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

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

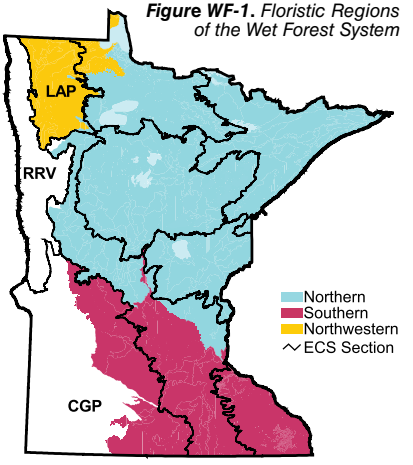

Figure WF-1. *Floristic Regions of the Wet Forest System*

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.

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

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.*

		Common Name	Scientific Name	frequency (%) WFn	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.*

		Common Name	Scientific Name	frequency (%) WFn	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

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%