	23	-	-
		Sensitive fern	*Onoclea sensibilis*	20	11	-
		Long-leaved chickweed	*Stellaria longifolia*	13	4	-
		White violets*	*Viola blanda or V. macloskeyi*	13	-	-
		Mad dog skullcap	*Scutellaria lateriflora*	13	-	-
		Rough cinquefoil	*Potentilla norvegica*	11	2	-
		Yellow loosestrife	*Lysimachia terrestris*	10	-	-
		Wild calla	*Calla palustris*	10	-	-
		Dotted smartweed	*Polygonum punctatum*	7	-	-
		Intermediate bladderwort	*Utricularia intermedia*	5	-	-
		Sweet-scented bedstraw	*Galium triflorum*	5	-	-

*Big-leaf white or Northern white violet

Table WM-1. *continued on next page*

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; in the PPA and TAP provinces, MH communities have combined cover of tree species in the canopy and understory that is typically 120% to 130%. 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 characteristic 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 low stores of the enzymes and pigments used in photosynthesis, combined with certain physical modifications to leaf tissue—such as clear cuticles—that allow for rapid photosynthesis as flecks of sunlight briefly pass over them. These adaptations minimize the energetic costs of maintaining the large stores of enzymes, high amounts of chlorophyll, and protective tissues typical of plants growing in full sunlight. Another adaptive strategy to low light levels 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.

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 plant hormones 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. Canopy trees in MH communities often exhibit symptoms of plastic response to changes in light during the life of the tree, such as boles that lean toward light gaps. 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 in deep shade in the shrub layer for 20 to 30 years 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 communities is concentrated in the soil surface and rich humus layer. Many herbaceous plants are rooted almost entirely in humus, and many woody plants have an abundance of roots near the surface. Sugar maple, for example, typically forms secondary roots or risers that grow upward from deeper roots and spread prolifically through the humus layer.

Landscape Setting, Soils, and History
The distribution of MH communities in the PPA and TAP provinces is strongly influenced by landscape features that provide protection from wildfires. Historically, in the prairie-dominated landscapes of these provinces the fire-sensitive trees characteristic of MH communities existed only in areas in the shadow of highly effective firebreaks. Sampling of remnants of MH communities and reconstructions of historic vegetation patterns from Public Land Survey (PLS) data indicate that MH communities were present in the provinces almost exclusively near water bodies and usually separated from nearby prairies by significant changes in topography. The public land surveyors' written descriptions often provide good documentation of the settings in which MH communities occurred in the prairie regions of Minnesota.

According to PLS records, MH communities commonly occurred within deeply incised river and stream valleys. The surveyors' notes typically place trees characteristic of MH communities, such as elm, basswood, and maple, on valley bottoms, as in the following description[1]:

> *The timber on the uplands is black and burr oak, on the bottoms we find elm, lind* [basswood]*, and maple.* [Township 108N, Range 27W, along the Minnesota and Blue Earth rivers in Nicollet and Blue Earth counties]

In some instances, MH communities were present on upland sites that were protected from prairie fire because they were surrounded by river valleys. This happened most often where tributaries parallel a larger river and then enter the main river valley at a sharp angle, as in the acute interfluve between the Snake and Red rivers in Marshall County:

> *There is a body of Oak, Elm, Ash and Basswood timber from 1/2 a mile to 2 miles in breadth in this Township East of Red River.* [Township 156N, Range 50W, Marshall County]

The most extensive MH communities in the PPA and TAP provinces occurred along a broad band of rugged moraines that parallel the eastern border of the PPA Province in Otter Tail, Grant, Douglas, Pope, Kandiyohi, and Meeker counties. These moraines were formed by stagnant ice sheets that created a rugged landscape of collapsed outwash, kames, drainage channels, and ice-walled lakes. The rugged terrain and numerous lakes impeded the spread of wildfire, enabling development of patches of MH communities in a matrix with woodlands, wetlands, and prairies:

> *This township has a large proportion of wood land stretching between the numerous lakes, sometimes in a dense forest growth, at others a sparse growth of scrubby timber interspersed with aspen thickets and brushy prairie.* [Township 119N, Range 32W, Meeker County]

Outside of this band of moraines, MH communities were also present on upland sites in association with lakes and large wetlands but were usually limited to the immediate shoreline (often with larger stands in the "fire shadow" downwind from the lake or wetland), to islands, to peninsulas, or to ridges between lakes or wetlands:

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[1]The trees most commonly mentioned in river valley bottoms by surveyors were elm, ash, and basswood, which could have been present either on regularly flooded sites, where they would have been components of FF communities, or on sites that did not flood, where they would have been present in MH communities. Species such as silver maple and cottonwood, which would clearly indicate the presence of FF communities, or sugar maple and ironwood, which are largely restricted to MH communities, were mentioned only infrequently by the surveyors or were combined in lists, making it difficult to determine whether these valley bottoms historically had distinct occurrences of FF and MH communities. It is possible that the contemporary presence of MH communities on these river bottoms is related to changes in river flood regimes following agricultural development in the landscape.

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) form dense tussocks that elevate rootlets above the water surface. These tussock-forming species 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, these species lack adaptations to prevent desiccation and do not persist during periods of low water.

Because minerals and nutrients are plentiful in WM communities, growth of vegetation is typically luxuriant. The characteristic sedges are wide-leaved, strongly rhizomatous species, such as lake sedge *(Carex lacustris)*, tussock sedge *(C. stricta)*, slough sedge *(C. atherodes)*, and beaked sedge *(C. utriculata)*, that can form dense monotypic stands and produce dense thatch. In many wet meadows, regular oscillations in water level and thick thatch limit plant diversity by reducing habitats available for forb species. 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.

The exotic species reed canary grass (*Phalaris arundinacea*), an aggressive invader of fertile wetland habitats, is problematic at many sites where WM communities occur. Invasion by reed canary grass is promoted by disturbance and altering of water-table levels. Reed canary grass spreads rapidly by rhizomes, begins growing very early in spring, is tolerant of a wide range of water levels as well as dry condidtions, and benefits from nitrates in agricultural runoff. Consequently, once established at a site, it often rapidly displaces native species from WM communities.

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 Southern Floristic (WMs) Region, and the Prairie Floristic (WMp) Region (Fig. WM-1). All three floristic regions are represented in the PPA and TAP provinces.

WMn communities are most common in the Eastern Broadleaf Forest (EBF) and Laurentian Mixed Forest provinces, both of which are characterized by regular, relatively high amounts of precipitation and low evapotranspiration rates. WMn communities occur throughout the TAP Province but are uncommon in the PPA Province, reaching the western limit of their range in the eastern part of the province. In the TAP Province, WMn communities often have shrub cover > 25% and are often associated with fen communities of the Open Rich Peatland (OP) System. In the PPA Province, WMn communities typically have shrub cover < 5% and appear to be associated with marshes and open-water basins where water levels are relatively stable.

WMs communities are present in both the EBF and TAP provinces but are most common in the PPA Province, where precipitation is sporadic and evapotranspiration rates are relatively high. Here, they are associated with areas of groundwater seepage or other

WM Wet Meadow/Carr System

photo by D.S. Wovcha, MN DNR

General Description

Wet Meadow/Carr (WM) communities are graminoid- or shrub-dominated wetlands that are subjected to moderate inundation by standing water 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)*, bluejoint *(Calamagrostis canadensis*), and Sartwell's sedge *(Carex sartwellii).* Shrubs, especially willows *(Salix* spp.) and dogwoods *(Cornus* spp.), are often dominant on sites that are not inundated by water throughout the summer and not exposed frequently to fire. Peak water levels are high and persistent enough to prevent trees 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, especially in riverine settings. Although organic matter can accumulate over time in WM communities, they are not "peat-accumulating" communities, because periodic oxidation from drought and fire limits net peat accumulation to depths less than 12in (30cm). WM communities can be present on deeper peat formed previously on the site by a peat-producing community—such as an Open Rich Peatland—that was flooded by beaver or human 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 occur throughout the Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces in wetland basins, along streams and drainageways, on seepage slopes, and as semi-floating mats along sheltered lake shorelines. Native wet meadows have become uncommon across much of the PPA and TAP provinces. Most of the loss has been from drainage and cultivation of wetland basins, but even meadows that have been spared are commonly dominated by non-native species such as reed canary grass *(Phalaris arundinacea)*, which displace native species in meadows subjected to heavy grazing or inflows of nutrient-rich, silt-laden runoff from agricultural land.

…the timber of the Great Oasis situated between a lake by that name on the South and Bear Lake on the North form a good inducement for settlers…the timber of the great Oasis is a good growth composed principally of Ash, Oak, Elm & Lind. [Township 107N, Range 42W, Murray County]

Statewide, MH communities are strongly correlated with well-drained soils that have clayey, compacted, or cemented soil horizons (semipermeable horizons) about 20–30in (50–75cm) below the ground surface. These layers impede 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 ground-layer plants. This helps to deter spring fires and allows MH communities to persist in matrices of vegetation more prone to burning. These soils, particularly those with clayey subsoil horizons, form under deciduous forests. Therefore, if FD communities with deciduous tree canopies become established on a site, they can promote development of moisture-retaining soil horizons that in turn promote development of MH communities on the site. Once established, MH communities tend to persist on such sites and further accentuate changes in the soil. The relationship of MH communities to soils with semipermeable horizons is obvious in northeastern and eastern Minnesota but is less clear in the prairie regions of the state. In the LMF Province, nearly 80% of the vegetation sample plots of MH communities used in developing this classification are present on soils with semipermeable horizons. In the EBF Province, only 60% of samples of MH communities occur on soils with semipermeable layers. In the PPA and TAP provinces, just 30% of samples of MH communities occur on such soils.

In spite of the comparatively low correlation of MH communities with soils with clayey horizons, it is obvious that many MH communities in the PPA Province are associated with landscape-scale zones where such soils occur, including linear bands within the stagnation moraines running from Otter Tail to Meeker counties, and shoulder slopes along major rivers that are dissected by numerous tributaries, especially along the Minnesota River from Montevideo to Mankato. In these areas, the clayey soils are intermixed with areas of "prairie" soils that have slight accumulations of clay in lower horizons, and with soils on slopes too steep to develop diagnostic horizons. It is most likely that water bodies and rugged or dissected terrain afforded protection from fire and allowed episodic existence of MH communities in these areas, initiating modest development of "forest" soils with clayey subsoil horizons.

There are few reconstructions of post-glacial vegetation history available for sites in the PPA and TAP provinces. This is because cyclic drought has caused repeated drawdown and refilling of most lakes, eliminating continuous records of deposition of fossil pollen and other plant material in lake sediments. As a result, the history of development of MH communities in the provinces is not thoroughly documented. In addition, the two tree species whose pollen enables differentiation of MH communities from other forest communities—sugar maple and basswood—produce much less pollen than tree and plant species present in FD communities and prairies, including oak, aspen, grasses, and sage. This makes it difficult to reliably determine from available pollen analyses the historic abundance of MH communities in the region relative to FD communities or prairies. Even so, sugar maple and basswood pollen do appear in sediment cores taken from several lakes in the eastern and northern Great Plains region, enabling speculation about the history of development of MH communities in the PPA and TAP provinces.

Sediment cores from lakes in parts of Iowa and South Dakota adjacent to the PPA Province in Minnesota indicate that spruce woodland began to form following melting of the glaciers about 14,000 to 12,000 years ago. Deciduous trees began invading this spruce woodland during the early-Holocene Epoch, about 10,000 years ago. Elms seem to have been the primary invader, along with ashes, oaks, and birch. Ironwood and hazelnut were probably present as well. This band of deciduous forest, perhaps mixed with some spruce, presumably extended from the PPA Province westward to the Black Hills. In addition, at this time there was low, but consistent, presence of sugar maple and basswood pollen in the sediment cores. Therefore, all of the tree species typical of MH communities were present in the PPA Province and probably at their greatest abundance during the early-Holocene Epoch. Beginning about 8,000 years ago and lasting until about 2,800 years ago, the central Great Plains region experienced severe drought, and forests were replaced by prairie. During this period, it is likely that trees were present in the valleys of persistent rivers and streams in the PPA Province but were not present around lakes. Fire-sensitive species like sugar maple and basswood were probably eliminated from the province. At about 4,000 years ago in Minnesota, the climate became more favorable for trees. Across the state, pollen diagrams record shifts at this time toward more mesic plant communities, including the formation of MH communities in the EBF Province. By about 3,000 years ago, pollen diagrams from the PPA Province once again show the consistent presence of basswood pollen and at least some maple pollen; these species then remain in the pollen diagrams until the present. Thus, MH communities could have developed in the province as early as 3,000 years ago along river bottoms and around more permanent lakes.

Examination of sediment cores from parts of Manitoba adjacent to the TAP Province in Minnesota indicate—as in the PPA Province—the first vegetation to develop at the end of glaciation was dominated by spruce with some birch and aspen. Presumably areas of lake-washed till on the recently exposed bed of Glacial Lake Agassiz supported spruce forest, whereas sandy lake sediments supported tundra or open spruce woodland. In contrast to the vegetational history of the PPA Province, during the early-Holocene Epoch (about 10,000 years ago) the spruce-dominated communities in the TAP Province were directly replaced by prairie. In addition, wetlands were present in the province on poorly drained lake clays and included peat-forming species such as sedges and grasses. During the period of about 10,000 to 8,000 years ago, such wetlands were probably restricted to the easternmost end of the Lake Agassiz basin in Minnesota and the central part of the basin in Manitoba. At about 3,500 years ago—around the time that basswood and sugar maple reappeared in the PPA Province—the vegetation of the central Lake Agassiz basin changed in response to increasingly wetter and probably cooler conditions, with development of spruce and tamarack swamps, establishment of mesic forests of spruce, birch, and aspen on lake-washed till, and establishment of fire-dependent jack pine forests on sandy lacustrine deposits. It appears that the critical event promoting development of forests was the appearance and eventual spread of wetlands across the landscape, which isolated and protected patches of uplands from prairie fires. Because the spread of wetlands occurred from east to west across the province, the eastern part of the province may have had forests for as long as 3,500 years, while forests along the western border of the province are probably much younger.

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 PPA and TAP provinces: the Northern Floristic (MHn) Region, the Northwestern Floristic (MHw) Region, and the Southern Floristic (MHs) Region. MHn and MHw communities are rare in the two provinces, being limited to wet-mesic habitats in the TAP Province. MHs communities are somewhat more common, but have been documented only in the PPA Province, especially along its eastern border with the EBF Province.

In general, MHn and MHw communities are composed of plant species with northern distributions in Minnesota, while MHs communities are composed of species with eastern and southern distributions. Species that are diagnostic for MHn and MHw communities (see ***Plant Indicators of MHn, MHw, and MHs Communities*** below) have ranges extending into the Boreal Forest region of Canada and into the northern Great

discharge points and have characteristic calciphilic plants such as Kalm's lobelia, marsh arrowgrass, and grass-of-Parnassus (*Parnassia* spp.). Prairie Rich Fens (OPp91) occur in glacial drainageways that are influenced by lateral movement of groundwater and lack the most strongly calciphilic species present in OPp93.

Succession

OP communities can develop from WM communities if conditions become suitable for sufficient accumulation of organic matter to form peat, minimizing contact of roots with the underlying mineral soil. 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; the presence of minerotrophic *Sphagnum* species causes changes to the peatland environment that can lead to invasion of the site by acidic *Sphagnum* species and eventual conversion of the OP community to an Acid Peatland (AP) community. In the TAP and PPA provinces, however, predominance of calcareous till and marginal climatic conditions limit the development of acidic *Sphagnum*; as a result, succession of OP communities to AP communities is uncommon in the TAP Province and does not occur in the PPA Province.

photo by R.P. Dana MN DNR

Norman County, MN

photo by Fred Harris, MN DNR

Yellow Medicine County, MN

species common in the more drought- and fire-prone landscapes of western Minnesota, including grass-leaved goldenrod *(Euthamia graminifolia)*, Buxbaum's sedge *(Carex buxbaumii)*, and narrow reedgrass (Table OP-2).

Table OP-2 *Plants useful for differentiating the Prairie from the Northern Floristic Region of the Open Rich Peatland System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

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

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

Plant Community Classes in the PPA and TAP Provinces

Three OP plant community classes are present in the PPA and TAP provinces: Northern Rich Fen (Basin) (OPn92), Prairie Extremely Rich Fen (OPp93), and Prairie Rich Fen (OPp91). OPn92 occurs only in the PPA Province, while OPp93 and OPp91 occur in both the PPA and TAP provinces. OPn92 is characterized by level or slightly concave peat surfaces and is restricted to rolling morainic landscapes in the northeastern part of the CGP in the PPA Province, where irregular topography allows the development of poorly drained, isolated depressions filled with peat or supporting floating peaty mats. Prairie Extremely Rich Fens (OPp93) develop at highly calcareous groundwater

Plains. They are widespread in the NSU and MOP of the LMF Province and reach their western range limits in wet-mesic MH communities in the TAP Province. Plant species diagnostic for MHs communities have ranges extending southeast from Minnesota into the Eastern Broadleaf Forest region of the United States and also into the central Great Plains. In Minnesota, these species are widespread in the EBF Province and in the MDL and WSU of the LMF Province, reaching their western range limits in riparian settings in the PPA Province.

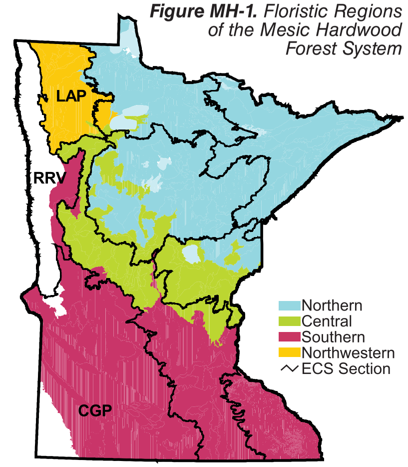


Figure MH-1. *Floristic Regions of the Mesic Hardwood Forest System*

Regional or continental patterns of distribution of mesic forest species are accentuated in western Minnesota because of the sharp contrast between the Glacial Lake Agassiz basin, which supports MHn and MHw communities, and the glaciated plains, which support MHs communities. These regions differ markedly in physiography, paleohistory, climate, glacial deposits, soil genesis, and major geologic processes (especially paludification versus dissection and drainage of the landscape), all of which influence differences in floristic composition. One of the most direct influences, however, appears to be the other types of vegetation adjacent to MH communities in these regions. MHn communities tend to occur next to conifer swamps and therefore are likely to have conifers such as spruce and fir as components, as well as understory species often associated with conifers. In comparison, MHw communities occur beyond the western extent of conifers in Minnesota, so lack conifers, but are often present in river valleys and beach-ridge complexes near open wet communities such as wet prairies and wet brush-prairies, with which they share species. MHs communities tend to occur along rivers with alluvial bottoms and around lakes with alluvial terraces, and for this reason share several species with FF communities.

Plant Indicators of MHn, MHw, and MHs Communities

Plant species with high fidelity for MHn relative to MHw and MHs communities are listed in Table MH-1. In general, nearly all of the species that differentiate the MHn Region are adapted to conifer-forest habitats. The MHn communities present in the TAP Province almost always have white spruce and balsam fir in the canopy and often in the understory. Presumably all of the other species diagnostic for MHn communities are present because of the effect that white spruce and balsam fir have on understory conditions, including sufficient acidification of soils and reduction in soil nutrients to favor plants with evergreen or overwintering leaves over species that lose and replace their leaves each year. Species with evergreen or overwintering leaves that are diagnostic for MHn communities include twinflower *(Linnaea borealis)*, naked miterwort *(Mitella nuda)*, bunchberry *(Cornus canadensis)*, spinulose shield fern or glandular wood fern *(Dryopteris carthusiana* or *D. intermedia)*, and long-stalked sedge *(Carex pedunculata)*. Most of the species diagnostic for MHn communities are also capable of growing on the peat or muck typical of FP or WF communities, including speckled alder *(Alnus incana)*, yellow lady's slipper *(Cypripedium calceolus)*, bunchberry, and twinflower, which are characteristic of FP communities; and balsam fir, naked miterwort, palmate sweet coltsfoot *(Petasites frigidus)*, swamp red currant *(Ribes triste)*, woodland horsetail *(Equisetum sylvaticum)*, graceful sedge *(Carex gracillima)*, drooping woodreed *(Cinna latifolia)*, and common marsh marigold *(Caltha palustris)*, which are characteristic of WF communities.

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

Region	Affinity	Group	Common Name	Scientific Name	MHn	MHs	MHw
Northern Floristic Region	Conifer Forest Affinity	Evergreen or Over-Wintering Leaves	Balsam fir (U)	*Abies balsamea*	72	-	-
			Naked miterwort	*Mitella nuda*	54	-	-
			Bunchberry	*Cornus canadensis*	32	-	-
			Spinulose shield fern	*Dryopteris carthusiana*	27	-	-
			White spruce (U)	*Thelypteris phegopteris*	16	-	-
			Twinflower	*Linnaea borealis*	10	-	-
			Crested fern	*Dryopteris cristata*	10	-	-
		Other	Mountain maple	*Acer spicatum*	67	-	-
			Paper birch (U)	*Betula papyrifera*	62	2	-
			Prickly or Smooth wild rose	*Rosa acicularis* or *R. blanda*	40	-	16
			Bush honeysuckle	*Diervilla lonicera*	35	2	-
			Starflower	*Trientalis borealis*	32	-	-
			Dwarf alder	*Rhamnus alnifolia*	24	-	-
			Large-leaved aster	*Aster macrophyllus*	21	1	-
			Bluebead lily	*Clintonia borealis*	18	-	-
			American vetch	*Vicia americana*	13	-	-
			Fly honeysuckle	*Lonicera canadensis*	10	1	-
			Speckled alder	*Alnus incana*	10	-	-
			Yellow lady's slipper	*Cypripedium calceolus*	10	3	-
	Wet Forest Affinity	*	Long-stalked sedge	*Carex pedunculata*	45	18	-
		Other	Palmate sweet coltsfoot	*Petasites frigidus*	51	-	-
			Swamp red currant	*Ribes triste*	21	-	-
			Woodland horsetail	*Equisetum sylvaticum*	18	-	-
			Graceful sedge	*Carex gracillima*	13	1	-
			Drooping woodreed	*Cinna latifolia*	13	-	-
			Fringed loosestrife	*Lysimachia ciliata*	10	-	-
			Common marsh marigold	*Caltha palustris*	10	-	

frequency (%)

*Evergreen or Over-Wintering Leaves (U) = understory tree

Most of the species with high fidelity for MHs versus MHn and MHw communities (Table MH-2) are common in both MH and FF communities. These species have affinity for nutrient-rich habitats and are among the most nutrient-demanding plant species in Minnesota. This is in strong contrast with the species that differentiate MHn communities, which can grow in nutrient poor and rather acidic conditions. The species characteristic of MHs communities are also among the most shade-tolerant species in Minnesota, in strong contrast with the many heliophytic species present in MHw communities. Herbaceous plants that develop early in the growing season before canopy leaves develop are a hallmark of the MH System; several of these species are diagnostic for MHs relative to MHn and MHw communities, including false rue anemone *(Enemion biternatum)*, jack-in-the-pulpit *(Arisaema triphyllum)*, sharp-lobed hepatica *(Anemone acutiloba)*, white trout lily *(Erythronium albidum)*, cut-leaved toothwort *(Cardamine concatenata)*, showy orchis *(Orchis spectabilis)*, Dutchman's breeches *(Dicentra cucullaria)*, and wild leek *(Allium tricoccum)*. The presence of these early-developing herbaceous plants in MHs communities is strong evidence that the river and lake terraces where they occur are not flooded or ponded for long in the spring.

MHw communities historically occurred in landscapes in which they were surrounded by open, nonforest vegetation, and nearly all of the species that distinguish MHw communities from MHn and MHs communities (Table MH-3) are also present in open habitats such as disturbed FD communities and brushy Wetland Prairie and Upland Prairie communities. These species include spreading dogbane *(Apocynum androsaemifolium)*, veiny meadow-rue *(Thalictrum venulosum)*, and tall thimbleweed *(Anemone virginiana)*, which are common in burned and brushy copses of balsam poplar

during periods of drought. Differences between the two regions in climate and fire regime are reflected in differences in species composition between the regions. OPn communities are characterized by species that are relatively intolerant of drought, including ericaceous shrubs such as leatherleaf *(Chamaedaphne calyculata)*, bog rosemary *(Andromeda glaucophylla)*, and small cranberry *(Vaccinium oxycoccos)*; insectivorous plants such as pitcher plant *(Sarracenia purpurea)*, sundews *(Drosera* spp.), and bladderworts *(Utricularia* spp.); and ferns and fern allies such as crested fern *(Dryopteris cristata)* and water horsetail *(Equisetum fluviatile)* (Table OP-1). OPp communities, in comparison, have

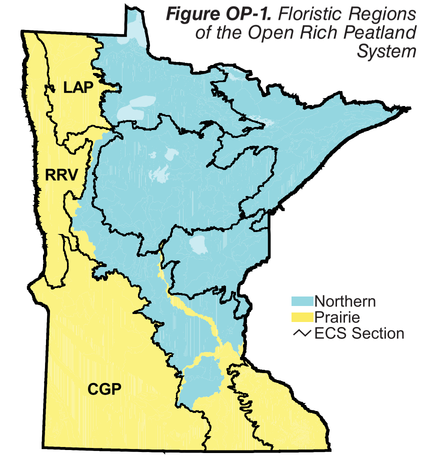


Figure OP-1. *Floristic Regions of the Open Rich Peatland System*

Table OP-1 *Plants useful for differentiating the Northern from the Prairie Floristic Region of the Open Rich Peatland System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

Region	Layer	Common Name	Scientific Name	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

frequency (%)

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

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 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. Even when WM communities are present on relatively deep peat, they are distinguishable from OP communities by their species composition and vegetation: OP communities are usually dominated by fine-leaved graminoids, mosses, or ericaceous shrubs such as large cranberry *(Vaccinium macrocarpon),* while WM communities are dominated by broad-leaved graminoids and lack significant moss cover and ericaceous shrubs.

Plant Adaptations

The plants characteristic of OP communities are adapted to full sunlight (because of absence of significant shade from trees and shrubs), sustained water levels, low nutrient levels, and high mineral levels. The lack of shade from trees and tall shrubs favors dominance in the ground layer by shade-intolerant species, especially graminoids; OP communities tend to have only sparse cover of forbs. 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 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 < 1/4 inch [6mm] wide), with species such as fen wiregrass sedge *(Carex lasiocarpa),* sterile sedge *(C. sterilis),* and narrow reedgrass *(Calamagrostis stricta)* most common. 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 Kalm's lobelia *(Lobelia kalmii),* marsh arrowgrass *(Triglochin palustris)*, and grass-of-Parnassus *(Parnassia* spp.), along with the rare species twig rush *(Cladium mariscoides)*, sterile sedge *(Carex sterilis)*, and hair-like beak rush *(Rhynchospora capillacea)*.

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 PPA Province, while only communities from the OPp Region are present in the TAP Province. The OPn Region is characterized by a cool, moist climate well suited for peatland development; communities in the OPp Region are at the western climatic limit of peatland formation in Minnesota and are subject to fires and water stress

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

		Common Name	Scientific Name	frequency (%) MHn	MHs	MHw
Southern Floristic Region	Floodplain Forest Affinity	Virginia waterleaf	*Hydrophyllum virginianum*	-	81	-
		Cleavers	*Galium aparine*	-	58	-
		Prickly ash	*Zanthoxylum americanum*	5	52	16
		Honewort	*Cryptotaenia canadensis*	2	50	16
		Hackberry (U)	*Celtis occidentalis*	-	46	-
		White avens	*Geum canadense*	-	37	-
		Canada moonseed	*Menispermum canadense*	-	29	-
		Missouri gooseberry	*Ribes missouriense*	-	29	-
		Blue phlox	*Phlox divaricata*	-	28	-
		Bland sedge	*Carex blanda*	-	24	-
		Sprengel's sedge	*Carex sprengelii*	-	23	-
		Gregarious black snakeroot	*Sanicula gregaria*	-	22	-
		False rue anemone	*Enemion biternatum*	-	12	-
	Mesic Hardwood Forest Affinity	Bitternut hickory (U)	*Carya cordiformis*	-	54	-
		Jack-in-the-pulpit	*Arisaema triphyllum*	8	54	-
		Wild leek	*Allium tricoccum*	-	47	-
		Red elm (U)	*Ulmus rubra*	-	40	-
		Stemless blue violets	*Viola* spp.*	-	33	-
		Red-berried elder	*Sambucus racemosa*	5	27	-
		Dutchman's breeches	*Dicentra cucullaria*	-	24	-
		Sharp-lobed hepatica	*Anemone acutiloba*	-	24	-
		Pointed-leaved tick trefoil	*Desmodium glutinosum*	2	21	-
		Black cherry (U)	*Prunus serotina*	-	19	-
		Heart-leaved aster	*Aster cordifolius*	-	15	-
		Cut-leaved toothwort	*Cardamine concatenata*	-	14	-
		White trout lily	*Erythronium albidum*	-	13	-
		Bearded shorthusk	*Brachyelytrum erectum*	-	12	-
		Showy orchis	*Orchis spectabilis*	-	11	-

(U) = understory tree   **Viola sororia* and similar *Viola* spp.

and gray dogwood *(Cornus racemosa)* that are often adjacent to MHw communities; and tall meadow-rue *(Thalictrum dasycarpum)*, Canada anemone *(Anemone canadensis)*, golden alexanders *(Zizia aurea)*, heart-leaved alexanders *(Z. aptera)*, and false gromwell *(Onosmodium molle)*, which are common in prairies.

Disturbance Regimes of MHn, MHw, and MHs Communities

MH communities across Minnesota historically had low rates of catastrophic disturbance from fires and windstorms. Along with WF communities, they have the lowest rates of natural disturbance of forest communities in the state. For the MH communities represented in the PPA and TAP provinces, rotation periods for catastrophic fire and wind were typically in excess of 430 and 360 years, respectively, and greater than 1,000 years in some instances (Table MH-4).[2] Disturbances that result in the partial loss of canopy trees, such as light surface fires and moderate windthrow, were far more frequent, with rotations ranging from 12 to 160 years. MHn communities had the lowest rates of partial canopy disturbance from surface fires and windthrow, with a rotation period of 160 years. For MHn communities, fire appears to have been more likely than windthrow as a source of moderate disturbance. MHs communities were somewhat more disturbed, with rotation periods for partial canopy disturbances of 35 to160 years. MHw communities had the highest rates of moderate disturbance, with a rotation period of just 12 years. For MHs and MHw communities, PLS notes contain more explicit references to windthrow than fire, suggesting that wind played a more important role than surface fires in regenerating these forests. Climatic data for the past 50 years are consistent with the notion that MHs

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

Region	Group	Common Name	Scientific Name	frequency (%) MHn	MHs	MHw
Northwestern Floristic Region	Fire-Dependent Forest Affinity	Spreading dogbane	*Apocynum androsaemifolium*	10	7	83
		Balsam popular (U)	*Populus balsamifera*	27	-	66
		Gray dogwood	*Cornus racemosa*	16	11	66
		Veiny meadow-rue	*Thalictrum venulosum*	2	-	50
		Tall thimbleweed	*Anemone virginiana*	-	1	33
		Virgin's bower	*Clematis virginiana*	-	1	16
		Stickseed	*Hackelia* spp.	-	5	16
		Interrupted wild rye	*Elymus diversiglumis*	-	-	16
		Canada plum (U)	*Prunus nigra*	-	-	16
		Sand or dog violet	*Viola adunca* or *V. conspersa*	5	-	16
	Prairie Affinity	Tall meadow-rue	*Thalictrum dasycarpum*	5	4	33
		Canada anemone	*Anemone canadensis*	5	-	16
		Pussy willow	*Salix discolor*	5	-	16
		Golden alexanders	*Zizia aurea*	-	5	16
		False gromwell	*Onosmodium molle*	-	-	16
		Heart-leaved alexanders	*Zizia aptera*	-	-	16
	Other	Flat-topped aster	*Aster umbellatus*	8	-	33
		Nodding fescue	*Festuca subverticillata*	-	12	33
		Big-leaved avens	*Geum macrophyllum*	-	-	16
		Mexican muhly grass	*Muhlenbergia mexicana*	-	-	16
		Northern black currant	*Ribes hudsonianum*	-	-	16
		Woodland millet grass	*Milium effusum*	2	-	16
		Common hops	*Humulus lupulus*	-	1	16
		Indian pipe	*Monotropa uniflora*	-	5	16

(U) = understory tree

and MHw communities are more frequently damaged by wind (probably exacerbated by ice-laden trees) than are deciduous forests in the MHn Region. The data report about four times as many damaging windstorms per acre for the MHs and MHw regions in comparison with the MHn Region.

[2] The rotation periods for catastrophic and moderate disturbances for the MH communities in the PPA and TAP provinces are estimated from PLS notes throughout the whole range of each community class represented in the two provinces. MHn and MHs communities are far more extensive to the east in Minnesota, and the proportion of the land survey records used in estimating disturbance frequencies that were within the PPA and TAP provinces is low. In these provinces, MH communities were historically present as small, isolated patches of forest embedded in landscapes that burned with regularity and experienced high wind speeds. It is quite likely that isolated patches of MH communities in the prairie regions were disturbed by fire and wind more frequently than the estimates in Table MH-4. Modern forestry data and early ecological studies in the Big Woods region of Minnesota indicate that trees that have distributions stretching across Minnesota are much shorter (about half as tall) in the PPA and TAP provinces than in eastern Minnesota. This reduction in height may be an adaptation to windthrow; frequent disturbance from wind or fire can cause some trees like bur oak, quaking aspen, balsam poplar, and perhaps basswood to invest more resources in roots and less in tree boles. It is possible that the short stature of trees in MH communities in western Minnesota is a consequence of more frequent disturbance than that indicated in Table MH-4; the reduction in tree height may also be related to the drier climate in the prairie region.

OP Open Rich Peatland System

photo by R.P. Dana MN DNR

Kittson 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 willows (especially sage-leaved willow *[Salix candida]* and bog willow *[S. pedicellaris]*), bog birch *(Betula pumila)*, or shrubby cinquefoil *(Potentilla fruticosa)*. Moss cover is variable in OP communities, but brown mosses may be abundant, particularly in the Tallgrass Aspen Parklands (TAP) Province. OP communities are widespread in the Laurentian Mixed Forest (LMF) 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 are also common in the TAP Province, which also has a cool climate and poorly drained lake plains, although amounts of precipitation are lower than in the LMF Province. In the Prairie Parkland (PPA) Province, where peatlands are at the southern and western limits of their range, OP communities are generally confined to floating mats in small watersheds or to settings where groundwater discharge is sufficient to offset higher rates of evapotranspiration caused by warmer temperatures; the relatively cold temperatures of groundwater also inhibit decomposition of plant litter and promote peat accumulation in these settings.

Peat Characteristics and Hydrology

(For a discussion of general peatland formation in Minnesota, see Peatland Formation under the Forested Rich Peatland System on page PPA/TAP-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. In the TAP and PPA provinces, the groundwater percolates through calcareous till and lacustrine deposits and therefore has high concentrations of minerals such as calcium. High rates of evaporation in these two provinces further concentrate minerals at the peat surface. Although OP communities in the TAP and PPA provinces may have relatively high concentrations of calcium or other minerals—especially in comparison with OP communities farther east in Minnesota—OP communities as a whole are generally not rich in nutrients, especially nitrogen and phosphorus.

Upland Prairie System

Table UP-1. *Plants useful for differentiating the Northern and Southern Floristic Regions of the Upland Prairie System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

Region	Common name	*Scientific Name*	frequency (%) UPn	frequency (%) UPs
Northern Floristic Region	Glaucous false dandelion	*Agoseris glauca*	24	1
	Tufted hair grass	*Deschampsia cespitosa*	24	-
	Veiny meadow-rue	*Thalictrum venulosum*	14	-
	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
	Aromatic aster	*Aster oblongifolius*	1	21
	Scribner's panic grass	*Panicum oligosanthes*	2	21
	Clammy ground cherry	*Physalis heterophylla*	-	16
	Hoary vervain	*Verbena stricta*	-	16
	Whorled milkweed	*Asclepias verticillata*	-	16
	False boneset	*Kuhnia eupatorioides*	-	13
	Round-headed bush clover	*Lespedeza capitata*	-	12
	Butterflyweed	*Asclepias tuberosa*	-	10

floristic region. None of these species has very high frequency within its respective floristic region. In part this is because the species occur preferentially in either dry or mesic prairie classes rather than in all of the UP classes in the region. In addition, many of the species listed for the UPs Region are not widespread geographically, being restricted to just a part of the region.

Additional data and analysis may support moving the boundary between these two regions 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, geographic variation in the 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 floristic region are greater than the floristic region differences within the dry and mesic classes.

Mesic Hardwood Forest System

Table MH-4. *Historic tree species composition and disturbance regimes in MHn, MHs and MHw 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 + Patchy Windthrow	Catastrophic Windthrow
Northern Floristic Region									
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
Southern Floristic Region						ranges ⟶	1000+	35 -160	360-1000+
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+ yrs	American elm** basswood *(sugar maple)*	--	--	--	--	--	160	>1000
Northwestern Floristic Region									
MHw36	0-95 yrs	**bur oak** *(balmsam poplar)*	>95 yrs	**bur oak** *(quaking aspen)* *(American elm)* *(basswood)* *(green ash)*	--	--	570	12	370

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

* includes red elm ** includes red and rock elm

MN DNR

Lac Qui Parle County, MN

General Description

Floodplain Forest (FF) communities are present on annually or occasionally 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 in the Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces, which are inundated most years during spring runoff, have forests dominated by trees tolerant of prolonged flooding and frequent deposition of sediment. In the CGP Section of the PPA Province, these species include silver maple, green ash, American elm, and cottonwood. Sites such as river or stream terraces that flood less frequently support mixed stands of American elm, basswood, bur oak, green ash, box elder, and, along the eastern margin of the CGP, black ash. In the RRV section of the PPA Province and in the TAP Province, forests on active floodplains and on terraces are similar to their southern counterparts, but silver maple is absent and black ash is limited to the eastern margin of this region. Statewide, the understories of FF communities are characteristically open, with few shrubs or saplings. FF communities in the PPA and TAP provinces, particularly those on higher terraces, are brushier than their counterparts in the Eastern Broadleaf Forest and Laurentian Mixed Forest provinces, primarily from presence of tree seedlings such as American elm, green ash, box elder, and, where these trees extend into the region, black ash and silver maple. Ground-layer cover is highly variable, ranging from areas of bare silt or sand to dense patches of wood nettle *(Laportea canadensis)*, ostrich fern *(Matteuccia struthiopteris*), or clearweed *(Pilea pumila* or *P. fontana)*. Woody vines are important in FF communities in the PPA and TAP provinces, with wild grape (*Vitis riparia*), Virginia creeper *(Parthenocissus* spp.), and Canada moonseed *(Menispermum canadense)* occurring commonly, and greenbrier (*Smilax tamnoides*) and virgin's bower *(Clematis virginiana)* present occasionally. Pools or mucky depressions in old channels are often present on actively flooded sites and support several annual plant species not present in other forested communities in Minnesota. FF communities are associated with streams and rivers throughout the PPA and TAP provinces. In the past, FF communities were extensive along the Minnesota River and lower stretches of its tributaries. They were intermittent along the Red River and smaller streams in general, occurring only in stretches with deposits of alluvium and where the valleys offered sufficient protection from wildfires. FF communities are still common in parts of these watersheds, although

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.

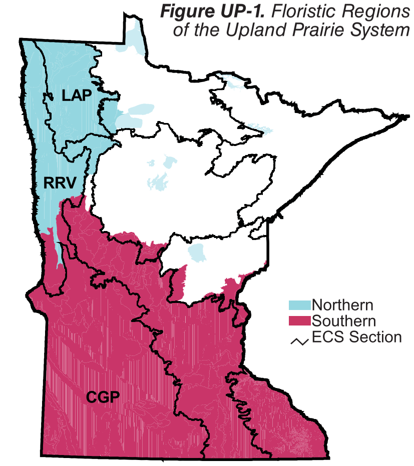
Another obvious adaptation of plants to the fire environment of the UP System is that the perennating organs—buds, tubers, root collars, and other tissue from which new growth originates—are generally deep enough below the soil surface to escape damage in prairie fires. In general, plants of the UP System invest heavily in belowground growth, with biomass below ground in these communities 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 these communities—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 and can replace lost leaf tissue simply by adding new cells to the leaf base to reelongate the blade.

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 is 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, high-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). UP communities in the southern part of the PPA Province (from Traverse County south) are recognized as being in the UPs Region; all UP communities north of this in the PPA Province and in the TAP Province are in the UPn Region. 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 UP-1 lists the most geographically widespread species with high fidelity for either the northern or southern

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



especially important for dispersals of more than a few meters. Mechanical disturbance of the soil by their hooves is critical for the regeneration of many of the short-lived plant species that are part of UP communities. Grazing also stimulates recruitment of new individuals of longer-lived plant species and affects competitive interactions among them. Reduction in the height and density of the grass canopy by grazing allows shorter plant species to persist in UP communities.

Grazing and fire apparently interacted in a way that helped distribute their effects evenly throughout the prairie and provided periods of respite from both disturbances. New plant growth following fire is more palatable and nutritious than older growth, so grazers tended to follow fires. Areas neglected by grazers accumulate greater fuel loads and thus burn more readily than grazed areas. Thus, in the past, a cycle of burning, followed by grazing, abandonment by grazers, and, after fuel buildup, burning again, characterized the UP system. UP communities are readily degraded by repeated season-long grazing; conversely, prolonged absence of grazing, even with periodic fire, probably results in greater dominance by taller species, as described above. Therefore, the movement of herds to new areas seeking the superior forage of recently burned prairie was likely important in maintaining the full component of species in upland prairie communities. It is not known whether the long-term absence of large grazers will result in the disappearance of species from UP communities.

Long-term patterns of variation in soil moisture are the strongest determinant of variation in species composition among plant communities in the UP System. The soil-moisture regimes in UP communities form a continuous gradient from wet-mesic to dry, but species composition responds less continuously. The wet-mesic to dry-mesic segment of the gradient is characterized by changes in the relative abundances of species, while a spike in species replacement marks the transition to the truly dry moisture regime. UP community classes in the mesic segment are dominated by tall grasses and have dense vegetation cover. Classes in the dry part of the moisture gradient are characterized by much greater abundance of midheight grasses and short grasses relative to tall grass species, and have sparser vegetation cover. The soil-moisture regime for a given climate is determined primarily by soil texture and composition, and topographic factors. Soils of the mesic prairie classes are generally finer-textured loams, although coarser-textured soils may support mesic prairies if the water table is shallow enough for plant roots to easily reach at least the capillary fringe during much of the growing season. In the dry prairie classes, soils are coarse textured and highly permeable, or if fine textured, are on steep slopes. The coarse-textured substrates include wind-reworked sands (dunes) and soils formed in glacial lakeshore, outwash, or ice-contact deposits. These soils are typically loamy sands with a substantial gravel fraction. The soils that support communities in the UP System are classified as mollisols (base-rich mineral soils with a deep, humus-rich surface horizon), except the sand substrates of dry communities, in which very high permeability and wind disturbance limit soil profile development.

Plant Adaptations

Adaptations to frequent fire are prominent in the flora of the UP System. Plants with herbaceous life-forms, unlike woody plants, do not lose much investment when fire destroys their aboveground parts, and therefore strongly dominate UP communities. The only generally common woody plants are semi-shrub species that do not form substantial aboveground woody structures. Stems of these plants deteriorate within 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. Bur oak has thickened, corky bark

significant areas have been cleared for cropland, and most sites have been affected by changes in the flooding regime caused by ditching and tiling of wetlands and conversion of native upland vegetation to cropland. FF communities on active floodplains have also experienced increased deposition of sediments from erosion of disturbed uplands.

In general, streams and rivers are 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 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 along the Minnesota and Red rivers. Hackberry, bur oak, American elm, 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 or in the Red River valley.

Most characteristic floodplain trees are capable of rapid growth and are adept colonizers of newly exposed or deposited sediments. Several of the typical tree species in FF communities, including silver maple, box elder, and basswood, can replace damaged stems by sprouting from the base of the stem or trunk. Multiple-stemmed old trees are common in FF communities as a result of resprouting from repeatedly damaged main trunks. In addition, most tree species are extremely resistant to the physical battering caused by spring ice floes. In the prairie regions of Minnesota, damage from large mammals appears to have been common as well. Historical accounts describe herds of bison in river valleys severely trampling small trees and rubbing the bark off larger trees.

Trees limited to upland habitats, such as sugar maple, northern red oak, paper birch, and yellow birch, 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, including silver maple, cottonwood, bur oak, American elm, green ash, black willow, and peach-leaved willow, tend to have seeds that can germinate immediately when shed from the tree or shortly thereafter. Most often, germination occurs early in the growing season after floodwaters have receded, leaving exposed mineral-soil seedbeds. 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 upland versus floodplain 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 peach-leaved willow. 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 floodplain forests statewide. 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.

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. This high presence of annual and biennial species appears related in part to the close association of FF communities with River Shore communities, in which annual and short-lived species are very common. Touch-me-not *(Impatiens* spp.), bur marigold and beggarticks *(Bidens* spp.), cleavers *(Galium aparine)*, clearweed *(Pilea* spp.), kidney-leaved buttercup *(Ranunculus abortivus)*, and stickseed *(Hackelia* spp.) 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. 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, 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.

absence of fire, they rapidly succeed to woodlands. Today, most brush-prairies occur in the Tallgrass Aspen Parklands (TAP) Province of northwestern Minnesota.

Historically, UP communities dominated the landscape of both the Prairie Parkland (PPA) and TAP provinces. Based on records from the Public Land Surveys that preceded intensive settlement, UP communities occupied about 80% of the PPA Province and 60% of the TAP Province. Most of the balance was occupied by Wetland Prairie, Wet Meadow, Open Rich Peatland, and Marsh communities that formed in low positions in the landscape. 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% of the presettlement upland prairie and savanna communities in the PPA Province, and more than 95% in the TAP 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 create a more favorable environment for 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 average fire-return interval in that landscape. Rivers, lakes, and rough topography inhibit the spread of fires. 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 dominance of the PPA and TAP provinces by UP communities before Euro-American settlement reflected these climatic and landscape influences. Both provinces are predominantly low-relief landscapes with relatively few, widely scattered, mostly small lakes. Natural lakes occupy less than 2% of the PPA Province and less than 1% of the TAP Province, compared with almost 5% of the EBF Province and more than 9% of the Laurentian Mixed Forest (LMF) Province. Limited areas of sharper relief, typically with a greater density of lakes as well, do occur in the PPA Province, but because they are surrounded by more level, fire-promoting topography, fires historically occurred within them frequently enough to prevent extensive forest formation. The greater importance of brush-prairie and woodland in the TAP Province probably reflects a cooler climate and greater duration of snow cover in the spring than in the PPA Province: the cooler, moister soil conditions at the time of spring fires afford some protection to the root crowns of woody plants

Grazing and browsing by large mammals, primarily bison and elk, were major processes in presettlement prairies, but it is unlikely that these played as significant a role as fire in the formation and maintenance of prairies. Bison and elk are primarily grazers, with a preference for grasses, which would have limited their role in suppressing woody vegetation. White-tailed deer are browsers and occurred in woodlands on the margins of prairies and along rivers, but their numbers were unlikely to have been sufficient to significantly influence the distribution of woody vegetation. Grazers probably influenced the relative abundances of plant species through their effects on regeneration and interspecific competition. These animals are major dispersers of seeds and are

UP Upland Prairie System

photo by Tim Whitfeld, MN DNR

Glacial Lakes State Park, Pope 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 midheight 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)*, both midheight grasses, are the most important associated graminoids. Sedges *(Carex* spp.) are sometimes common in UP communities but are typically a minor graminoid component. The most common and widespread woody species are the low semi-shrubs leadplant *(Amorpha canescens)* and prairie rose *(Rosa arkansana)*, and the tall shrub wolfberry *(Symphoricarpos occidentalis)*. Purple prairie clover *(Dalea purpurea)*, heath aster *(Aster ericoides)*, and stiff goldenrod (*Solidago rigida*) are common forbs. The main vegetation layer in UP communities is usually less than 40in (1m) high, although some forbs and the flowering stalks of the tall grasses exceed this height as the growing season progresses.

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, shrubs and fire-tolerant trees can persist, forming brush-prairie and savanna communities. 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. Taller shrubs typical in brush-prairies include Bebb’s willow *(Salix bebbiana)*, American hazelnut *(Corylus americana)*, and Saskatoon juneberry *(Amelanchier alnifolia)*, which contribute to a patchy shrub layer that is usually less than 5ft (1.5m) tall. Savannas typically have scattered trees, sometimes clumps of trees, growing in a prairie matrix. There is typically a patchy shrub layer up to 6ft (2m) tall, while trees are seldom more than 33ft (10m) tall. Bur oak is the most common and widespread tree, but northern pin oak is sometimes present in savannas close to the edge of the Eastern Broadleaf Forest (EBF) Province. Small, open-grown, often gnarled bur oaks are most distinctive. Savanna and brush-prairie communities intergrade. In the

FF -continued- Floodplain Forest System

The most prominent stress on plants in FF communities is lack of oxygen needed for respiration. During flooding, 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.

In addition to experiencing annual or occasional flooding, floodplains and river terraces have persistently high water tables. 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 are 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 soil invertebrates. 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 in forests—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 because plant growth in most temperate forests is limited by the availability of nitrogen. Knowledge of nitrogen mineralization rates is 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 annual rate and seasonal timing of nitrogen mineralization and the prevalent form of nitrogen available to plants are quite specific compared with the 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 have been greatly enriched in nitrates over the past 100 to 150 years from human activities, especially the burning of fossil fuels and use of commercial 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. Specifically, when nitrate-laden groundwater enters organic-rich river backwaters, nitrates are converted by microbes under anaerobic conditions 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 the oceans.

Glacial History of the Red River and Minnesota River Valleys

The valleys and drainages of the two largest rivers in the prairie region of Minnesota, the Red River and the Minnesota River, have strong influence on the character and abundance of floodplain forests in the PPA and TAP provinces. The Red and the Minnesota rivers flow through markedly different valleys with very different flooding regimes and alluvial landforms. The differences in physiography of the Red River and Minnesota River drainages originate from geologic processes that occurred near the end of the last glaciation in Minnesota.

About 12,000 years ago, when Glacial Lake Agassiz was at its greatest extent and its outflow, Glacial River Warren, was cutting what is now the Minnesota River valley, the current Red River watershed was covered by the lake. During the first 700 years of the draining of Glacial Lake Agassiz, the outlet of the lake into the Glacial River Warren eroded to several successively lower positions and correspondingly lowered the elevation of the great lake. Thus, the lands of the Agassiz basin were exposed gradually; beach ridges or strand lines document at least five major episodes of drawdown from about 11,700 to 11,000 years ago. At about 11,000 years ago the outlet stabilized. The elevation of Glacial Lake Agassiz then remained about the same for at least the next 1,000 years. During this period, rivers in Minnesota that drained westward into Lake Agassiz cut through the beach ridges and eroded significant valleys in the freshly exposed sediment. Beginning about 10,000 years ago, the history of Glacial Lake Agassiz is complicated by short episodes of advance and melting of glacial ice masses, which opened drainages to the north. By about 9,500 years ago, the ice and the lake had retreated into Canada, exposing clayey, deep-water sediments in Minnesota. Because the Agassiz lake bed is incredibly flat, the Red River and most of its tributaries in Minnesota have very little fall (about 1 foot per mile) and lack the erosive power to form deep valleys. In addition, within

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 and RV Community Classes in the PPA and TAP Provinces

RV communities have not been extensively surveyed in Minnesota, and unlike other ecological systems in this classification, the RV System is not divided into floristic regions. Surveys of RV communities have been especially limited in the PPA and TAP provinces. Three plant community classes are recognized in the RV System. Two of these—Sand/Gravel/Cobble River Shore (RVx32) and Clay/Mud River Shore (RVx54)—are likely present throughout most of the PPA and TAP provinces. The third—Rocky River Shore (RVx43)—is rare in the PPA Province and has not been recorded in the TAP Province.

matter by new deposits of silt or sand. Normal erosion also commonly removes existing shoreline vegetation, leaving bare sediment for recolonization by plants. Clearing or other alteration of native vegetation on uplands adjacent to river shore communities 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.

Most rivers and streams in the PPA and TAP provinces have been heavily influenced by changes to the land in surrounding watersheds, with corresponding effects on river shore communities. Major portions of most watersheds in the two provinces have been converted from native grassland to cropland, non-native pasture, urban land, and other uses. This conversion, along with an extensive network of ditches that has drained over 90% of the wetlands in the prairie regions of Minnesota, has resulted in greatly increased rates of runoff and soil erosion, as well as disruption of natural seasonal cycles of flooding and drawdown. Without the buffering effect of native grasslands and wetlands, precipitation now moves off the landscape quickly, causing prairie rivers and streams to rise and fall much more rapidly than before intensive Euro-American settlement. At present, rivers and streams in the PPA and TAP provinces are commonly deeply cut, with steep-sided silt banks, and often lack the mudflats and sand or gravel bars typical of natural river bottoms.

Natural disturbance regimes have been further altered along many rivers by dams. Downstream from dams, flooding can be markedly reduced, especially the flooding that typically follows heavy summer rains. Upstream from dams, river shore 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. In some areas along major rivers, RV communities have been increasingly exposed to erosive wave action over the past few decades. This is a fairly recent phenomenon caused by increasing boat traffic, especially from larger and faster boats and other watercraft. Channel dredging, stream channelization, and mining of gravel bars have also had major impacts on streams in the PPA and TAP provinces.

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 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

about 1,000 years of exposure of the lake bed, Minnesota entered a period of extreme aridity that lasted until about 4,000 years ago, during which there was probably little development of valleys and drains, further slowing valley and drainage development in the flat landscape of northwestern Minnesota.

During the period of about 12,000 years ago to about 9,500 years ago, when the Red River watershed was covered by Glacial Lake Agassiz, lands in the current Minnesota River drainage were exposed to erosion. The relatively wet climate during this period and the increasing gradient of streams flowing into the deepening valley eroded by the Glacial River Warren caused early development of river valleys and delivery of alluvium to the major valleys in the Minnesota River drainage. When the northern outlets of Glacial Lake Agassiz were uncovered and the lake began to drain into Canada, the erosive and powerful flow of Glacial River Warren stopped rather abruptly. The river that succeeded Glacial River Warren, the Minnesota River, lacked the volume and energy to remove the sediment delivered by tributaries that plunge from rolling till plains into the deep valley. At the mouths of these streams, deltas blocked the flow of the Minnesota River and served as natural dams creating strings of natural lakes (Big Stone Lake, Marsh Lake, and Lac qui Parle, formed by deltas of the Whetstone, Pomme de Terre, and Lac qui Parle rivers, respectively, are present-day examples of this phenomenon). As the tributaries continued to deliver sediment to the valley, much of it settled in the quiet water of these lakes until alluvium covered the floor of the Minnesota River valley. High-energy floods have since shaped and reshaped the alluvium across the floor of the Minnesota River valley.

The deep-water deposits of Glacial Lake Agassiz provide a setting for FF communities that is rather distinctive in Minnesota. Where the valleys of the Red River and its tributaries are strongly winding and sufficiently deep to interrupt the spread of prairie fires (typically at least 25ft [8m] below the surrounding Agassiz lake plain), the rivers were lined in the past by gallery forests consisting almost entirely of terrace forest communities (i.e., Northern Terrace Forest [FFn57]). These FF communities occurred on patches of silty or clayey alluvium nearly encircled by hairpin river bends, which protected them from prairie fires. Outside bends in the rivers were not sufficiently protected from fire to support forest development and were occupied by prairie or fire-dependent woodland communities. Alluvial deposits along the Red River and the lower reaches of its tributary rivers tend to be well drained because of local relief within the channel, favoring the formation of terrace forest or even Mesic Hardwood Forest (MH) communities over the true floodplain forests characteristic of active floodplain sites, which have poorly drained soils. The unusual flooding regime of the Red River also favors development of terrace forest communities over true floodplain forest communities. Flooding along the Red River is caused largely by inflow of spring meltwater along upper reaches of the river while lower reaches to the north are still frozen or dammed with ice. In springs where snowmelt is more rapid in Minnesota and North Dakota than in Canada, the river backs up and spills for tens of miles beyond its banks across the flat Agassiz lake plain. The flooding regime along the Red River amounts to intermittent, low-energy ponding accompanied by the deposition of fine alluvium, not unlike the extreme backwaters of other rivers in Minnesota where terrace forest communities are present on occasionally flooded sites. The tributaries of the Red River that lie entirely within the Glacial Lake Agassiz basin, including the Roseau, Two Rivers, Tamarac, Snake, and Thief rivers, are sluggish, with shallow valleys and poorly developed channels. These rivers had only scattered areas of FF communities along their banks and instead were flanked mainly by prairies or fire-dependent woodlands. In contrast, tributaries with headwaters in the high moraines east of the Agassiz basin, including the Red Lake, Clearwater, Sand Hill, Wild Rice, Buffalo, and Otter Tail rivers, have sufficient fall and volume to have cut deeper, winding valleys across the deep-water sediments. These rivers often have galleries of FF communities much like the Red River. Most of these rivers also cut through the sandy, shallow-water deposits and beach ridges that ring the Agassiz basin. In these stretches, the valleys are deeper, tributaries are more common, the land is rolling and dissected, and bottomlands have at least some sandy alluvial features. According to the early surveyors, these stretches of river were continuously lined with forest. At present, terrace forest communities are most common along these stretches, although there are a few examples of true floodplain forest communities on sites with sufficient alluvium.

The landscape context of FF communities along the Minnesota River and its tributaries contrasts sharply with that of FF communities in the Red River drainage, primarily because the Minnesota River valley is so deeply incised into the landscape. The depth of the Minnesota River valley provides tributary streams with much greater energy than those in the Red River drainage. These streams have eroded deep valleys and deposited sediment in valley bottoms in a complex array of fluvial landforms. The large volumes of sediment deposited in the bottoms of the Minnesota River by the Glacial River Warren and afterward by tributaries of the Minnesota provide continuous habitat for FF communities as the river flows through the PPA Province, including floodplain forests on low, annually flooded alluvial bottoms and terrace forests on higher, occasionally flooded sites such as terraces and levees. Other river valleys in the watershed have more limited habitat for development of FF communities. Many of the tributaries of the Minnesota River are characterized by headwaters high in the Prairie Coteau region southwest of the Minnesota River or in moraines to the northeast of the river. These tributaries, including the Lac qui Parle, Redwood, Cottonwood, Pomme de Terre, and Chippewa rivers, erode down through the uplands of the Coteau and the moraines and then cross flat plains before falling rapidly through deep valleys just before they enter the Minnesota. The headwater stretches of these rivers have deep valleys but limited amounts of alluvium, enabling development of terrace forests but not true floodplain forests. Where these rivers cross the flat plains, often in broad glacial meltwater channels, the channels are shallow, and prairies and marshes historically adjoined the rivers. Although the early surveyors described scattered timber and narrow bands of cottonwood, willow, ash, elm, and box elder along these stretches, it is unlikely that these characteristic FF trees formed large forest stands. Where these rivers fall to the Minnesota River, their valleys are deep, with alluvial bottoms that provide habitat for either terrace or true floodplain communities. In the southeastern corner of the PPA Province, the tributaries of the Minnesota River drain what is essentially the basin of Glacial Lake Minnesota. These rivers, including the Blue Earth, Maple, Cobb, and Le Sueur, form a well-developed, fan-shaped system of drainages cut well into the old lake bed. Because of this dissection, forests were historically rather common in the region, with FF communities lining the lower valleys of these rivers and occurring intermittently upstream as the valleys become shallower and offered less protection from prairie wildfires.

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). Communities of the FFn Region are present in the TAP Province and the eastern edge of the RRV in the PPA Province, where rivers course through the sandier, shallow-water deposits of the Glacial Lake Agassiz basin. Communities of the FFs Region are present in the PPA Province in the Minnesota River drainage and in the headwaters of rivers tributary to the Mississippi and Missouri rivers in the CGP. FF communities along the Red River and the portions of its tributaries that traverse the Glacial Lake Agassiz basin in northwestern Minnesota are currently included in the FFn Region. However, there were few vegetation samples in this area suitable for inclusion in development of the classification presented in this field guide. The distinct character of the Red River valley makes it likely that these FF communities are more similar to floodplain forests to the northwest in Manitoba than to FF communities to the east in northern Minnesota (i.e., FFn communities). If this is supported by collection and analysis of additional vegetation samples, FF communities in the LAP and much of the RRV may be placed in a separate, northwestern floristic region within the FF System,

RV River Shore System

photo by Fred Harris, MN DNR

Blue Earth River, Blue Earth 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 occur (or at least occurred historically) throughout the Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces.

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 fluctuate 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 (by mid-August in average years), 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. It is the lower beach zone that supports many of the more characteristic RV System plants.

The most common pattern of natural disturbance in RV communities is repeated erosion and deposition of materials by flowing water. This process generally results in removal of organic matter and nutrients from substrates along river shores, and burial of organic or gravel beaches, plants in the upper zone tend to grow in a series of parallel bands, each containing a different assemblage of species and each resulting from a different storm earlier in the growing season. 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 distinct upper, middle, and lower zones. The upper zone on very large lakes 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. 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 lower zone, as in smaller lakes, is constantly influenced by waves and has few vascular plants.

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 PPA and TAP provinces. 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.

LK Community Classes in the PPA and TAP Provinces

LK communities in the PPA and TAP provinces have not been thoroughly described. Two LK plant community classes are known to occur in the provinces, Inland Lake Sand/Gravel/Cobble Shore (LKi32) and Inland Lake Clay/Mud Shore (LKi54).

analogous to northwestern floristic regions in the Fire-Dependent Forest/Woodland (FD) and MH systems.

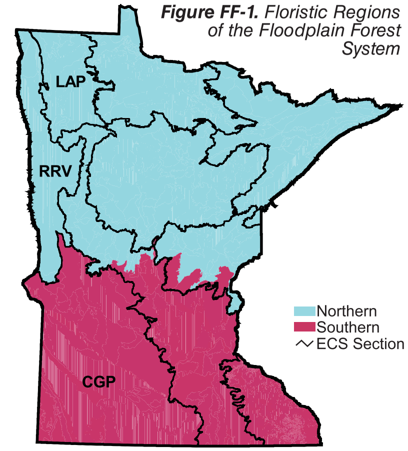


Figure FF-1. *Floristic Regions of the Floodplain Forest System*

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. Because of this, FFn communities are more likely than FFs communities to occur in proximity to plant communities from a variety of other systems and consequently are more likely to contain plant species characteristic of these systems. For example, plant species characteristic of WF communities are common in FFn communities in the TAP Province because WF communities are often present in the province on river terraces cut into fresh glacial drift. Among these species are sweet-scented bedstraw *(Galium triflorum)*, black ash, highbush cranberry *(Viburnum trilobum)*, and side-flowering aster *(Aster lateriflorus)*. Another group of species more common in FFn than FFs communities include species characteristic of FD communities, which commonly occurred as a buffer between northern riparian forests and prairies. Among these species are bur oak, Canada mayflower *(Maianthemum canadense)*, beaked hazelnut *(Corylus cornuta)*, and American hazelnut *(C. americana)*. A surprising number of plants diagnostic for FFn relative to FFs communities have their highest presence in Minnesota in MH communities. MH communities are not common in the PPA and TAP provinces, so the presence of characteristic MH species in FFn communities is not likely to be related to proximity with MH communities. It is likely that these species have become increasingly abundant in the region as a result of fire suppression, including species such as Clayton's sweet cicely *(Osmorhiza claytonii)*, chokecherry *(Prunus virginiana)*, and early meadow-rue *(Thalictrum dioicum)*. Of the species that help to separate FFn from FFs communities, only ostrich fern, nannyberry *(Viburnum lentago)*, starry false Solomon's seal *(Smilacina stellata)*, starry sedge *(Carex rosea)*, prickly ash *(Zanthoxylum americanum)*, common hops *(Humulus lupulus)*, and tall scouring rush *(Equisetum hyemale)* have their peak presence in the FF System.

Plant species with high fidelity for FFs relative to FFn communities are listed in Table FF-2. Nearly all of the plants in this table are diagnostic for FFs communities because of their affinity for extensive alluvial bottoms, which are more common in the FFs than the FFn region. FFs communities are characterized by a rather large group of species that reach their peak presence in the FF System, including plants such as silver maple, Ontario aster *(Aster ontarionis)*, hackberry, clearweed *(Pilea* spp.), white grass *(Leersia virginica)*, ambiguous sedge *(Carex amphibola)*, and greenbrier. All of these plants have much higher presence in FF communities than in other systems, making them rather good indicators of the FF System in general as well as indicators of FFs relative to FFn communities. FFs communities are also characterized by higher presence of species typical of marsh, meadow, and prairie communities, including bur marigold or beggarticks *(Bidens* spp.), tall bellflower *(Campanula americana)*, rice cut grass *(Leersia oryzoides)*, woundwort *(Stachys palustris)*, and fragrant cyperus *(Cyperus odoratus)*. Although historical descriptions of bottomlands in the FFs Region mention marshes, meadows, and prairies mixed with FF communities, these open communities are now infrequent in bottomlands in the PPA Province, in part because they have

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

Region	Affinity	Common Name	Scientific Name	frequency (%) FFn	frequency (%) FFs
Northern Floristic Region	Fire-Dependent Forest /Woodland Affinity	Bur oak (U)	*Quercus macrocarpa*	52	7
		Canada mayflower	*Maianthemum canadense*	41	-
		Beaked hazelnut	*Corylus cornuta*	35	-
		American hazelnut	*Corylus americana*	29	-
		Prickly or smooth wild rose	*Rosa acicularis* or *R. blanda*	29	-
		Poison ivy	*Toxicodendron rydbergii*	29	-
		Columbine	*Aquilegia canadensis*	23	-
		Gray dogwood	*Cornus racemosa*	23	-
		Quaking aspen (U)	*Populus tremuloides*	23	-
		Common strawberry	*Fragaria virginiana*	23	-
		Lindley's aster	*Aster ciliolatus*	17	-
		Snowberry or wolfberry*	*Symphoricarpos* spp.	17	-
		Tall meadow-rue	*Thalictrum dasycarpum*	52	-
		Canada anemone	*Anemone canadensis*	41	-
		Northern bedstraw	*Galium boreale*	23	-
		Giant goldenrod	*Solidago gigantea*	17	-
	Floodplain Forest Affinity	Ostrich fern	*Matteuccia struthiopteris*	64	-
		Nannyberry	*Viburnum lentago*	47	-
		Starry false Solomon's seal	*Smilacina stellata*	41	-
		Starry sedge	*Carex rosea*	23	-
		Prickly ash	*Zanthoxylum americanum*	23	-
		Common hops	*Humulus lupulus*	17	-
		Tall scouring rush	*Equisetum hyemale*	17	-
	Mesic Hardwood Forest Affinity	Clayton's sweet cicely	*Osmorhiza claytonii*	58	7
		Chokecherry	*Prunus virginiana*	58	7
		Early meadow-rue	*Thalictrum dioicum*	52	7
		Red baneberry	*Actaea rubra*	41	-
		Hog peanut	*Amphicarpaea bracteata*	35	7
		Basswood (U)	*Tilia americana*	35	7
		Wild sarsaparilla	*Aralia nudicaulis*	29	-
		Dewey's sedge	*Carex deweyana*	29	-
		Pennsylvania sedge	*Carex pensylvanica*	29	-
		Bloodroot	*Sanguinaria canadensis*	29	-
		Downy arrowwood	*Viburnum rafinesquianum*	23	-
		Wood anemone	*Anemone quinquefolia*	17	-
		Pale bellwort	*Uvularia sessilifolia*	17	-
		Large-flowered bellwort	*Uvularia grandiflora*	17	-
		Lopseed	*Phryma leptostachya*	17	-
	Wet Forest Affinity	Sweet-scented bedstraw	*Galium triflorum*	64	7
		Black ash (U)	*Fraxinus nigra*	52	-
		Highbush cranberry	*Viburnum trilobum*	41	-
		Side-flowering aster	*Aster lateriflorus*	35	-
		Nodding trillium	*Trillium cernuum*	35	-
		Bladder sedge	*Carex intumescens*	29	-
		Jack-in-the-pulpit	*Arisaema triphyllum*	29	-
		Meadow horsetail	*Equisetum pratense*	23	-
		Philadelphia fleabane	*Erigeron philadelphicus*	23	-
		Dwarf raspberry	*Rubus pubescens*	23	-
		Spinulose shield fern	*Dryopteris carthusiana*	17	-
		Balsam popular (U)	*Populus balsamifera*	17	-

(U) = understory tree *Snowberry or wolfberry (*Symphoricarpos albus* or *S. occidentalis*)

LK Lakeshore System

photo by Karen Myhre, MN DNR

Becker 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 Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces, LK communities are most common in the CGP, parts of which have numerous basins created in pitted moraines, outwash plains, and other landforms during the last glaciation. LK communities are much less common in the RRV and LAP, both of which are characterized by the nearly level and largely featureless terrain of the Glacial Lake Agassiz basin.

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 blown ashore during spring breakup can remove existing vegetation and push sand, gravel, and cobbles into beach ridges. When present, these ice-thrust ridges often mark the ecotone between LK communities and adjacent terrestrial communities. In prairie landscapes, ice-thrust ridges are often covered by prairie forbs and graminoids. In wooded landscapes they tend to be covered by woodland forbs 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 lie above the normal water level and are influenced by waves mainly during storms; they are also subject to scouring by ice during spring breakup. On broad sand communities along the Minnesota River valley, rarely burn. In general, 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 and the complexes in which they occur will succeed over centuries to woodland or forest.

With fire suppression since Euro-American settlement, woody plant cover is increasing in native plant communities throughout the PPA Province, including RO communities. Historically, RO communities were likely refugia for native woody plants in prairie landscapes because, as noted above, large areas of exposed rock and low fuel levels slowed the intensity and spread of fire. Although woody plant cover on rock outcrops usually was not eliminated by fire, fires did burn through matrices of RO communities in the past, controlling the vigor and abundance of woody vegetation. At present, as woody plants increase in abundance across the PPA Province, the seed source for species that colonize RO communities has likewise increased, exacerbating the effect of fire suppression. Notable examples include eastern red cedar (*Juniperus virginiana*) and exotic species such as European honeysuckles (*Lonicera tatarica*, *L. bella*, and *L. morrowii).*

Grazing and browsing by large mammals, primarily bison and elk, were major processes in prairie landscapes prior to Euro-American settlement and likely impacted the structure and composition of RO communities. Because bison and elk prefer grasses over forbs and woody plants, it is unlikely that they affected the vegetation of RO communities directly through grazing and browsing, but they may have suppressed vegetation by trampling or by rubbing on woody plants or rock surfaces. They very likely helped to disperse seeds and, by disturbing the soil with their hooves, probably contributed to regeneration of short-lived species characteristic of RO communities. Because they are too rocky for cultivation, complexes of outcrop communities and prairie are often used at present as pastures for domestic livestock. Confined grazing of outcrops by domestic livestock facilitates invasion by exotic species and by eastern red cedar, which is avoided by cattle.

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 the PPA and Eastern Broadleaf Forest 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, devil's tongue, small-flowered fameflower, false pennyroyal, rusty woodsia, rock spikemoss *(Selaginella rupestris)*, bulbostylis *(Bulbostylis capillaris)*, Carolina foxtail, disk hyssop *(Gratiola neglecta)*, mousetail *(Myosurus minimus)*, Carolina cranesbill *(Geranium carolinianum)*, slender knotweed *(Polygonum tenue)*, and water hyssop *(Bacopa rotundifolia)*. Only one native plant community class is recognized in the ROs Region, Southern Bedrock Outcrop (ROs12). 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*

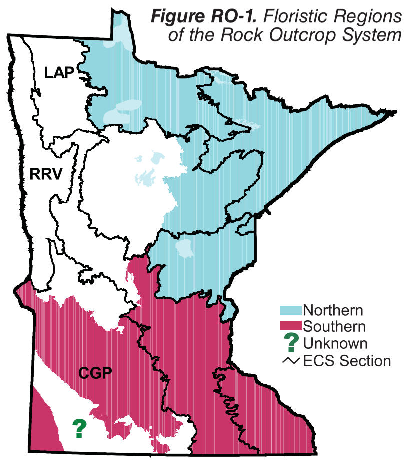


Table FF-2. *Plants useful for differentiating the Southern from the Northern Floristic Region of the Floodplain Forest System.*

		Common Name	Scientific Name	frequency (%) FFn	FFs
Southern Floristic Region	Floodplain Forest Affinity	Silver maple (U)	*Acer saccharinum*	5	69
		Ontario aster	*Aster ontarionis*	-	61
		Hackberry (U)	*Celtis occidentalis*	5	53
		Clearweed	*Pilea* spp.	5	53
		White grass	*Leersia virginica*	-	46
		Ambiguous sedge	*Carex amphibola*	-	30
		Greenbrier	*Smilax tamnoides*	-	30
		White snakeroot	*Eupatorium rugosum*	-	23
		Cleavers	*Galium aparine*	-	23
		Blue monkey flower	*Mimulus ringens*	-	15
		Aniseroot	*Osmorhiza longistylis*	-	15
		Blue phlox	*Phlox divaricata*	-	15
		Gregarious black snakeroot	*Sanicula gregaria*	-	15
		Broad-glumed brome	*Bromus altissimus*	-	7
		Maple-leaved goosefoot	*Chenopodium simplex*	-	7
		Woodland goosefoot	*Chenopodium standleyanum*	-	7
		False rue anemone	*Enemion biternatum*	-	7
		Southern or yellow wood sorrel	*Oxalis dillenii* or *O. stricta*	-	7
		Lady's thumb	*Polygonum persicaria*	-	7
		Peach-leaved willow	*Salix amygdaloides*	-	7
		Black willow	*Salix nigra*	-	7
		Canadian black snakeroot	*Sanicula canadensis*	-	7
	Marsh, Meadow & Prairie Affinity	Bur marigold and beggarticks	*Bidens* spp.	5	38
		Tall bellflower	*Campanula americana*	-	23
		Rice cut grass	*Leersia oryzoides*	-	15
		Woundwort	*Stachys palustris*	-	15
		Fragrant cyperus	*Cyperus odoratus*	-	7
		Germander	*Teucrium canadense*	-	7
		Sandbar willow	*Salix exigua*	-	7
		Tall thistle	*Cirsium altissimum*	-	7
		Witch grass	*Panicum capillare*	-	7
		Virginia ground cherry	*Physalis virginiana*	-	7
		Autumn sneezeweed	*Helenium autumnale*	-	7
	Other	Mad dog skullcap	*Scutellaria lateriflora*	-	38
		Bitternut hickory (U)	*Carya cordiformis*	-	7
		Sharp-lobed hepatica	*Anemone acutiloba*	-	7
		Giant Solomon's seal	*Polygonatum biflorum*	-	7
		Red-berried elder	*Sambucus racemosa*	-	7

(U) = understory tree

been converted to fields and in part because they have been flooded by dams. The continued presence of marsh, meadow, and prairie species in FF communities is likely from persistence of these species in small openings in forests, along treeless overflow channels, on shorelines, and on sand bars in river bottomlands. FFs communities are also more likely to have annual species such as clearweed, cleavers, maple-leaved and woodland goosefoots *(Chenopodium simplex* and *C. standleyanum)*, lady's thumb *(Polygonum persicaria)*, bur marigold and beggarticks, fragrant cyperus *(Cyperus odoratus)*, and witch grass *(Panicum capillare)*, possibly because the bottomlands of rivers in the FFs Region experience more flooding and erosion than FFn rivers, creating increased areas of the ruderal habitats favorable for annual plants.

WF Wet Forest System

photo by R.P. Dana, MN DNR

Skull Lake Wildlife Management Area, Kittson County, MN

General Description

Wet Forest (WF) communities occur most often 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 the Prairie Parkland (PPA) and Tallgrass Aspen Parklands (TAP) provinces are characterized by a relatively dry climate, WF communities are uncommon, occurring mainly in areas with high water tables. WF communities are most often dominated by black ash or quaking aspen, which may be mixed with one another, and in some parts of the TAP Province by northern white cedar. Balsam poplar, paper birch, and American elm are commonly present, although not typically dominant, with balsam fir and white spruce present in some stands in the TAP Province. In the TAP Province, tamarack and black spruce may also be present because of the tendency of WF communities to occur next to tamarack- and spruce-dominated communities of the Forested Rich Peatland (FP) System. American elm was historically more important in WF communities in the PPA and TAP provinces, but elm populations have declined dramatically across Minnesota due to Dutch elm disease. Historic records suggest that tamarack also was more common in the past, as an associate in WF communities dominated by quaking aspen and balsam poplar, but was cut for railroad ties and other uses and did not recolonize most sites. Characteristically, the understories of WF communities are shrubby, commonly containing dogwoods *(Cornus* spp.), gooseberries or currants *(Ribes* spp.), dwarf alder *(Rhamnus alnifolia)*, speckled alder *(Alnus incana)*, highbush cranberry *(Viburnum trilobum)*, prickly or smooth wild rose *(Rosa acicularis* or *R. blanda)*, juneberries *(Amelanchier* spp.), and nannyberry *(Viburnum lentago)*. 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 continuous inputs 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

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 colder at night and much hotter during midafternoon on sunny days than in surrounding prairies, woodlands, and forests. 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 when moisture levels are high enough to make it likely that the plants will be able to complete their life cycle; 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, such as brittle prickly pear, tend to flower and produce seeds only during periods of above-average rainfall. RO communities often share a number of plants with communities in the Cliff/Talus (CT) System due to similarities in environmental conditions.

Landscape Setting and Disturbance Regime

RO communities are present where local bedrock highs are exposed in level to strongly rolling landscapes composed variously of alluvium, terrace deposits, outwash, glacial till, or loess-mantled till. In most of the PPA Province, RO communities occur in fire-prone landscapes dominated by Upland Prairie communities. Along the Minnesota River valley downstream from Montevideo, RO communities occur in landscapes dominated by a mix of Floodplain Forest, Fire-Dependent Forest/Woodland, Mesic Hardwood Forest, Upland Prairie, and Marsh communities.

RO communities are small features, rarely covering more than 10 acres (4ha) and most often less than 5 acres (2ha). Exposed (bare) rock often makes up just a portion of a typical community occurrence, with individual exposures rarely larger than 2 acres (1ha) and usually much smaller (often 1/4 acre or less). Most RO communities are embedded in a matrix of prairie, savanna, woodland, forest, or marsh vegetation. Because of their small size, RO communities are often mapped as complexes or described as inclusions within prairie, savanna, woodland, forest, or, occasionally, cliff and talus communities. Complexes with these communities may be larger than 10 acres but are rarely more than 25 acres (10ha).

Because RO communities are typically small and surrounded by more expansive prairie, woodland, and forest communities, they are often affected by disturbances originating in these other settings. For example, 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, can also burn through and around RO communities, removing shallow accumulations of organic matter along margins of exposed rock. Removal of this organic matter prevents soil development over the rock surface, which if not checked would eventually lead to the replacement of the outcrop community by prairie or woodland communities (this occurs over decades or centuries, depending on the height of the bedrock above the surrounding terrain). Severe fires can remove at least the aboveground portions of most vascular plants from outcrops, and repeated severe fires effectively reduce woody cover and eliminate other fire-sensitive species. Even during severe fires, however, areas in outcrop communities with thin soils and bare rock burn infrequently because of their sparse vegetation cover and low levels of fuel. As a result, the specialized plants characteristic of outcrops—which are typically present on microsites with very low levels of fuel—often escape combustion. RO communities that are surrounded by forest or wetland communities likely experience lower fire frequencies and intensities than those surrounded by prairies. Because of their lack of fuels, the largest and most continuous patches of exposed bedrock, such as in some RO exposed during the most recent period of glaciation when the Glacial River Warren drained Glacial Lake Agassiz, carrying enormous volumes of ice and meltwater that scoured out the present-day Minnesota River valley. The erosive force of this torrent cut a deep trench through the thick blanket of drift down to the underlying bedrock, leaving numerous exposures along the valley floor flanking the much smaller Minnesota River, which succeeded the glacial river once Lake Agassiz had drained. (The glacial history of the Minnesota River valley is described in more detail on page PPA/TAP-FF5). Over the past 10,000 years, further erosion has exposed some additional areas of bedrock in the PPA Province, especially along streams. RO communities occur locally on quartzite bedrock outcrops in the Minnesota River Prairie Subsection of the CGP in Cottonwood County and in the Inner Coteau Subsection in Rock and Pipestone counties. These areas were not covered by ice during the Wisconsin glaciation, and these outcrops have been exposed thousands of years longer than many other bedrock outcrops in the state. RO communities do not occur in the Tallgrass Aspen Parkland (TAP) Province as there are no bedrock exposures to support them.

Vegetation Structure and Composition

The vegetation of RO communities is quite variable, although vascular plant cover is typically very sparse because of scarcity of soil. RO communities can be dominated by lichens, graminoids, or shrubs. Lichens are the dominant life form on most outcrops. Crustose and foliose lichens cover exposed rock surfaces. Fruticose species may also be 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. Woody plants sometimes occur in areas of deeper soil and may dominate RO communities where patches of deep soil are prevalent. Even in these shrub-dominated outcrop communities, however, soil depths are much less than in surrounding prairie or woodland communities. On many outcrops, the amount of soil is closely tied to the degree of bedrock fracturing, with soil accumulating in cracks and crevices and providing rooting areas for plants.

In general, RO communities are perhaps more usefully treated as heterogeneous assemblages of several plant communities rather than as a single vegetation type. A typical example may include a bare rock community composed mostly of lichens such as *Candelariella vitellina* and *Rhizocarpon disporum*, a crevice and thin soil community with specialized vascular plants such as brittle prickly pear *(Opuntia fragilis)* and false pennyroyal *(Isanthus brachiatus)*, a deeper soil community with prairie or woodland species such as big bluestem (*Andropogon gerardii)* and prairie wild onion *(Allium stellatum)*, and a shallow pool community supporting aquatic plants such as water hyssop (*Bacopa rotundifolia*) and Carolina foxtail (*Alopecurus carolinianus*). Overall, the flora of RO communities is distinctive, containing many species of vascular plants, mosses, and lichens that occur in no other habitat in Minnesota. One such species is devil's tongue (*Opuntia humifusa)*, which in Minnesota is restricted to RO communities (although to the west in the Great Plains it is distributed more widely, occurring in prairies as well as in rock outcrop communities).

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 due to the low moisture-holding capacities of substrates and exposure to direct sunlight and strong winds. Many of the characteristic plants of RO communities utilize the C_4 metabolic pathway in photosynthetic carbon fixation, a physiological mechanism that makes photosynthesis more efficient with respect to water use in the typically high-light, high-temperature, and water-limited environment of RO communities. Fleshy water-storing tissues are present in such vascular plant outcrop specialists as prickly pears *(Opuntia* spp.) and small-flowered fameflower *(Talinum parviflorum)*. During periods of drought some

moves laterally below the surface but often upwells to create springs or seeps 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.

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 as a result, 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 plant species have adapted to this problem by producing both normal roots and adventitious roots with gas-conducting cells.

Soils and 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 the thick layers of peat present in Acid 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 (often 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 communities. Because of waterlogged and cold soils, very little nitrogen is mineralized in WF communities 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

WF communities in Minnesota form three floristically distinct groups that are generally separated from one another by geography. These groups 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). Communities of both the WFn Region and the WFw Region are common in the TAP Province (although WFw communities are more prevalent, and so the TAP Province is mapped mostly as part of the WFw Region). Communities of the WFs Region may be present in the PPA Province, but there is little information available on WF communities in the province and no vegetation plot data.

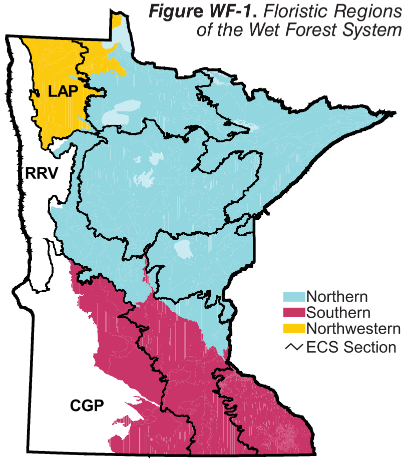


Figure WF-1. *Floristic Regions of the Wet Forest System*

In the TAP Province, WFw and WFn communities occur in close proximity and are limited to zones of upwelling groundwater associated with beach ridges and intervening shallow-water deposits of Glacial Lake Agassiz. These zones supply sufficient groundwater to sustain WF as well as FP communities in a climate that strongly favors prairies and fire-dependent woodlands. Although WFw and WFn communities differ floristically (see below), they generally occur in similar habitats, with most settings having soils developed on hydrologically conductive fine sands that overlay rather dense till. WFn communities tend to have deeper and more fibric peat than WFw communities, and some WFw communities lack organic surface horizons and instead have organic matter mixed deeply into the mineral soil. Springs and seepage zones are more evident in WFn than WFw communities, although all WF communities in the TAP Province tend to have concentrations of carbonates in upper mineral soil horizons, suggesting upwelling of groundwater. Both WFw and WFn communities occur in association with peatlands that extend into the TAP Province from the peat-dominated Agassiz Lowlands Section of the MOP. In these settings, WFn communities tend to occur within the cores of extensive peatland areas, where the vegetation consists mainly of forests of the FP System. In comparison, WFw communities tend to occur on the periphery of these peatland areas in landscapes where they are mixed mostly with brushy Upland Prairie and Wetland Prairie (WP) communities and with open peatlands of the Wet Meadow/Carr (WM) and OP systems. In addition to the settings described above, limited areas of WFn communities occur in association with peaty, rich fens along the contact between the McIntosh moraine and the Glacial Lake Agassiz plain in Polk County.

Floristic differences between WFn and WFw communities seem to be related to differences in their natural disturbance regimes, particularly events that affect tree density (see ***Disturbance Regimes of WFn and WFw Communities*** below). The ground layers of WFn communities have several shade-tolerant, fire-sensitive herbs. These plants are common throughout the forested regions of Minnesota and occur mostly in communities where fire was a rare event. Analysis of Public Land Survey (PLS) records suggests that in the 1800s WFn communities in the TAP Province were composed of trees averaging about 8in (20cm) in diameter, 100 years in age, and with densities similar to those in the LMF Province, indicating that WFn communities in the TAP Province were well insulated from fire and were true forests not much different from their counterparts to the east. In contrast, the ground layers of WFw communities have several plants that are tolerant of fire and that favor more open habitats. The PLS records suggest that WFw communities were composed of fast-growing trees averaging about 7in (18cm) in diameter, 50 years in age, and with densities that were

RO Rock Outcrop System


photo by Carmen Converse, MN DNR

Plover Prairie, Lac Qui Parle 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 where bedrock is at or just above the ground surface. Crustose and foliose lichens typically cover bare rock surfaces, with fruticose lichens also often present. Vascular plant cover is sparse to patchy, with abundance and distribution dependent on the amount of fracturing of bedrock surfaces and accumulation of soil in cracks, crevices, and shallow depressions. In this classification, RO communities are classified by bedrock type and geography, which are major determinants of plant community composition.[1]

In most of the Prairie Parkland (PPA) Province, bedrock is buried beneath glacial sediments generally greater than 100ft (30m) deep—often from 200ft to 500ft (60m to 150m) deep. RO communities are confined to a few localized areas in the province where glacial sediments are not deep enough to cover local bedrock highs or where glacial deposits have been removed by flowing water. In the Minnesota River Prairie Subsection of the CGP, RO communities occur fairly frequently along major portions of the Minnesota River valley between Ortonville and New Ulm, predominantly on Precambrian granite, gneiss, and diorite. RO communities also occur on gabbro, amphibolite, schist, quartz monzonite, quartzite, basalt, and sandstone bedrock in the Minnesota River valley, although much less commonly. Most of these outcrops were

[1]Although not specifically addressed in this classification, lichen-covered boulders and glacial erratics are present sporadically in upland and wetland communities across the PPA and TAP provinces. These boulders, which have been transported to their current locations by glacial ice and meltwater, are varied in mineral composition, with origins ranging from local bedrock, to limestone bedrock in Manitoba, to bedrock on the Canadian Shield of Ontario and northeastern Minnesota. The lichen flora of these boulders is often similar to that of local bedrock exposures. For example, granitic boulders typically support lichens common on granitic outcrops, while quartzite boulders support lichens characteristic of Sioux quartzite outcrops. Boulders and glacial erratics composed of rock types not represented in the bedrock outcrops of the PPA Province (such as limestone) typically have a lichen flora that is starkly different from that of local RO communities. The degree of similarity of lichen species composition between boulders and outcrops also appears to be related to distance between boulder and outcrop. The lichen communities on boulders and erratics have not been systematically studied in Minnesota; further collection and analysis of lichen data are needed to better understand species composition and patterns of distribution.

Forest (EBF) provinces. The other two floristic regions, the Northern Floristic (CTn) Region and the Lake Superior Floristic (CTu) Region, occur within the Laurentian Mixed Forest Province.

Cliffs in the PPA Province have not been systematically surveyed. Despite limited data, there appear to be marked differences between CTs communities in the PPA Province and CTs communities in the EBF Province. Further sampling and analysis of CTs communities in the two provinces may warrant division of the CTs Region. Two CT plant community classes have been documented in the PPA Province, Southern Dry Cliff (CTs12) and Southern Mesic Cliff (CTs33).

about half those of more fire-protected forests in the TAP Province, specifically WFn and FPn communities. It is likely that infrequent severe droughts dried out the sites where WFw communities occur to the point where fires could burn through the stands, removing surface organic material and thinning the tree canopy. Early surveyors described extensive areas of wet, burned aspen timber and wet brush-prairie where WFw communities are now present. Because quaking aspen and balsam poplar aggressively colonize open, nonforested sites, it is possible that contemporary WFw communities include forests that have developed on sites formerly occupied by wet brush-prairies as a result of fire suppression.

Plant Indicators of WFn Communities

Plants with high fidelity for the WFn Region in comparison with the WFw Region are presented in Table WF-1. Most of these species are tolerant of shade, and a number of them are sensitive to fire. Several species common throughout the WFn Region have their peak presence in Minnesota in WF communities, including alpine enchanter's nightshade *(Circaea alpina)*, common marsh marigold *(Caltha palustris)*, mountain maple *(Acer spicatum)*, bladder sedge *(Carex intumescens)*, awl-fruited sedge *(Carex stipata)*, and jack-in-the-pulpit *(Arisaema triphyllum)*. In the TAP Province, WFn

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

Region	Affinity	Common Name	Scientific Name	frequency (%) WFn	frequency (%) WFw
Northern Floristic Region	Wet Forest Affinity	Alpine enchanter's nightshade	*Circaea alpina*	60	11
		Common marsh marigold	*Caltha palustris*	57	11
		Mountain maple	*Acer spicatum*	45	11
		Bladder sedge	*Carex intumescens*	27	3
		Awl-fruited sedge	*Carex stipata*	27	-
		Jack-in-the-pulpit	*Arisaema triphyllum*	21	3
		Bur marigold and beggarticks	*Bidens* spp.	21	3
		Common oak fern	*Gymnocarpium dryopteris*	18	-
		Willow-herbs*	*Epilobium* spp.	15	3
	Forested Rich Peatland Affinity	Interior sedge	*Carex interior*	30	3
		Northern marsh fern	*Thelypteris palustris*	30	-
		Three-leaved false Solomon's seal	*Smilacina trifolia*	30	3
		Labrador tea	*Ledum groenlandicum*	24	3
		Twinflower	*Linnaea borealis*	24	-
		Bristle-stalked sedge	*Carex leptalea*	21	-
		White cedar (U)	*Thuja occidentalis*	21	-
		Goldthread	*Coptis trifolia*	18	-
		Mountain fly honeysuckle	*Lonicera villosa*	15	3
		Tall Northern bog orchid	*Platanthera hyperborea*	15	-
		Black spruce (U)	*Picea mariana*	15	-
		Water horsetail	*Equisetum fluviatile*	12	-
	Mesic Hardwood Forest Affinity	American spikenard	*Aralia racemosa*	30	3
		Rose twistedstalk	*Streptopus roseus*	27	3
		Northern red oak (U)	*Quercus rubra*	21	-
		Bottlebrush grass	*Elymus hystrix*	18	-
		Zigzag goldenrod	*Solidago flexicaulis*	18	-
		Pagoda dogwood	*Cornus alternifolia*	15	3
		Lopseed	*Phryma leptostachya*	12	-
	Other	Virginia creeper	*Parthenocissus* spp.	24	-
		Ostrich fern	*Matteuccia struthiopteris*	18	3
		Bluebead lily	*Clintonia borealis*	15	3
		Lowbush blueberry	*Vaccinium angustifolium*	12	-

*American, purple-leaved, or northern willow-herb *(Epilobium ciliatum, E. coloratum,* or *E. glandulosum)*
(U) = understory tree

communities are usually adjacent to or occur in regions dominated by FP communities and therefore share several species with FP communities, including interior sedge *(Carex interior)*, northern marsh fern *(Thelypteris palustris)*, three-leaved false Solomon's seal *(Smilacina trifolia)*, Labrador tea *(Ledum groenlandicum)*, twinflower *(Linnaea borealis)*, bristle-stalked sedge *(Carex leptalea)*, white cedar, and goldthread *(Coptis trifolia)*. WFn communities in the TAP Province are also more likely than WFw communities to have species common in well-drained, rich MH communities, including American spikenard *(Aralia racemosa)*, rose twistedstalk *(Streptopus roseus)*, northern red oak seedlings, bottlebrush grass *(Elymus hystrix)*, zigzag goldenrod *(Solidago flexicaulis)*, pagoda dogwood *(Cornus alternifolia)*, and lopseed *(Phryma leptostachya)*. Because MH communities are rare in the province, the presence of characteristic MH species does not seem to be related to physical proximity of WFn with MH communities. Apparently, other factors promote the presence of these species in WFn communities in the TAP province, perhaps including the nutrient richness of these sites.

Plant Indicators of WFw Communities

Selected plant species with high fidelity for the WFw Region in comparison with the WFn Region are presented in Table WF-2. In general, these species are tolerant of fire and favor open habitats, and are characteristic of the prairie, brushland, or sparsely wooded communities often adjacent to WFw communities. Among these species are American vetch *(Vicia americana)*, fireweed *(Epilobium angustifolium)*, Virginia thimbleweed *(Anemone virginiana)*, veiny pea *(Lathyrus venosus)*, and bracken *(Pteridium aquilinum)*, which have their peak presence in Fire-Dependent Forest/Woodland communities but occur also in WFw communities. Another group of species that distinguish WFw from WFn communities are species more likely to occur in WP communities, including yarrow *(Achillea millefolium)*, arrow-leaved sweet coltsfoot *(Petasites sagittatus)*, Bebb's willow *(Salix bebbiana)*, heart-leaved willow *(Salix eriocephala)*, and marsh vetchling *(Lathyrus palustris)*.

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

Region	Affinity	Common Name	Scientific Name	frequency (%) WFn	frequency (%) WFw
Northwestern Floristic Region	Fire-Dependent Forest/Woodland Affinity	Quaking aspen (U)	*Populus tremuloides*	18	88
		Spreading dogbane	*Apocynum androsaemifolium*	-	33
		American vetch	*Vicia americana*	3	25
		Fireweed	*Epilobium angustifolium*	3	18
		Virginia thimbleweed	*Anemone virginiana*	3	14
		Veiny pea	*Lathyrus venosus*	-	11
		Bracken	*Pteridium aquilinum*	-	7
	Open Prairie/Wetland Affinity	Bebb's willow	*Salix bebbiana*	6	44
		Arrow-leaved sweet coltsfoot	*Petasites sagittatus*	9	37
		Heart-leaved willow	*Salix eriocephala*	-	22
		Marsh vetchling	*Lathyrus palustris*	-	11
		Yarrow	*Achillea millefolium*	-	11
		Aquatic sedge	*Carex aquatilis*	-	7
		Woolly sedge	*Carex pellita*	-	7
		Shrubby cinquefoil	*Potentilla fruticosa*	-	7
		Woolgrass	*Scirpus cyperinus*	-	7
		Slender wedge grass	*Sphenopholis obtusata*	-	7
	Other	Downy arrowwood	*Viburnum rafinesquianum*	3	18
		Elliptic shinleaf	*Pyrola elliptica*	-	11
		Shining willow	*Salix lucida*	-	7

(U) = understory tree

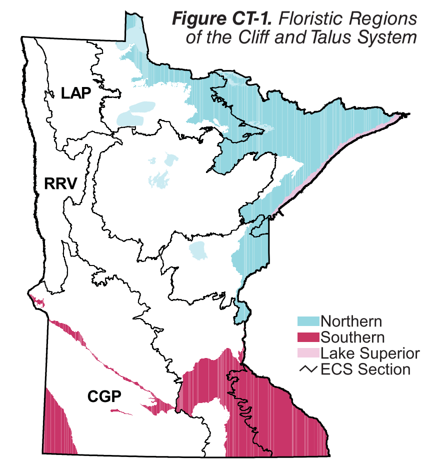
Plant Adaptations

Plants in CT communities are generally tolerant of greater environmental extremes than species in surrounding terrestrial communities. Many plants on cliffs 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 colder at night than in surrounding communities and often much warmer during midafternoon on sunny days. Limited availability of nutrients on many cliffs 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 or runners and tend to persist from year to year once established at a site; species that disperse and propagate primarily by seed are less common. Ferns, which reproduce by spores, are fairly common on most cliffs. Dry cliff communities share a number of vascular plant and lichen species with RO and Upland Prairie (UP) communities. Many of the lichen species present in cliff communities are also often present on large boulders or glacial erratics in prairies, forests, and other habitats. Moister cliffs often have vascular plants that are common in Mesic Hardwood Forest (MH) communities.

Landscape Setting and Disturbance Regime

In the broader landscape, CT communities are small features, rarely covering more than 5 acres (2ha). In the PPA Province, they generally occur in landscapes dominated by UP communities. CT communities may also occur in association with small patches of woodlands or forests of the Fire-Dependent Forest/Woodland and MH systems, especially along the Minnesota River valley. The disturbance regimes that shape these prairies, woodlands, and forests often affect CT communities. Fires that originate in prairies, woodlands, or forests 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. In general, cliff communities are fairly stable over time as a result of low rates of natural disturbances, combined with limited habitat for plant establishment and growth and with prevalence of species that persist once established. Cliff and talus communities are some of the least human-disturbed habitats in Minnesota. Since the late 1800s, some cliff and talus communities have been destroyed or altered by quarrying. 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 and erosion and sedimentation from upslope areas that have been developed or otherwise cleared.

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



Floristic Regions and Plant Community Classes in the PPA Province

Communities in the CT System are divided into three floristic regions based on geographic variation in climate, bedrock type, and composition of vascular plant, bryophyte, and lichen species (Fig. CT-1). The Southern Floristic (CTs) Region occurs in the PPA and Eastern Broadleaf

MN DNR

Blue Mounds State Park, Rock County, MN

General Description

Communities in the Cliff/Talus (CT) System are present on steep-sided bluffs, along streams, on margins of bedrock ridges, and in other settings with sheer bedrock exposures. The vegetation of CT communities is generally open. Lichens and mosses are often the dominant life-forms, with vascular plants sparse or patchy largely 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 cool and wet depending on cliff aspect, surrounding vegetation, proximity to streams or lakeshores, and presence of groundwater seepage on the cliff face.

In the Prairie Parkland (PPA) Province, CT communities are very rare. Throughout most of the province, bedrock is buried deep below glacial drift. Cliff communities have been documented on Sioux quartzite, a metamorphic sandstone of Early Proterozoic origin, at several locations in the Inner Coteau and Minnesota River Prairie subsections of the CGP, and on the Paleozoic sandstone along ravines of the Minnesota River valley in the Minnesota River Prairie Subsection. Small cliffs may also be present as part of igneous and metamorphic outcrop complexes that occur sporadically along the Minnesota River. There are no documented talus slopes in the PPA Province but small examples may be present in association with cliffs in the areas mentioned above. CT communities do not occur in the Tallgrass Aspen Parklands Province.

Vegetation Structure and Composition

Lichens, mosses, and liverworts cover rock surfaces in CT communities and colonize areas exposed by erosion. Lichens are especially diverse in CT communities. Many of these species also occur in Rock Outcrop (RO) communities, but some species, such as *Xanthoria sorediata* and *Peltula euploca*, appear to be limited to vertical bedrock exposures (i.e., 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 wetter 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 woody plant cover is variable.

Disturbance Regimes of WFn 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 cause conversion to WM or Marsh communities. Other potential disturbances include fire and windthrow. Historically, WFn 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 communities, a result of being surrounded by fire-prone woodlands, prairies, and open wetlands that burned severely during drought periods. In Minnesota, wind played its greatest role in regenerating forests in the TAP Province, where forests were windthrown roughly two to four times more often than anywhere else in the state. These high rates of wind damage are likely related to the fact that nearly all forest communities in the province—including FD and MH communities in addition to WF communities—are dominated by weak-boled quaking aspen and balsam poplar trees that are shallowly rooted above high water tables. The rotation of catastrophic windthrow for WFw communities is 250 years, compared with 370 years for WFn communities. It is likely that WFw communities had greater wind damage than WFn communities because WFw communities occurred as small patches in a generally treeless landscape, whereas WFn communities are present within large patches of forest that help to buffer them from wind. Relative to WFn 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+	140-340	365-370
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
WFn55	0 - 75 yrs	**black ash**	75 - 195 yrs	**black ash**	> 195 yrs	black ash *(tamarack)* *(white spruce)*	>1000	140	370
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%

FP Forested Rich Peatland System

photo by Norm Aaseng, MN DNR

Roseau 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 (LMF) Province and extend across the northern half of the Eastern Broadleaf Forest (EBF) Province. They reach their western limit in the Tallgrass Aspen Parklands (TAP) Province, where they are uncommon, and along the border of the northern part of the EBF Province with the Prairie Parkland (PPA) Province, where they are extremely rare. In the PPA and TAP provinces, high rates of evapotranspiration—caused by warmer climate and relatively low precipitation—combined with historical prevalence of fires limit peat development and restrict FP communities to wetlands fed by upwelling groundwater.

Peatland Formation

Most of Minnesota's peatlands began to form following climate cooling and increased precipitation about 5,000 to 6,000 years ago; peatland development in western Minnesota in the TAP and PPA provinces is much more recent, beginning around 3,000 years ago. Cooler, wetter climates led to stabilization of 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 0.4–0.8mm 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 increasingly dependent on external inputs of essential minerals from precipitation, surface runoff from adjacent uplands, and groundwater-derived subsurface flow. Groundwater supplies to peatlands can have high concentrations of minerals in settings where groundwater has percolated through calcareous substrates; high rates of evaporation also concentrate minerals at the peat surface in peatlands in the TAP and PPA provinces. As a result, both FP and Open Rich Peatland (OP) communities can

Non-Mineotrophic Peatland Species

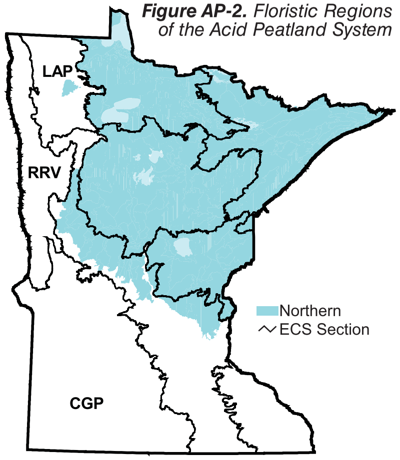
Because only those species listed below can persist in the ombrotrophic conditions of bogs, the occurrence of any other species can be considered an indicator of minerotrophic conditions. However, some seedlings, particularly of tree species, can germinate in bogs but are short-lived and should not be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

Only two of the four plant community classes in the AP system occur in the TAP 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 appear to extend west into the TAP Province. It is possible that Northern Spruce Bogs (APn80) were present in the TAP Province in the past but were converted to more minerotrophic peatlands (i.e., Northern Poor Conifer Swamps) over the past 100 years by mineralization of peat from ditching and increased fire frequency, and by mineral inputs from windblown dust from the vast agricultural areas to the west of the province.

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



The two AP Classes that occur in the TAP Province are distinguished from one another in part 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 TAP 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 other 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 TAP Province apparently prevent succession of poor fens or poor conifer swamps to true bogs.

have surface water with relatively high concentrations of minerals such as calcium and magnesium. The precipitation, surface runoff, and groundwater that feed peatlands, however, usually have only very low concentrations of the essential nutrients nitrogen and phosphorus.

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 sufficiently dry and aerated 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; in addition, relatively dry hummocks in FP communities provide areas of suitable habitat for forb species not present in OP communities. 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 balsam fir, and ericaceous shrubs, such as Labrador tea *(Ledum groenlandicum)* and bog rosemary *(Andromeda glaucophylla)*, 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 FP communities, such as pitcher plant *(Sarracenia purpurea),* 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 FPw Region, are represented in the TAP Province. The FPs Region barely extends into the PPA Province, with a few isolated occurrences in the CGP. (See *Field Guide to the Native Plant Communities of Minnesota: The Eastern Broadleaf Forest Province* [Minnesota Department of Natural Resources 2005] for a description of how the FPs Region differs from the FPn Region.)

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 Northern Cedar Swamp (FPn63) occurs in the TAP Province, in well-protected areas that rarely burn. The FPw Region is represented by one native plant community class, Northwestern Rich Conifer Swamp (FPw63). FPw63 is limited in distribution to the TAP Province and the western portion of the MOP in the LMF Province. FPw63 is associated with areas of groundwater seepage and is confined to sites that offer some protection from fires but that probably burn occasionally.

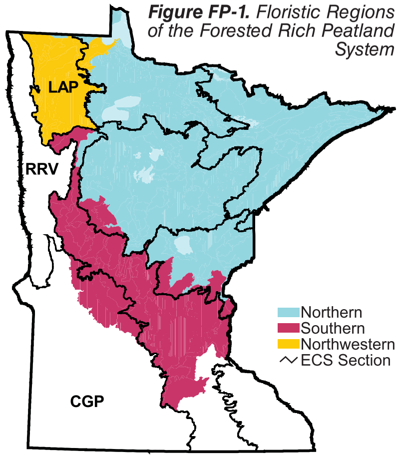


Figure FP-1. *Floristic Regions of the Forested Rich Peatland System*

Differences in species composition between FPn and FPw communities are presented in Table FP-1 and Table FP-2. Species with greater affinity for FPn communities include ericaceous shrubs such as creeping snowberry *(Gaultheria hispidula)* and leatherleaf *(Chamaedaphne calyculata)*, orchids such as stemless lady's slipper *(Cypripedium acaule)* and heart-leaved twayblade *(Listera cordata)*, and insectivorous plants such as round-leaved sundew *(Drosera rotundifolia)* and pitcher plant. It is likely that the diminished presence in the FPw Region of species common in the FPn Region is related to more frequent drought, with prolonged drawdown of the water table; low snow cover, resulting in desiccation of evergreen shrubs during the winter; and more frequent fire. Species with greater affinity for FPw communities include species typical of shallow peat, wet mineral soil, or even upland habitats.

Table FP-1*. Plant species useful for differentiating the Northern from the Northwestern Floristic Region of the Forested Rich Peatland System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

		Common Name	Scientific Name	frequency (%) FPn	FPw
Northern Floristic Region	Tree	White cedar (C)	*Thuja occidentalis*	44	4
		Balsam fir (C)	*Abies balsamea*	30	4
		Red maple (U)	*Acer rubrum*	40	-
		Mountain ashes (U)	*Sorbus* spp.	17	-
	Tall Shrub	Fly honeysuckle	*Lonicera canadensis*	22	-
		Bog willow	*Salix pedicellaris*	21	-
		Round-leaved dogwood	*Cornus rugosa*	10	-
	Low Shrub	Creeping snowberry	*Gaultheria hispidula*	53	8
		Lowbush blueberry	*Vaccinium angustifolium*	32	4
		Leatherleaf	*Chamaedaphne calyculata*	32	-
		Bog laurel	*Kalmia polifolia*	12	-
	Forb	Stemless lady's slipper	*Cypripedium acaule*	20	-
		Arrow-leaved tearthumb	*Polygonum sagittatum*	15	-
		One-flowered pyrola	*Moneses uniflora*	14	-
		Round-leaved sundew	*Drosera rotundifolia*	12	-
		Heart-leaved twayblade	*Listera cordata*	12	-
		Early coralroot	*Corallorhiza trifida*	10	-
		Small northern bog orchid	*Platanthera obtusata*	10	-
		Lesser rattlesnake plantain	*Goodyera repens*	10	-

Table FP-1 *continued on next page*

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.

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 Labrador tea *(Ledum groenlandicum)* or leatherleaf *(Chamaedaphne calyculata)*. 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 overtopped by accumulating peat. Black spruce, for example, is able to layer, or reproduce vegetatively, from branches that become covered by moss.

Because the AP communities in the TAP Province are at the western edge of the range of peatland development in Minnesota, several peatland species characteristic of the numerous and expansive AP communities in the LMF Province, such as pitcher plant *(Sarracenia purpurea),* sundews *(Drosera* spp.), bog laurel *(Kalmia polifolia),* bog wiregrass sedge *(Carex oligosperma),* tussock cottongrass *(Eriophorum vaginatum)*, and tawny cottongrass *(E. virginicum)*, are scarce or absent.

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.

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 the pH to 5.0. Humic acid–buffered peatlands are transitional and relatively short-lived, quickly succeeding to poor fens (i.e., Northern Poor Fen [APn91]) or poor swamp forests (i.e., Northern Poor Conifer Swamp [APn81]), 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.

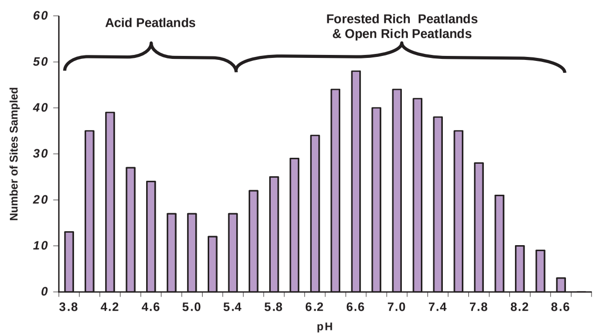


Figure AP-1. *Histogram of surface water pH from wetland sites in Minnesota. The natural bimodal distribution corresponds to separation of Acid Peatlands from Rich Peatlands.*

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.

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. Within the AP System, bogs (i.e., Northern Spruce Bog [APn80] and Northern Open Bog [APn90]), which have the most acidic and nutrient-poor conditions, are inhabited by a set of only 25 species (see page PPA/TAP-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 concentrations of minerals such as calcium and magnesium. The dominant 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. In addition, many plants in AP communities have thickened outer leaf membranes and alkaloids in leaf tissues that help to reduce herbivory. The low

Table FP-1. *continued*

Northern Floristic Region	Forb	Bluebead lily	*Clintonia borealis*	32	4
		Wild calla	*Calla palustris*	24	4
		Pitcher plant	*Sarracenia purpurea*	18	4
	Fern	Cinnamon fern	*Osmunda cinnamomea*	24	-
		Bristly clubmoss	*Lycopodium annotinum*	10	-
	Graminoid	Three-fruited bog sedge	*Carex trisperma*	46	4
		Poor sedge	*Carex paupercula*	42	4
		Creeping sedge	*Carex chordorrhiza*	10	-

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

Table FP-2. *Plant species useful for differentiating the Northwestern from the Northern Floristic Region of the Forested Rich Peatland System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

				frequency (%)	
		Common Name	***Scientific Name***	**FPn**	**FPw**
Northwestern Floristic Region	Tree	American elm (U)	*Ulmus americana*	4	46
		Bur oak (C)	*Quercus macrocarpa*	4	21
		Balsam poplar (C)	*Populus balsamifera*	1	17
		Box elder (C)	*Acer negundo*	-	13
	Tall Shrub	Chokecherry	*Prunus virginiana*	5	33
		Highbush cranberry	*Viburnum trilobum*	3	29
		Shrubby cinquefoil	*Potentilla fruticosa*	1	29
		Wild black currant	*Ribes americanum*	4	17
	Low Shrub	Poison ivy	*Toxicodendron rydbergii*	4	33
	Vine	Wild honeysuckle	*Lonicera dioica*	-	29
	Forb	Spotted Joe pye weed	*Eupatorium maculatum*	19	75
		Alpine enchanter's nightshade	*Circaea alpina*	7	38
		Swamp thistle	*Cirsium muticum*	2	33
		Starry false Solomon's seal	*Smilacina stellata*	1	33
		Side-flowering aster	*Aster lateriflorus*	2	29
		Tall meadow-rue	*Thalictrum dasycarpum*	2	29
		Arrow-leaved sweet coltsfoot	*Petasites sagittatus*	5	21
		Wood strawberry	*Fragaria vesca*	2	21
		Cut-leaved bugleweed	*Lycopus americanus*	1	21
		Fireweed	*Epilobium angustifolium*	3	17
		Canada goldenrod	*Solidago canadensis*	2	13
		Elliptic shinleaf	*Pyrola elliptica*	1	13
	Graminoid	Fringed brome	*Bromus ciliatus*	6	58
		Common reed grass	*Phragmites australis*	3	21
		Prairie sedge	*Carex prairea*	3	17
		Fowl bluegrass	*Poa palustris*	3	13
		Golden-fruited sedge	*Carex aurea*	2	13

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

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 for their removal by *Sphagnum*.

photo by E.R. Rowe, MN DNR

Becker County, MN

AP Acid Peatland System

photo by Tim Whitfeld, MN DNR

Clearwater County, MN

General Description

The Acid Peatland (AP) System is characterized by conifer- or low shrub–dominated communities that develop in association with peat-forming *Sphagnum*. AP communities are acidic (pH < 5.5), are extremely low in nutrients, and have hydrological inputs dominated by precipitation rather than groundwater. These communities are floristically depauperate, with the vascular 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 AP communities and open, low shrub–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, sporadic in the northern half of the Eastern Broadleaf Forest Province, and rare in the Tallgrass Aspen Parklands (TAP) Province; they are absent from the Prairie Parkland Province. Because of marginal climatic conditions for peatland formation in the TAP Province, with precipitation barely exceeding evapotranspiration, AP communities are limited to a few localities and are not as well developed as in the main part of their range in Minnesota in the LMF Province. The development of AP communities in a landscape with widespread occurrence of prairie communities—as occurs in the TAP Province—is unusual for acid peatlands in North America.

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* adsorbs dissolved mineral cations, particularly calcium, and exchanges them for hydrogen ions, releasing organic acids and lowering