



Tettegouche State Park, Lake County, MN

General Description

Mesic Hardwood Forest (MH) communities are present in the Laurentian Mixed Forest (LMF) Province on upland sites with moist soils, usually in settings protected from fire. They are characterized by continuous, often dense, canopies of deciduous trees, including sugar maple, basswood, paper birch, and northern red oak, and understories with shade-adapted shrubs and herbs. Plants in MH communities have access to predictable supplies of water and nutrients, but they are often limited by light because of the dense forest canopy. Typical sites are buffered from seasonal drought by fine-textured, moisture-retaining soils or dense subsoil layers that perch snowmelt and rainfall. At the same time, soils are well drained and do not experience water logging or saturation except after spring snowmelt or heavy 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 twice the rate of that in either Fire-Dependent Forest/Woodland (FD) or Wet Forest (WF) communities. As a result, nutrients in dead plant material quickly become available again for uptake by plants. Resource availability in MH communities follows an annual or seasonal pattern that is more predictable than in FD forests, where nutrients are released mainly following episodic fires. Tree mortality in MH communities is also rather constant, with stand-regenerating disturbances such as wildfires and windthrow uncommon. The death of established trees most often involves individual canopy trees or small patches that are affected by minor windthrow, disease, or other fine-scale disturbances.

Plant Adaptations

Competition for light appears to have strong influence on the species composition of MH communities. Older forests commonly have several, nearly closed layers of woody plants, including well-defined forest canopies, subcanopies, and shrub layers. These layers combine to produce cover that is often continuous, filtering most of the sunlight 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 that of direct sunlight. As a result, the species characteristic of the System tend to be extremely tolerant of shade, at least in their juvenile stages, or develop rapidly in early spring, capturing and storing most of their annual energy needs before trees become fully leaved.



In MH communities, nutrients and organic matter accumulate at the soil surface in leaf litter and humus. This contrasts with FD communities, for example, where nutrients are leached deeply into the soil and the humus layer is periodically consumed by fire, and with WF and Floodplain Forest (FF) communities, which are sinks for nutrients transported from uplands in groundwater or runoff. Deeply rooted plants in MH communities extract base elements such as calcium, magnesium, and potassium from deep in the mineral soil and deposit them on the surface in plant litter. Species such as sugar maple, basswood, and elm, which are abundant in many stands, shed leaves with high amounts of nutrients, contributing to high nutrient content in the humus. As a result, much of the plant activity in MH forests is concentrated around the soil surface and rich humus layer. Many of the herbaceous plants are rooted almost entirely in humus, and woody plants have a high proportion of their roots near the surface. Several species characteristic of MH communities have adaptations, such as decumbent growth forms or extensive rhizome systems, that allow them to expand laterally through these upper soil layers in search of unexploited nutrients and light reaching the forest floor.

Soils and Soil Moisture

The distribution of MH communities in the LMF Province is strongly correlated with the presence of impermeable horizons about 20 to 30 inches (50 to 75cm) below the soil surface that perch snowmelt or rainfall. Close to 80% of the vegetation plots from MH communities in this analysis occurred on soils with impermeable lower horizons, and more than 80% of sites with impermeable soil layers were occupied by MH communities to the exclusion of other communities. These soil layers are impermeable either because they are firmly packed or because of accumulation of clay particles. Soils above the impermeable horizons typically are saturated in the spring, keeping humus wet and promoting rapid green-up of ground-layer plants, which helps to deter spring fires.

Plant communities in the MH System vary strongly along a gradient of soil moisture and nutrients from drier and poorer sites to wetter and richer ones. In this classification, the moisture and nutrient gradient is divided into three segments: dry-mesic, mesic, and wet-mesic. The mesic segment consists of communities dominated by northern hardwood species such as sugar maple, basswood, paper birch, and ironwood. These trees are also present but less dominant in wet-mesic and dry-mesic MH communities. Dry-mesic MH forests are intermediate in moisture between mesic MH forests and forests in the FD System. Dry-mesic MH communities are occasionally exposed to light surface fires when adjacent to fire-prone sites and tend to be dominated by northern red oak mixed with northern hardwood species and often have scattered red pine or white pine. Wet-mesic MH forests are intermediate between mesic MH forests and forests in the WF System. Wet-mesic MH communities usually consist of mixed stands of quaking aspen, balsam poplar, black ash, American elm, white spruce, and balsam fir.

Floristic Regions

MH communities in Minnesota are grouped into four "floristic" regions, based on general differences in species composition (Fig. MH-1). Two of these Floristic Regions are represented in the LMF Province: the Northern Floristic (MHN) Region and the Central Floristic (MHC) Region. Communities from the other two Floristic Regions, the Southern (MHS) and the Northwestern (MHW), are present only occasionally along the southern and western edges of the LMF Province.

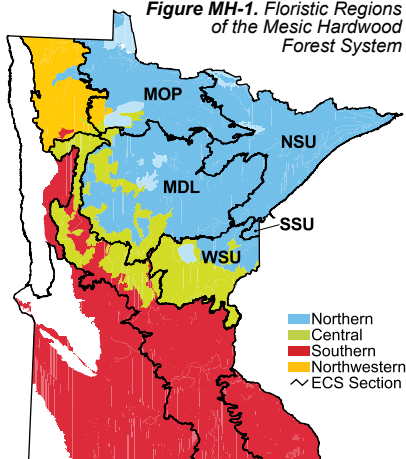
In comparison with communities of the MHC Region, MHN communities are wetter, falling mainly in the mesic and wet-mesic segments of the moisture gradient in the MH System. About 66% of the vegetation plots in the MHN Region are in mesic communities, while 34% are in wet-mesic communities. There are no dry-mesic community classes in the MHN Region; all "northern" dry-mesic community classes are in the FD System rather than in the MH System. In the MHN Region in general, upland habitats protected from fire are present in settings with wet soils or with numerous lakes or peatlands. This may explain, in part, why many of the plants characteristic of MHN communities also oc-



cur in WF and Forested Rich Peatland (FP) communities.

Communities in the MHC Region are mainly represented in the mesic and dry-mesic segments of the moisture gradient in the MH System. In this analysis, about 52% of the vegetation plots in the MHC Region are in mesic communities, and 43% are in dry-mesic communities; just 5% of the plots are in wet-mesic communities. In the MHC Region, upland habitats protected from fire tend to occur in very rugged terrain with well-developed drainages and river valleys. Proximity to rivers and streams may explain why many plants characteristic of MHC communities also occur in FF communities.

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



Plant Indicators of MHN and MHC Communities

Plant species with high fidelity for MHN relative to MHC communities are listed in Table MH-1. MHN communities are much more likely than MHC communities to have plants characteristic of the WF and FP systems, for example common oak fern (*Gymnocarpium dryopteris*), yellow birch, naked miterwort (*Mitella nuda*), white spruce, swamp red currant (*Ribes triste*), and bunchberry (*Cornus canadensis*). Another noticeable difference between MHN and MHC communities is the greater diversity of conifers in MHN, including white cedar, balsam fir, and white spruce, in addition to white pine and red pine. MHC communities rarely have conifers in the tree canopy; if present, conifers are limited to occasional white pines, or rarely, red pines.

Many of the plant species that have high fidelity for MHC relative to MHN communities are common in Southern Mesic Hardwood (MHs) communities and, in fact, have higher affinity for MHs than MHC communities (Table MH-2). Among these species are black cherry, white oak, bitternut hickory, butternut, and sharp-lobed hepatica (*Anemone acutiloba*). The low number of species in the MH System with high affinity for the MHC Region relative to the MHN or MHs Regions strongly suggests that the MHC Region is mainly a zone of transition between the MHN and MHs Regions. That is, MHC communities are composed of mixtures of plants from the MHN and MHs Regions, rather than plants that are unique to the MHC Region. The few species that have their highest frequency within the MH System in MHC communities are pointed-leaved tick trefoil (*Desmodium glutinosum*), large-flowered trillium (*Trillium grandiflorum*), blue beech, smooth juneberry (*Amelanchier laevis*), black-fruited rice grass (*Oryzopsis racemosa*), and poke milkweed (*Asclepias exaltata*). Several species with high affinity for MHC forests are also common in FF communities, including nodding fescue (*Festuca subverticillata*), greenbrier (*Smilax tamnoides*), and honewort (*Cryptotaenia canadensis*).

Disturbance Regimes of MHN vs. MHC Communities

MH communities historically had low to very low rates of catastrophic disturbance from fires and windstorms, with rotation periods in excess of 400 years and often greater than 1,000 years, and there were not strong differences between the MHN and MHC Regions in rotation periods (Table MH-3). Moderate disturbances from light surface fires and patchy windthrow were frequent to occasional, with rotation periods generally ranging from 40 to 300 years. Such moderate disturbances were more common among MHC than MHN communities, probably because of a warmer and drier climate in the southern and western parts of the LMF Province.



Table MH-1. Plants useful for differentiating the Northern from the Central Floristic Region of the Mesic Hardwood Forest System

		Common Name	Scientific Name	MHn	MHc
Northern Floristic Region	Wet Forest or Forested Rich Peatland Affinity	Balsam fir (U)	<i>Abies balsamea</i>	2	6
		White spruce (U)	<i>Picea glauca</i>	25	2
		Bunchberry	<i>Cornus canadensis</i>	24	3
		Common oak fern	<i>Gymnocarpium dryopteris</i>	23	—
		Naked miterwort	<i>Mitella nuda</i>	22	2
		Yellow birch (C)	<i>Betula alleghaniensis</i>	19	1
		Swamp red currant	<i>Ribes triste</i>	19	2
		Palmate sweet coltsfoot	<i>Petasites frigidus</i>	17	—
		Alpine enchanter's nightshade	<i>Circaea alpina</i>	16	3
		Yellow birch (U)	<i>Betula alleghaniensis</i>	15	1
		White spruce (C)	<i>Picea glauca</i>	14	—
		Balsam fir (C)	<i>Abies balsamea</i>	13	—
		Drooping woodreed	<i>Cinna latifolia</i>	13	1
		Woodland horsetail	<i>Equisetum sylvaticum</i>	12	1
		Long beech fern	<i>Phegopteris connectilis</i>	11	—
		Meadow horsetail	<i>Equisetum pratense</i>	10	2
		Shining firmoss	<i>Huperzia lucidula</i>	10	1
		Mountain ashes (U)	<i>Sorbus</i> spp.	10	—
		Big-leaf white & northern white violet	<i>Viola blanda/macloskeyi</i> group	9	1
	Balsam poplar (U)	<i>Populus balsamifera</i>	8	—	
Red-osier dogwood	<i>Cornus sericea</i>	7	—		
White cedar (C)	<i>Thuja occidentalis</i>	7	—		
Speckled alder	<i>Alnus incana</i>	6	—		
White cedar (U)	<i>Thuja occidentalis</i>	6	—		
Kidney-leaved violet	<i>Viola renifolia</i>	6	—		
Other	Groundpine	<i>Lycopodium dendroideum/hickeyi</i> grp.	31	2	
	Trailing blackberries	<i>Rubus flagellaris</i> & similar <i>Rubus</i> spp.	10	2	
	Thimbleberry	<i>Rubus parviflorus</i>	9	—	
	White baneberry	<i>Actaea pachypoda</i>	6	—	
	Goldthread	<i>Coptis trifolia</i>	6	1	

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

Table MH-2. Plants useful for differentiating the Central from the Northern Floristic Region of the Mesic Hardwood Forest System

		Common Name	Scientific Name	MHn	MHc
Central Floristic Region	Southern Mesic Hardwood Forest Affinity	Black cherry (U)	<i>Prunus serotina</i>	5	45
		Bitternut hickory (U)	<i>Carya cordiformis</i>	—	26
		White oak (C)	<i>Quercus alba</i>	—	9
		Bitternut hickory (C)	<i>Carya cordiformis</i>	—	8
		White oak (U)	<i>Quercus alba</i>	—	7
		Sharp-lobed hepatica	<i>Anemone acutiloba</i>	—	6
		Butternut (C)	<i>Juglans cinerea</i>	—	5
	Central Mesic Hardwood Forest Affinity	Pointed-leaved tick trefoil	<i>Desmodium glutinosum</i>	3	55
		Large-flowered trillium	<i>Trillium grandiflorum</i>	8	51
		Blue beech (U)	<i>Carpinus caroliniana</i>	4	35
		Smooth juneberry	<i>Amelanchier laevis</i>	3	15
		Black-fruited rice grass	<i>Oryzopsis racemosa</i>	—	10
		Poke milkweed	<i>Asclepias exaltata</i>	—	9
	Floodplain Forest Affinity	Nodding fescue	<i>Festuca subverticillata</i>	7	32
		Virginia waterleaf	<i>Hydrophyllum virginianum</i>	1	11
		Honewort	<i>Cryptotaenia canadensis</i>	—	9
		Greenbrier	<i>Smilax tamnoides</i>	—	9
		Prickly ash	<i>Zanthoxylum americanum</i>	—	9
		Gregarious black snakeroot	<i>Sanicula gregaria</i>	—	6
		Side-flowering sandwort	<i>Arenaria lateriflora</i>	—	5
Other	Wild geranium	<i>Geranium maculatum</i>	—	32	
	Common enchanter's nightshade	<i>Circaea lutetiana</i>	3	27	
	Lopseed	<i>Phryma leptostachya</i>	3	20	
	Maidenhair fern	<i>Adiantum pedatum</i>	1	18	
	Two-leaved miterwort	<i>Mitella diphylla</i>	3	18	
	Tall blackberries	<i>Rubus allegheniensis</i> & similar spp.	2	16	
	White ash (U)	<i>Fraxinus americana</i>	—	8	
	Woodland sunflower	<i>Helianthus strumosus</i>	—	7	
	White ash (C)	<i>Fraxinus americana</i>	—	5	

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



Table MH-3. Historic tree species composition & disturbance regimes in Mesic Hardwood Forest Classes.

Historic Tree Species Frequency by Class and Stand Age				Historic Disturbance Rotation Periods by Class (in years)		
young forest age		mature forest age		old forest age		
	young forest species		mature forest species		old forest species	
						Stand-Regenerating Fire Moderate Surface Fire + Patchy Windthrow Catastrophic Windthrow

Northern Floristic Region						ranges →			
MHn35	0 - 55 yrs	paper birch quaking aspen (sugar maple) (northern red oak)	95 - 205 yrs	paper birch (sugar maple) (white spruce)	> 295 yrs	white pine sugar maple (paper birch)	430-1000+	130-1000+	800-1000+
MHn44	0 - 35 yrs	quaking aspen	95 - 195 yrs	white spruce (quaking aspen) (paper birch) (balsam fir)	> 195 yrs	white spruce quaking aspen (paper birch) (balsam fir)	430	160	960
MHn45	0 - 75 yrs	sugar maple (yellow birch) (paper birch)	95 - 155 yrs	white spruce white cedar (sugar maple) (yellow birch)	> 195 yrs	white spruce (yellow birch) (sugar maple)	none	>1000	none
MHn46	0 - 35 yrs	quaking aspen	> 95 yrs	quaking aspen (white spruce) (American elm)	...		600	160	800
MHn47	0 - 55 yrs	sugar maple (paper birch)	75 - 195 yrs	sugar maple (paper birch)	> 195 yrs	sugar maple white pine	>1000	300	>1000

Central Floristic Region					ranges➡		370-1000+	40 -160	380-1000+
MHc26	0-35 yrs	quaking aspen* (paper birch)	55 - 135 yrs	paper birch (quaking aspen*) (red oak)	> 135 yrs	quaking aspen* (paper birch) (white spruce) (red oak) (white pine)	370	160	910
MHc36	0-35 yrs	red oak (basswood) (quaking aspen*)	> 95 yrs	sugar maple (basswood) (American elm)	...		1000	40	380
MHc37	0-35 yrs	quaking aspen (paper birch) (American elm) (basswood)	55 - 135 yrs	sugar maple (basswood) (American elm) (red oak) (paper birch)	> 135 yrs	(quaking aspen) (American elm) (sugar maple) (white spruce)	515	70	>1000
MHc47	0-55 yrs	(basswood) (bur oak) (quaking aspen) (paper birch) (sugar maple)	55 - 155 yrs	(basswood) (bur oak) (sugar maple) (paper birch)	> 155 yrs	basswood (bur oak) (white pine) (sugar maple)	>1000	140	>1000

bold = >50%

normal = 25-50%

(italics) = 10-25%

*includes big-toothed aspen