MH Mesic Hardwood Forest System

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

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.

> *…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

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.

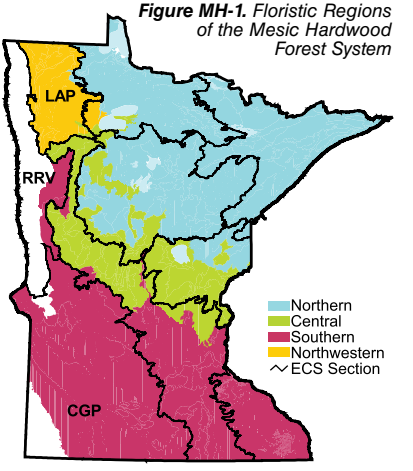

Figure MH-1. *Floristic Regions of the Mesic Hardwood Forest System*

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.*

			Common Name	Scientific Name	frequency (%) 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	-	

*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

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.*

				frequency (%)		
		Common Name	Scientific Name	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.

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