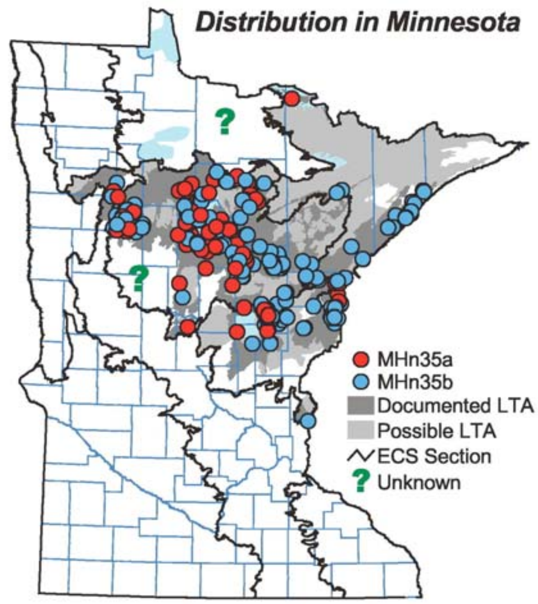
MHn35

MHn35 – Northern Mesic Hardwood Forest

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights

Northern Mesic Hardwood Forests (MHn35) are a common hardwood community found mostly within the Northern Minnesota Drift and Lake Plain, Western Superior Uplands, and Northern Superior Uplands ecological Sections of Minnesota (see map). Detailed descriptions of this community and ecological maps are presented in the DNR Field Guides to Native Plant Communities of Minnesota.



The range of MHn35 forests in Minnesota (shaded) and distribution of releve samples (red and blue dots).

Commercial Trees

As a commercial forest, MHn35 sites offer a wide selection of crop trees and possible structural conditions. Sugar maple, basswood, northern red oak, paper birch, quaking aspen, and red maple are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on MHn35 (see Suitability Tables). Big-toothed aspen and white pine are ranked as good crop trees, and stands can be managed to perpetuate these trees as co-dominants, especially when present or with evidence of former presence (e.g. stumps) in a particular stand. Bur oak, yellow birch, and balsam fir are ranked as just fair choices of crop trees, but stands can be managed to maintain their presence as minor trees for purposes other than timber production.

Among these species, paper birch, quaking aspen, red oak, white spruce, and sugar maple were the dominant native trees that have occupied MHn35 sites for a long time and have had the opportunity through successive generations to adapt to physical site conditions typical of these sites. Balsam fir, basswood, and white pine are likewise native to MHn35 sites but occurred naturally at lower abundance. The consequence of fire suppression, commercial logging, and settlement in the past century has been to promote much more sugar maple, basswood, and understory ironwood than was usual. Past history and land use as also encouraged the ingress of species that were not significant in native MHn35 stands such as red maple. The increased abundance sugar maple, basswood, ironwood and red maple complicates our interpretations and the use of natural regeneration models as silvicultural strategies.

Natural Silvicultural Approaches

In the historic landscape, most MHn35 stands (51%) were transitioning between the young and mature growth-stages. Roughly these were stands 55-95 years old. At this time, senescence of the initial-cohort trees created regeneration opportunities for trees ranging from single-tree gaps to large gaps up to an acre. Several silvicultural systems could be used to approximate the natural loss of initial-cohort trees and regeneration typical of transitioning MHn35 forests. Selective harvesting matches best the small-gap mortality pattern, and on MHn35 sites would favor sugar maple over all other species. Shelterwood variants or group selection match best with trees like basswood, which can use large or small gaps on MHn35 sites. Red oak, red maple, and possibly paper birch should do well in the larger gaps created by patch cutting or variants of seed-tree harvests.

A large proportion (39%) of native MHn35 stands were young forest <55 years old. Given that less than 3% of MHn35 forests were described as having been burned or windthrown, it is clear that destructive agents other than these obvious catastrophes were involved to create so much young, small diameter MHn35 forest. We suspect chronic disease and surface fire. What seems clear from the historic records is that young, re-initiated MHn35 stands were patchy and created a mixture of situations where seeding, sprouting, and release of advance regeneration worked together to initiate the next forest. It is highly unlikely that re-initiated MHn35 forests resembled something as uniform as a clear-cut. Clear-cutting with reserves, patch cutting, and variants of seed-tree cutting could all approximate the natural pattern of disturbances that created young MHn35 forests. Clear-cutting with reserves would favor quaking aspen and white pine, which are open regeneration strategists on MHn35 sites. Patch cutting or variants of seed-tree harvests are silvicultural strategies that should work to re-initiate MHn35 stands and favor trees that do well in the open or in large gaps such as paper birch, red oak, and red maple.

Just about 10% of the MHn35 landscape was forest older than 95 years. The hallmark of these forests was the skeletal presence of supercanopy white pine and white spruce over mixed stands of paper birch, basswood, and sugar maple. Below the conifers, the deciduous forests were maintained indefinitely by gap processes. Silvicultural systems that create large gaps such as group selection should favor paper birch and red oak, and also increase the chances of white pine remaining on the site. Silvicultural systems that focus on small gaps like any of the selective systems would favor sugar maple and basswood, and increase the chances of white spruce remaining on the site.

Management Concerns

MHn35 communities occur mostly on medium textured soils where there are legitimate concerns about heavy equipment compacting or rutting the soil. On stagnation moraines, this community consistently occurs on till that is of sandy loam texture or finer. Soil compaction is always a concern with these textures. Because of the usual high relief of stagnation moraines, drainage is good, and when dry, the soils may have adequate strength for heavy equipment. Almost always the soils have firm, subsoil horizons which make rutting a serious risk when the upper horizons are saturated. MHn35 communities are also common on till plains, with soils similar to those on stagnation moraines with regard to texture and firm subsoil horizons. Compaction and rutting are always a concern for the same reasons. In this situation, MHn35 sites are less-well drained because the till plains are flatter and require drying periods far longer than on stagnation moraines. Rarely, MHn35 forests occur on stony till overlying glacially scoured bedrock. Soil texture ranges from coarse sandy loam to quite silty. Field verification of the texture is required to determine if compaction is a concern or not. The bouldery parent material often gains enough skeletal strength from stones to support heavy equipment. In such cases, rutting is not likely.

The landscape balance of growth-stages and stand ages for the MHn35 community is not much different than it was historically. Today, there is slightly less young forest (<55 years) and slightly more mature forest (>95 years) than in pre-settlement times. We believe that wildlife populations are probably reacting to MHn35 habitat as they always have apart from reducing the natural patch size to that of commercial stands. Compositional changes are more of a concern. Most obvious is the loss of white spruce and white pine as a significant component of mature and old MHn35 forests. These species should be conserved or enhanced when opportunities arise. Sugar maple, red maple, and ironwood are the benefactors of modern conditions because logging does not selectively kill these trees as did natural processes. Paper birch, basswood, and white pine now have diminished success because of the maple and ironwood competition. Silvicultural strategies designed to set back these competitors might help to improve the success of paper birch, basswood, and white pine.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 5,887 corners within the primary range of the MHn35 community. At these corners there were 14,788 trees one commonly finds in MHn35 forests.

The PLS field notes described about 2% of the MHn35 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands with some references to post-fire thickets. From these data, a rotation of 970 years was calculated for stand-replacing fire.

Elsewhere in the MHn35 landscape, the surveyors described lands as windthrown or as scattered timber without suitable-sized trees for scribing. Such corners were encountered at about 1% of the time, yielding an estimated rotation of 1,280 years for windthrow.

Far more common at MHn35 sites were references to what we have interpreted as some kind of partial canopy loss, without any explicit mention of fire or windthrow. Most references were to scattered timber, thickets, or sparse forest with distances to bearing trees that were intermediate between the distances for burned/windthrown lands and what is typical for fully stocked mesic hardwood forests. About 4% of the survey corners were described as such, resulting in a calculated rotation of 130 years for disturbances that maintained early and mid-successional trees on MHn35 sites. That more corners were described as burned (85) compared to windthrown (37) suggests that surface fires were the more prevalent cause of partial canopy loss.

Natural Rotations of Disturbance in MHn35 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**970 years**
Catastrophic windthrow photograph	**1,280 years**
Partial Canopy Loss, photograph	**130 years**

MHn35 is similar to most other mesic hardwood (MH) communities in Minnesota in that the rotations of catastrophic disturbance exceed the longevity of any initial cohort species. This means that natural stand dynamics will usually involve a few generations of trees and a shift from large regeneration gaps to smaller ones as stands mature. The rotations of catastrophic fire in northern MH communities form a gradient with MHn35 as the middle member, with richer forests burning less often and wetter forests burning catastrophically more often because of their tendency to have conifers. The rotation of 1,280 years for stand-regenerating wind is typical of MH communities in the northern (MHn) and central (MHc) floristic regions where wind was not an important disturbance agent. This differs from MH communities in the southern and northwestern floristic regions where wind played a significant role. The rotation of 130 years for maintenance disturbances is typical of MHn communities. Maintenance disturbance was sufficient to keep local populations of early successional trees like paper birch and quaking aspen on MHn35 sites and prevent total domination by sugar maple.

Natural Stand Dynamics & Growth-stages

Following stand-regenerating fire or possibly windstorms, young MHn35 forests exhibited modest, but distinctive compositional change from that of the older, parent community. Young forests included a significant legacy of late-successional trees and older forests maintained a significant component of early successional trees **(PLS-1)**. Catastrophe was muted in MHn35 forests, and did not totally eliminate disturbance-sensitive trees. Moderate-scale disturbances were effective in maintaining mixed stands with the full compliment of MHn35 trees. Aspen and paper birch are favored in young forests, and most compositional change is the result of their successive decline beginning with the a decline in aspen followed by a decline in paper birch thus creating a long period of transition **(PLS-4)**. The tendency of old MHn35 stands to have scattered, large white pines and white spruce is the primary reason we chose to recognize compositional movement late in stand development and describe a very old growth-stage.

Views and Summaries for MHn35 sidebar	
PLS-1	**Summary of historic growth-stages:** relative abundance of bearing trees
PLS-2	**View line-graph of historic change:** bearing tree abundance across age-classes
PLS-3	**Summary of historic disturbance:** abundance of bearing trees at burned, windthrown or disturbed sites
PLS-4	**View historic rates of change:** ordination of bearing tree age-classes
PLS-5	**Summary of historic regeneration:** Species ratings regarding their ability to regenerate after disturbance, in gaps, and beneath a canopy
R-1	**Summary of tree suitability for a Native Plant Community:** Species ratings based upon modern forests
R-2	**Summary of understory recruitment in modern forests:** indices of species' success in the understory
FIA-1	**Summary of regeneration in modern forests:** FIA trees in multiple-cohort situations
PLS/FIA-1	**Summary of differences between modern and pre-settlement forests:** relative abundance of bearing trees and FIA trees by growth-stage.

Incredibly, all MHn35 trees had their greatest regenerative success in the young growth-stage ... even though they are quite different with regard to shade-tolerance, successional position, and regeneration strategy. The post-disturbance MHn35 environment must have offered quite a variety of conditions for seeding, sprouting, and release of advance regeneration.

Early in the process of stand maturation, MHn35 stands achieved tree densities that were incredibly stable. Young forests had mean distances from survey corners to bearing trees on the order of 22 feet. The following transition and mature growth stages (55-205 years) had identical means of 20 feet, which is slightly tighter but not significantly different. Only in the second transition and very old MHn35 forest (>205 years) did spacing increase to about 24 feet, which is most likely not significant but possibly the consequence of a supercanopy of white pine or white spruce. The absolute values of these means and the pattern of little or no change during stand maturation is typical of closed-canopy, multi-layered, northern mesic-hardwood communities in general. Even in the post-disturbance years, trees don't lose growing space to other plant growth-forms on MHn35 sites. MHn35 trees never achieve massive crowns, nor do stands thin due to crown-competition. Changes in canopy architecture did not contribute to species' succession on MHn35 sites.

Young Growth-stage: approximately 0-55 years

About 39% of the MHn35 landscape in pre-settlement times was covered by forests estimated to be under 55 years old **(PLS-1)**. By far, most of the young stands were of mixed composition (78%) and monotypic conditions involved almost any species regardless of their successional position. Amazingly, it was about as common for survey corners to be attended only by young sugar maples as it was for only young quaking or big-toothed aspen. Paper birch, basswood, and red oak could also represent all of the bearing trees at young MHn35 survey corners. Fire clearly favored paper birch, quaking aspen, big-toothed aspen, and red oak in the initial cohort (PLS-3). Wind favored paper birch and red oak. Either disturbance must have left some patches of intact groundlayer vegetation as advance regeneration of sugar maple and basswood were able to respond positively to open conditions.

The ability of paper birch and aspen to gain importance in young MHn35 forests is a consequence of their persistence in the mature and old growth-stages. For a pioneer species, quaking aspen shows surprisingly good success in maintaining a bank of suckers and modest success in recruiting some to mid-canopy and canopy heights (R-2). Apparently quaking aspen was successful enough to maintain clone rootstocks that could rapidly repopulate burned or windthrown areas. Big-toothed aspen is considerably less able to do this as it has poor ability to maintain suckers under a canopy. Paper birch on MHn35 sites show poor ability to establish seedlings under a canopy, yet it maintained fairly high presence in mature and very old MHn35 forests enabling it to succeed in young forests. We believe that maintenance disturbances, involving the death of at least several trees perpetuated birch in older stands. In fact, MHn35 sites are such good paper birch habitat that disturbance at any scale resulted in regeneration (PLS-3). Our interpretation is that maintenance disturbance kept a significant presence of paper birch in stands of all ages and that it was always positioned to succeed when a disturbance achieved noteworthy intensity and size.

Our impression is that the post-disturbance environment in MHn35 forests was naturally patchy. In no way could fire have had the homogenizing effect that it can in fire-dependent forests, creating large areas of similar, mineral soil surfaces where quaking aspen and jack pine can totally dominate. It is the nature of MHn35 sites and northern hardwood sites in general to occur on topographically variable landforms where slope, depth to water-perching soil horizons, soil drainage class, and density of included wetlands vary at a fairly fine scale and can affect the behavior and effect of wildfire. We believe also that these site variants have some control over the distribution and abundance of ever-present, native disease vectors (e.g. *Armillaria*) that weaken roots and tree boles. The patchy nature of these diseases and weakened trees probably allowed for a patchy response of MHn35 forest to windthrow. Our general impression is that the "average" stand-regenerating event in MHn35 affected just a little more than half the site, leaving substantial amounts of legacy from the parent forest in the form of trees and advance regeneration in the groundlayer.

Transitional Stage: approximately 55-95 years

Over half, 51%, of the historic MHn35 landscape was forest undergoing considerable compositional change (PLS-1, PLS-5). That most MHn35 stands seemed to be in flux is not at all surprising given our impression that most MHn35 forests were a patchy balance of early and late-successional species. Stands in this stage were more often mixed (87%) than monotypic. Monotypic conditions were represented mostly by survey corners where all bearing trees were paper birch, sugar maple, red oak, or basswood. At survey corners with mixed composition, paper birch was the most cited species and it was mixed with a wide variety of trees including early successional species like aspen and red oak, and also late-successional trees like sugar maple, basswood, elm, and some balsam fir.

The transition stage is driven initially by a precipitous decline in aspen (PLS-2). This decline actually started at the close of the young growth-stage, with the relative abundance of aspen declines significantly between the 30 and 60-year age classes. Because the aspen decline starts early, it is possible that early aspen mortality was due to self-thinning and that the initial drop in relative abundance at about age 30 is just the consequence of other initial-cohort trees having better survivorship. The magnitude of the aspen decline though is such that by the start of the transition stage (55 years), we believe initial-cohort aspen in the canopy were senescing and dying until most were gone by about age 80. After age 80, the relative abundance of aspen was at low, but persistent levels. On the heels of the collapse of initial-cohort aspen is a steady decline of initial-cohort paper birch. This trend started at about age 70 and continued throughout the mature and very-old growth stages. The successive decline of initial-cohort aspen followed by that of paper birch is the main reason for a prolonged transition stage.

The benefactors of the decline in aspen and paper birch were species that we consider more tolerant of shade than aspen and birch. Sugar maple and basswood abundances increase throughout the transition stage **(PLS-1, PLS-2)**, but not as much as one might expect because paper birch was still the dominant tree and was able to replace itself with success comparable to that of sugar maple and basswood. Increases in white spruce and white pine during the transition stage contributed to compositional flux **(PLS-4)** as much as the shade-tolerant hardwoods. For white pine, there is no good evidence that its increase in the transition stage was due to establishment and recruitment of seedlings. Nearly all white pine regeneration was detected during the young growth-stage and its increase during the transition stage must have been due to incredibly good survival and longevity. Ingress of small-diameter white spruce was detected throughout the transition stage and it started to appear as large trees near the close of the transition.

Normally, the first transition in Minnesota forests involves fairly synchronous mortality of initial-cohort trees that were essentially the same age and condition. Succession proceeded because the regeneration opportunities beneath a declining canopy favored more tolerant species in comparison to the open, post-disturbance environment that favored light-loving species. It is common and expected to see small-diameter regeneration of the tolerant species during the transition. For MHn35 this is not the case at all. All important species had their best regenerative opportunities in the young growth-stage **(PLS-5)**, and their regenerative performance in the transition stage was rather balanced among species of quite different shade-tolerance. Only white spruce showed the typical pattern of ingress and success in response to the decline of paper birch. Our best guess is that historically, stand-replacing disturbance and maintenance disturbances on MHn35 sites were of similar intensity and differed only in size. Both must have resulted in patchy and varied regeneration opportunities for MHn35 trees.

Mature Growth-stage: approximately 95 – 205 years

Just 8% of the historic MHn35 landscape was mature forest where the rate of successional change slowed greatly **(PLS-1, PLS-4)**. Stands in this stage were far more likely to be mixed (95%) than monotypic. Patches of pure sugar maple, basswood, and paper birch were most common. Nearly all mixed corners involved paper birch mixed with some other tree. Trees mentioned most often as minor components within the paper birch matrix were sugar maple, basswood, and what must have been the remnants of initial-cohort aspen.

The most striking feature of mature MHn35 forests is that they were a mixture of late-successional and early successional trees. This is in spite of the initial presence of shade-tolerant trees like sugar maple and basswood, where we would assume that they could quickly assert dominance. Though in steady decline throughout the growth-stage, paper birch was able to hold dominance in mature MHn35 forests **(PLS-1)**. It is hard to imagine that it was able to do this without some continued regeneration and recruitment, but we did not detect small-diameter paper birch regeneration past the age of 80 **(PLS-5)**. Paper birch's poor regenerative performance in modern forests **(R-2)**, suggests also that paper birch seedlings need substantially more sunlight to recruit than is offered beneath the canopy of a mature MHn35 forest. We have concluded that only maintenance disturbances, affecting fairly large patches of mature forest (>1 acre) could have slowed the demise of paper birch and perhaps offered a few regenerative opportunities for aspen, red oak, and maybe white pine. Such disturbances must have killed enough sugar maple, or at least sugar maple regeneration to prevent maple dominance. We believe that surface fires accomplished this more so than windthrow or disease. It is significant also that there really was very little mature and very old MHn35 forest. The landscape balance was far more in favor of more recently disturbed stands younger than 95 years (90%, **PLS-1**). Proximity to coniferous forest likely to burn might explain why sugar maple dominance was never achieved in MHn35 forests in contrast to the maple-basswood forests of the central and southern floristic regions. Consistent with this idea is the fact that northern mesic-hardwood forests, and MHn35 in particular, were far more likely to have coniferous components. In this case, both white pine and white spruce were important in the mature growth-stage.

Second Transition Stage: approximately 205 – 295 years
About 1% of the historic MHn35 landscape was forest undergoing considerable compositional change as it approached the very old growth-stage **(PLS-1)**. All survey corners estimated to be this old were of mixed composition. Paper birch is still the most cited tree and could be mixed with almost any other MHn35 species.

Compositional movement in this second transition was driven mostly by the loss of white spruce and to some extent, balsam fir. It is exceedingly unusual in northern Minnesota forests to see substantial ingress and success of white spruce, only to then disappear in older age-classes **(PLS-1)**. More normally, white spruce just continues to show increased regeneration and tree dominance as stands get very old ... to the point where we usually conclude that white spruce is the climax species. Sugar maple though, is the alternative climax species, especially in communities farther south and west of the core part of spruce's range in northeastern Minnesota. The range of MHn35 forests is exactly in the zone of transition between forests to the northeast where spruce dominance seems obvious and forests to the southwest where sugar maple dominance is normally assumed. Because of the varied topography and soils of MHn35 sites, we recognize the patchy nature of forests on these sites. It seems that some patches, probably the slightly wetter and poorer patches resembling the spruce-dominated MHn44 community, could start to succeed towards white spruce climax, but never succeeded. Sugar maple and white pine were the obvious benefactors of spruce's failings during the second transition stage.

Very Old Growth-stage: approximately >295 years
Very little of the historic MHn35 landscape, just 1%, was estimated to have been MHn35 stands older than 295 years **(PLS-1)**. Nearly all (94%) of the corners with these large old trees were mixed in composition. Sugar maple was the only species to occur at monotypic survey corners. Trees that one would find in the initial cohort – paper birch, aspen, and red oak – are still present in very old MHn35 forests. As discussed above, maintenance disturbance must have been involved in maintaining these species. Their presence in very old forests allowed for slight presence to translate into considerable success after stand-regenerating disturbance.

A curiosity is the behavior of white spruce and balsam fir on MHn35 sites. Neither species is important today in MHn35 forests, which is why they were not covered in the MHn35 species behavior accounts. Historically though, both species show their typical behavior on upland sites in the northern floristic region. In the transition stage there is a pulse of balsam fir recruitment, to as much as 10% relative abundance followed by its collapse and persistence at about 1-2% abundance. White spruce, as usual, ingresses at about age 80 **(PLS-5)** and seems well on its way towards dominance in the following age-classes. Usually, the ingress of these species is a sure sign that they will be important, if not dominant in very old forests (but see also MHn47). On MHn35 sites though, they eventually disappear and sugar maple emerges as the ultimate climax species. We don't know why.

There are very few bearing trees contributing to our concept of very old (>295 years) MHn35 forests. The very old growth stage is the consequence of white pine having success when MHn35 forests are left without large disturbances. Also, white pine was the only trees to attain large enough diameters to suspect that a survey corner represented a stand that had escaped disturbance for over nearly 300 years.

Growth Stage Key

Understanding natural growth-stages is important because it offers the opportunity to maintain stands indefinitely by mimicking maintenance disturbance regimes, or to direct succession during transitional episodes of mortality and replacement by other species. Use the following descriptions to determine the growth-stage of the stand you are managing.

Young Forests	•
Transitional Forests	•
Mature Forests	•
Old Forests	•

Tree Behavior

Tree “behavior” is an important element of silviculture and we are interested in it because we want to predict how a tree or stand of trees will respond given a management activity. For example, can we increase the relative abundance or yield of certain crop trees by doing this? Will individual trees grow, die, branch, make seeds, sprout, etc. if we do that?

Behavior is influenced by many things comprising a wide variety of scientific disciplines such as: genetics, physiology, population ecology, and community ecology. Tradition has been to focus on the first three of these as they are properties of a species. Nearly all silvicultural information is currently organized about species – but most authors admit that species properties vary substantially as they interact with other plants and the environment.

Our Native Plant Community (NPC) Classification allows us to contemplate a few elements of community-dependent behavior which can then be blended with the traditional silvics to create a fuller understanding of tree behavior. We view our NPC Classification as an empirical measure of the mind boggling interaction of trees with soil moisture conditions, nutrient availability, competing plants, diseases, pests, and wildlife that occupy the same place. Using this framework is an important paradigm shift because maintenance of these complex interactions is now a stated goal in forest management – in contrast to agricultural approaches where disrupting these interactions was the primary means of getting uniform and desired responses from crop trees.

To this end, we have performed analyses Public Land Survey records, FIA subplots, and releves to answer three very basic questions as to how trees behave in their community context:

- Suitability – for each NPC Class, how often and in what abundance do we see certain tree species in stands where there has been no obvious effort to silviculturally alter abundance or remove competition?
- Succession – for each NPC Class, what was the natural reaction to fire and windthrow and how did the different species succeed one another?

Regeneration strategies – for each common species within a NPC Class, what were/are the natural windows of opportunity for regeneration throughout the course of succession?

Sugar Maple

- ***excellent habitat suitability rating***
- ***late-successional***
- ***small-gap regeneration strategist***
- ***regeneration window at 0-50 years***

Suitability
MHn35 sites provide ***excellent habitat*** for sugar maple trees. The perfect ***suitability rating*** of 5.0 for sugar maple is influenced mostly by its very high presence (81%) as trees on these sites in modern forests **(R-1)**. When present, sugar maple is an important co-dominant and sometimes dominant tree, contributing 32% mean cover in mature stands. The ranking is perfect, because no other tree or plant has a higher presence and cover on MHn35 sites as sampled by releves. Northern mesic hardwood communities in general offer excellent-to-good habitat for sugar maple (see Suitability Tables). Sugar maple is the highest ranked tree when it occurs in the better drained communities: MHn35, MHn45, MHn47.

Young Growth-stage: 0-55 years
Historically, sugar maple was an important tree in young MHn35 stands **(PLS-1, PLS-2)**. Amazingly, young sugar maples represented 11% of the trees at survey corners described as burned **(PLS-3)**. This result is not at all consistent with its well-known sensitivity to fire. Sugar maple was also an important tree at windthrown corners, representing 8% of the trees at such survey corners. This result is expected if the effect of windthrow was to remove canopy trees and release the ever-present advance regeneration of sugar maple in older stands. This is also the tree's reaction to logging in modern forests as sugar maple tends to dominate post-logging MHn35 forests **(PLS/FIA-1)**. It is important to note that the actual number of trees recorded at survey corners directly described as burned or windthrown is low (335 corners) and perhaps unreliable **(PLS-3)**. For such few direct observations of disturbed forests there was a surprising amount of young MHn35 forest (39%), meaning that the surveyors didn't often ascribe any disturbance to the small-diameter stands **(PLS-1)**. Sugar maple regeneration coming in among larger trees was substantial in the post-disturbance recruitment window **(PLS-5)** and remains at similar levels throughout the young growth-stage. Almost all occurrences of smaller-diameter maples were at survey corners of mixed composition. These young trees could come in under almost any other species, but did so more often beneath larger quaking aspen and paper birch. Although it is tempting to dismiss what seems to be unusual behavior of sugar maple to low sample numbers in the initial age-class, the following age-classes are well-populated samples and they are obviously a continuation of sugar maple's immediate success in disturbed MHn35 forests. Our interpretation is that the success of sugar maple in the young growth-stage is the consequence of releasing the pervasive bank of seedlings common in older MHn35 forests. The historic reaction of the seedling bank to windthrow and modern reaction to canopy removal through logging is quite in line with this hypothesis. Regeneration of MHn35 stands by fire is problematic in that such fires needed to be intense enough to kill trees, but not eliminate the advance regeneration of sugar maple. We favor the idea that the effect of fire burning through hardwoods was patchy and at a fine scale, leaving enough of a maple legacy in wet depressions and swales to repopulate the stand. Alternatively, the surveyors were mistaken. A common field error is to mistake the jet black, maple boles and branches on the forest floor for charred wood. The black color comes from a fungus that lives on the surface of dead maple debris.

Transition: 55-95 years
As stands transitioned to mature conditions sugar maple increased in abundance **(PLS-1)**. We estimate that this increase started immediately after disturbance and continued throughout the life of the stand until sugar maples were dominant **(PLS-2)**. Small-diameter, sugar maple regeneration was often observed coming in among larger trees during the transition stage until the 90-year age-class **(PLS-5)**. In most cases, young sugar maples were coming in under paper birch and quaking aspen. However, there is a long list of species below which we recorded sugar maple

regeneration, meaning that maple was having no problem replacing any species on MHn35 sites. Most important, and different from the young growth-stage, is that a substantial amount of regeneration was beneath older maples presumably belonging to the initial-cohort. We interpret this as good success at establishment and recruitment of seed-origin maples under a canopy, and initial development of the multi-layered structure that helps sugar maple dominate less-tolerant trees. This interpretation is strongly supported by sugar maple's perfect indices of regeneration in modern forests **(R-2)** and its performance on FIA plots **(FIA-1)** were it does well in all subordinate situations (12, 13, 23).

Mature Growth-stage: 95-205 years

The mature growth-stage is really the last episode where we have adequate numbers of bearing trees to interpret the historic behavior of sugar maple. The relative abundance of sugar maple stablilized at about 14% during the mature growth-stage **(PLS-1, PLS-2)**, and this is why we consider sugar maple a ***late-successional*** species on MHn35 sites. Its steady presence was the result of good establishment and recruitment for the first 90 years of stand maturation **(PLS-5)**, followed by good survivorship. Surprisingly using our restrictive half-diameter rule, small-diameter sugar maple regeneration was not detected during the mature growth-stage, whereas it was common until the 90-year age-class **(PLS-5)**. At mature survey corners, sugar maples were far more common as the smaller tree at a survey corner compared to when it was the larger tree. We interpret this as sugar maple continuing to build its abundance in the subcanopy. When sugar maple was the smallest tree, it was coming in among a long-list of almost any tree that can occur on an MHn35 site. It was most common for sugar maple to be beneath paper birch, basswood, and white pine. Less often, it was subordinate to American elm, quaking aspen, and itself. We interpret this as sugar maple demonstrating its eventual dominance of MHn35 sites as it was successful in all strata of a mature forest with any overstory composition.

Second Transition and Very Old Growth-stage: 205-295 years and older

Very few bearing trees contribute to our concept of second transition and very old MHn35 forests. Both stages are the consequence of white pine having some success when MHn35 forests are left without large disturbances. Also, white pines were the only trees to attain large enough diameters to suspect that a survey corner represented a stand that had escaped disturbance for over 200 years. The relative abundance of sugar maple in the very old growth-stage is quite high (29%) and second only to white pine **(PLS-1)**. More reliable though are the age-class estimates throughout the mature growth stage were it seems clear that sugar maple abundance was stable at about 14% and if anything was declining slightly as white spruce and white pine made some gains **(PLS-2)**. Our interpretation is that very old MHn35 forests had a skeletal presence of supercanopy white spruce and white pine that probably had little influence on sugar maple's ability to dominate the lower strata. Sugar maple abundance probably did increase in these very old forests, but mostly in response to losses in paper birch.

Regeneration Strategy

Sugar maple's primary regenerative strategy on MHn35 sites is to develop a pervasive bank of seedlings capable of recruiting in ***small-gaps***. However, sugar maples were successful at this following almost any degree of canopy removal, ranging from catastrophic events to single-tree gaps. They were able to do this in the presence of any other species of tree, including other sugar maples. In the historic PLS data this interpretation is supported by: (1) the fact that sugar maple is important in the mature and very-old growth-stages of the community **(PLS-1, PLS-2)**, and (2) it is most abundant at survey corners showing no canopy loss or disturbance **(PLS-3)**. The high percent of sugar maples as seedlings in subordinate canopy situations (situations 12 and 13) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate best in small gaps. The releve sampling of mature MHn35 forests shows that sugar maple is unequalled at establishing and recruiting individuals in all understory strata, eventually resulting in canopy dominance **(R-2)**.

Historic Change in Abundance

Today, sugar maple is substantially more abundant and more dominant on MHn35 sites than it was historically **(PLS/FIA-1)**. Its populations have essentially doubled in historic time. The increase from 11% abundance in young, native stands to 24% in modern stands suggests that it has benefited from typical forest management. It increase from historic abundance of 14% to 32% in modern mature stands suggests that it has also benefited from passive management. Its 82% presence in releves, which are a biased sampling of unmanaged stands, suggests that it has benefited from no management at all **(R-1)**. Sugar maple is king on MHn35 sites. We believe that the odd surface fire was the only check on its populations in the past. Though present at burned survey corners at unexpected abundance (11%, **PLS-3**), such levels were the minimum abundance that one would have seen throughout the course of natural stand maturation. We anticipate that sugar maple's strong dominance of MHn35 sites will complicate our attempts to manage these sites for any other species.

Basswood

- ***excellent habitat suitability rating***
- ***mid- (late) successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at 0-40 years***

Suitability
MHn35 sites provide ***excellent habitat*** for basswood trees. The ***suitability rating*** of 4.8 for basswood is influenced mostly by its high presence (65%) as trees on these sites in modern forests **(R-1)**. When present, basswood is an important co-dominant tree, contributing 15% mean cover in mature stands. The ranking is second, behind sugar maple on MHn35 sites as sampled by releves. Northern mesic hardwood communities in general offer excellent-to-good habitat for basswood (see Suitability Tables). Among these, MHn35 offers the best opportunity for growing basswood.

Young Growth-stage: 0-55 years
Historically, basswood was a tree of modest importance in young MHn35 stands **(PLS-1, PLS-2)**. Young basswood represented 7% of the trees at survey corners described as burned **(PLS-3)**. This result is consistent with its well-known ability to sprout when fire or another agent kills the main stem. Basswood was equally successful at windthrown corners where it also represented 7% of the trees present. Small-diameter, basswood ***regeneration*** coming in among larger trees was abundant in the post-disturbance window, peaking immediately and lasting until the ***40-year*** age-class **(PLS-5)**. Our interpretation is that a substantial bank of basswood seedlings and stump sprouts were available to re-colonize MHn35 stands following removal of the canopy.

Transition: 55-95 years
As stands transitioned to mature conditions basswood increased in abundance **(PLS-1)**. We estimate that this increase started immediately after disturbance and continued for the life of the stand until basswoods were important co-dominants in old stands **(PLS-2)**. Small-diameter basswood regeneration was common early in the transition and lasting until the 70-year age-class **(PLS-5)**, but at levels far less than in the young growth stage. In most cases, young basswoods were coming in under other quaking aspen, paper birch or American elm, however the list of species includes just about any tree that can grow on MHn35 sites. We interpret this as good success at establishment and recruitment of seed-origin basswood during the transition under a canopy of any species, and also high survivorship of trees established in the young growth-stage. This interpretation is supported by basswood's excellent indices of regeneration in modern forests **(R-2)** and its performance on FIA plots **(FIA-1)** were it does well in all subordinate situations (12, 13, 23).

Mature Growth-stage: 95-205 years
The mature growth-stage is really the last episode where we have adequate numbers of bearing trees to interpret the historic behavior of basswood. The relative abundance of basswood peaks at about 9% during the mature growth-stage and declines in very old forests **(PLS-1, PLS-2)**. This is why we consider basswood to be primarily a ***mid-successional*** species. Its steady presence was the result of establishment and recruitment for the first 70 years of stand maturation **(PLS-5)** and high survivorship as trees. Using our restrictive half-diameter rule, small-diameter basswood regeneration was not detected during the mature growth-stage, whereas it was common throughout the earlier stages. At this time, basswoods were slightly more common as the smaller tree at a survey corner compared to when it was the larger tree. We interpret this as basswood having good success in the subcanopy, relying more on survivorship than a large pool of small trees like sugar maple. When basswood was the smallest tree, it was coming in among a long-list of almost any tree that can occur on an MHn35 site. It was most common for basswood to be beneath paper birch, white pine, American elm and older basswood. We interpret this as

basswood demonstrating its eventual co-dominance on MHn35 sites as it was successful in all strata of mature forests with any overstory composition.

Second Transition and Very Old Growth-stage: 205-295 years and older
Very few bearing trees contribute to our concept of second transition and very old MHn35 forests. Both stages are the consequence of white pine having some success when MHn35 forests are left without large disturbances. Also, white pines were the only trees to attain large enough diameters to suspect that a survey corner represented a stand that had escaped disturbance for over 200 years. The relative abundance of basswood in the very old growth-stage is lower (6%) than it was during the mature growth-stage **(PLS-1)**. More reliable though are the age-class estimates throughout the mature growth stage were it basswood abundance oscillated between 5 and 10%. Its ability to persist in very old forests is why we consider basswood to have also some properties of ***late-successional*** species. Our interpretation is that very old MHn35 forests had a skeletal presence of supercanopy white spruce and white pine that probably had little influence on basswood's ability to maintain its presence in lower strata.

Regeneration Strategies
On MHn35 sites basswood exhibits regenerative flexibility, which allows it to be a minor, but ever-present tree throughout the full course of stand maturation. Basswood sprouts effectively following disturbances that kill the main stem, and it is able to carry its density as a tree into young growth stages. Its slightly lower abundance in the young growth stage **(PLS-1)** could be due to the fact that other species, especially quaking aspen and paper birch, react to disturbance by creating many more new aerial stems or seedlings than does basswood. Basswood also maintains a bank of seedlings capable of recruiting in gaps of any size. Basswoods were successful at this beneath other tree species and well as under larger basswoods. We believe that basswood was most successful increasing its presence locally by recruiting seedling in ***large canopy gaps***. In the historic PLS data this interpretation is supported by the fact that basswood abundance peaks in response to the decline of initial-cohort quaking aspen **(PLS-1, PLS-2)**, when we presume some fairly large canopy gaps. The high percent of basswood poles among trees in the FIA data (situation 23) is especially characteristic of species that tend to regenerate best in large gaps **(FIA-1)**. The releve sampling of mature MHn35 forests shows that basswood excels at establishing and recruiting individuals in all regenerating strata **(R-2)**. Its regenerative indices (4.3-4.5) are more in line with trees that use ***smaller gaps***.

Historic Change in Abundance
Today, basswood is more abundant and more dominant on MHn35 sites than it was historically **(PLS/FIA-1)**. Its populations have essentially doubled in historic time, paralleling the gains of its co-associate, sugar maple. We believe that fire suppression, though infrequent historically, is the primary reason for seeing basswood populations increase on MHn35 sites at paper birch's expense. Its high presence as a tree in the releves **(R-1)** would indicate that it will probably continue to increase in abundance relative to other trees in unmanaged stands.

Northern Red Oak

- ***excellent habitat suitability rating***
- ***early (mid-) successional***
- ***large-gap (open) regeneration strategist***
- ***regeneration window at 0-50 years***

Suitability
MHn35 sites provide ***excellent habitat*** for red oak trees. The ***suitability rating*** of 4.7 for red oak is influenced mostly by its high presence (49%) as trees on these sites in modern forests **(R-1)**. When present, red oak is an important co-dominant tree, contributing 20% mean cover in mature stands. The ranking is third behind sugar maple and basswood on MHn35 sites as sampled by releves. Northern mesic hardwood communities in general offer good-to-excellent habitat for red oak within its native range (see Suitability Tables). Among these, MHn35 offers the best opportunity for red oak.

Young Growth-stage: 0-55 years
Historically, red oak was an important tree in young MHn35 stands recovering from stand-regenerating disturbance **(PLS-1, PLS-2)**. Young red oaks represented 18% of the trees at survey corners described as burned, which is behind only paper birch and quaking aspen **(PLS-3)**. Red oak was also a very important species following windthrow, representing 28% of the trees at such survey corners. However, windthrow was not an important means of regenerating MHn35 forests. Young MHn35 corners with red oak trees present were almost always mixed (95%) with attending bearing trees being combinations of red oak mixed mostly with quaking aspen and some paper birch. Small-diameter, red oak regeneration coming in among larger trees was common throughout the entire growth-stage and at its peak in the post-disturbance window **(PLS-5)**. During this stage, red oak showed a preference for coming in among larger quaking aspen. Less often, red oak regeneration would come in among paper birch and larger red oaks. Because red oak has peak presence and was so abundant at disturbed survey corners, we consider it to be primarily an ***early successional*** species on MHn35 sites (but see Transition Stage below).

Transition: 55-95 years
As stands transitioned to mature conditions red oak generally decreased in abundance **(PLS-1)**. However, the young and transition growth-stages are long, and averaging the relative abundance of red oak masks a definite peak of red oak abundance between the 40 and 70 year age-classes **(PLS-2)**. Because of this peak, it is fair to ascribe some ***mid-successional*** behavior to red oak on MHn35 sites. We believe that some of this peak was the consequence of red oaks established in the young growth-stage just outliving initial-cohort quaking aspen and paper birch. Small-diameter, red oak regeneration was still detectable in the early years of the transition stage and young red oaks were coming in among larger trees up until about age 70 **(PLS-5)**. In most cases red oak regeneration was still coming in under aspen, but at this stage far more red oak regeneration was showing the tendency to come in among paper birch and other red oaks compared to the young growth-stage. We interpret this as limited success at establishment and recruitment of seed-origin oak under a partial canopy of initial-cohort trees. Also, it seems likely that the collapse of the initial-cohort aspen released red oak seedlings established during the young growth-stage.

Mature Growth-stage: 95-205 years
The mature growth-stage is really the last episode where we have adequate numbers of bearing trees to interpret the historic behavior of red oak. The relative abundance of red oak declines throughout the growth-stage, but the percentages are low and it would be more accurate to describe its presence as at sustainable, background abundances in the vicinity of 5% **(PLS-1, PLS-2)**. Small-diameter red oak regeneration was not detected during the mature growth-stage, whereas it was steadily present until age 70 **(PLS-5)**. At this time, red oaks were more common as the smaller tree at a survey corner compared to when it was the larger tree. We interpret this as

red oak having limited success recruiting advance regeneration, though no red oak bearing trees met our half-diameter rule. Red oak's excellent-to-good performance in regenerating strata in modern forests supports the idea that red oak could maintain presence in mature stands by regeneration and recruitment **(R-2)**. When red oak was the smaller tree at a survey corner, there was a surprising tendency for the larger trees to be white pine and even some red pine. Our best guess is that maintenance surface-fires affected some patches of MHn35 habitat in a way that promoted limited opportunities for pine and red oak that was not typical of the broader MHn35 landscape.

Second Transition and Very Old Growth-stage: 205-295 years and older
Very few bearing trees contribute to our concept of second transition and very old MHn35 forests. Both stages are the consequence of white pine having some success when MHn35 forests are left without large disturbances. Also, white pines were the only trees to attain large enough diameters to suspect that a survey corner represented a stand that had escaped disturbance for over 200 years. The relative abundance of red oak in the very old growth-stage is just 1%, suggesting that it might eventually disappear from very old MHn35 forest **(PLS-1)**. However, it was exceedingly rare for MHn35 sites to avoid maintenance disturbances capable of regenerating some red oak for such a long time.

Regeneration Strategies
Red oak's primary regenerative strategy on MHn35 sites is to fill ***large-gaps***. It was most successful at this when gaps were forming within a declining canopy of initial-cohort quaking aspen and to some extent paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that red oak abundance peaks in response to the decline of the initial cohort species **(PLS-2)**, (2) it is most abundant at survey corners showing partial canopy loss **(PLS-3)**, and it shows measurable establishment in a gap window **(PLS-5)**. The high percent of red oak poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate best in large gaps. The releve sampling of mature MHC26 forests shows that red oak has some success beneath a canopy. Its regenerant and seedling indices are excellent, however its sapling index is just good. This means that there is a bottleneck in red oak recruitment as it has difficulty getting seedlings to heights over 2m. The bottleneck and just good sapling index (3.3) is typical of large-gap species. It is important to note though that red oak was most abundant in young MHn35 forests and that its window of establishment was best in the post-disturbance years. Impressive also is red oak presence at survey corners described as having been catastrophically burned or windthrown. Red oak clearly has regenerative strategies that allow it to perform in ***open habitat***. Our interpretation is that the best opportunity for seed-origin oaks was in large-gaps, and stump sprouts served as a reliable mechanism to re-colonizing MHn35 forests destroyed by fire or wind.

Historic Change in Abundance
Today, it seems that red oak on MHn35 sites is in some peril based upon FIA data because there are very few sapling and pole stands with red oak in comparison to older stands **(FIA-1)**. The decline in red oak is most evident in the young growth-stage as it now represents just 6% of the FIA trees as compared to 10% of the bearing trees **(PLS/FIA-1)**. There is, however, substantially more red oak in mature MHn35 forests (11%) than there was historically (5%). An examination of the age-class data shows that the point in time where there is consistently more or less red oak now than historically is at age 70. Our interpretation is that red oak has done better than they did historically in unmanaged stands and poorly where, most likely, MHn35 stands have been managed for quaking aspen. The high presence of red oak trees **(R-1)** and especially its high presence in the understory **(R-2)** in the little-disturbed stands sampled by releves supports this idea. Our general impression is that red oak would benefit from silvicultural attention when MHn35 stands are regenerated and that there should be plenty of opportunities to do so.

Paper Birch

- ***excellent habitat suitability rating***
- ***early successional***
- ***open (large-gap) regeneration strategist***
- ***regeneration window at 0-40 years***

Suitability
MHn35 sites provide ***excellent habitat*** for paper birch trees. The ***suitability rating*** of 4.6 for paper birch is influenced mostly by its high presence (61%) as trees on these sites in modern forests **(R-1)**. When present, paper birch is an important co-dominant and sometimes dominant tree, contributing 13% mean cover in mature stands. The ranking is fourth behind sugar maple, basswood, and northern red oak on MHn35 sites as sampled by releves. Northern mesic hardwood communities in general offer excellent habitat for paper birch, and MHn35 sites are as good as any (see Suitability Tables).

Young Growth-stage: 0-55 years
Historically, paper birch was the dominant tree in young MHn35 stands recovering from stand-regenerating disturbance **(PLS-1, PLS-2)**. Young paper birch represented 32% of the trees at survey corners described as burned, which is more than any other tree **(PLS-3)**. Paper birch was also the leading species following windthrow, representing 36% of the trees such survey corners. Young MHn35 corners with paper birch trees present were mostly of mixed composition (87%), which is unusual for a dominant tree and means that it was widespread and important throughout the community's range. Its dominance in the young growth-stage and its leading abundance following fire and windthrow is why we consider paper birch to be an ***early successional*** species on MHn35 sites. Small-diameter, paper birch regeneration was most often observed coming in among larger trees in the post-disturbance window **(PLS-5)**. Most birch regeneration was coming in beneath quaking aspen, but it was common also for paper birch to be beneath older paper birch. We interpret paper birch's regenerative success in the post-disturbance years as it showing excellent ability to recruit into under-stocked areas of burned or windthrown stands.

Transition: 55-95 years
Transitioning of young MHn35 forests was driven by the steady loss of initial-cohort aspen early in the stage, followed by some loss of the longer-lived paper birch as stands approached age 95 **(PLS-1, PLS-2)**. We estimate that this decline started at about age 70 and continued until stands became very old. However, this decline is slow and paper birch remained an important tree in older growth-stages. Small-diameter, paper birch regeneration was coming in among larger trees until about age 80 **(PLS-5)**. Most often, paper birch was coming in under other paper birch and quite old quaking aspen. Be believe that near the end of the transition period, it was common for some rather pure stands of paper birch to form on MHn35 sites as initial-cohort quaking aspen dropped out. The 80-year regeneration window is unusually long for a post-disturbance dominant, and this long window is the main reason that paper birch maintained a presence in older MHn35 forests.

Mature Growth-stage: 95-205 years
The mature growth-stage is really the last episode where we have adequate numbers of bearing trees to interpret the historic behavior of paper birch. The relative abundance of paper birch declines throughout the growth-stage, but the decline is slow from about 40% at the beginning to about 10% at the conclusion of this long growth-stage (average 28%; **PLS-1, PLS-2)**. Small-diameter paper birch regeneration was not detected during the mature growth-stage, whereas it was steadily present throughout the earlier stages. At this time, paper birches were more common as the larger tree at a survey corner compared to when it was the smaller tree. By far, smaller-diameter birches were most often coming in under older paper birch and some quaking aspen. We interpret this as paper birch having some recruitment beneath itself, and having very little regenerative success in stands that were well on their way to being dominated by sugar

maple. Paper birch's poor performance in regenerating strata in modern forests supports the idea that paper birch could maintain presence in mature stands by regeneration and recruitment in just a few limited areas **(R-2)**. We believe that maintenance surface-fires affected some patches of MHn35 habitat in a way that promoted limited opportunities for paper birch that was not typical of the broader, maple-dominated MHn35 landscape.

Second Transition and Very Old Growth-stage: 205-295 years and older
Very few bearing trees contribute to our concept of second transition and very old MHn35 forests. Both stages are the consequence of white pine having some success when MHn35 forests are left without large disturbances. Also, white pines were the only trees to attain large enough diameters to suspect that a survey corner represented a stand that had escaped disturbance for over 200 years. The relative abundance of paper birch in the very old growth-stage was still rather high (12%), which seems to have been the consequence of it replacing itself in pure pockets of paper birch and probably some regenerative success reacting to maintenance surface fires **(PLS-1)**.

Regeneration Strategies
Paper birch's primary regenerative strategy on MHn35 sites is to dominate ***open habitat*** after stand-regenerating disturbance. It was about equally successful at this following fire or windthrow **(PLS-3)**. In the historic PLS data this interpretation is supported by: (1) the fact that paper birch was the most abundant tree in young forests **(PLS-1)**, (2) paper birch represented the largest proportion of bearing trees at burned and windthrown corners **(PLS-3)**, and (3) paper birch's peak regeneration was in the post-disturbance window **(PLS-5)** with it's absolute peak being the initial age-class. The high percent of paper birch as poles in pole stands (situation 22) in the FIA data is also characteristic of species that regenerate effectively in the open but its low percentage as saplings in sapling stands (situation 11) suggests that it is not as effective in the open as quaking aspen **(FIA-1)**. Most likely this is the consequence of most modern stands being regenerated by clear-cut logging rather than fire or windthrow. Paper birch's poor regenerant and seedling indices (1.7-1.3) in modern stands sampled by releves is also very consistent with the idea that it prefers open habitat **(R-2)**.

The persistence of paper birch in older stands is the main reason to suspect that paper birch has some regenerative ability in ***large gaps***. This idea is supported by the long, 80-year regeneration window **(PLS-5)**. The high percentage of paper birch poles in tree stands (situation 23) is particularly characteristic of trees that are successful at recruiting in large gaps **(FIA-1)**. Ultimately paper birch lost to small-gap specialists like sugar maple, but the process was long and drawn out because maintenance events like surface fires were effective in killing sugar maple.

Historic Change in Abundance
Today, it seems that paper birch on MHn35 sites is in some peril based upon FIA data because there are very few sapling stands with paper birch in comparison to older stands **(FIA-1)**. The decline in paper birch is evident in all growth-stages. In the young growth-stage it now represents just 9% of the FIA trees compared to 38% of the bearing trees **(PLS/FIA-1)**. This strongly suggests to us that paper birch is not regenerating after logging nearly as well as it did in response to fire or windthrow. Mature MHn35 forests also have considerably less paper birch (7%) than they had historically (28%). There are no very old MHn35 forests today. Although paper birch has 61% presence as a tree in little-disturbed MHn35 forests **(R-1)**, its limited presence in the understory **(R-2)** indicates that it is stumbling without active management as well. Our general impression is that paper birch would benefit from silvicultural attention when MHn35 stands are regenerated.

Quaking and Big-toothed Aspen

- ***excellent habitat suitability rating for quaking aspen***
- ***good habitat suitability rating for big-toothed aspen***
- ***early successional***
- ***open regeneration strategists***
- ***regeneration window at 0-40 years***

Identification Problems
The PLS surveyors did not distinguish between quaking and big-toothed aspen. Thus, interpretations of PLS data for the more common quaking aspen should always be done knowing that some of these trees were likely big-toothed aspen. MHn35 releve samples show that for plots with aspen present: 9% have both species present; 23% are big-toothed aspen without quaking aspen; 68% are quaking aspen without big-toothed aspen. We consider quaking and big-toothed aspen to be ecologically equivalent for most silvicultural considerations.

Suitability
MHn35 sites provide ***excellent habitat*** for quaking aspen trees. The ***suitability rating*** of 4.4 for quaking aspen is influenced mostly by its high presence (31%) as trees on these sites in modern forests **(R-1)**. When present, quaking aspen is an important co-dominant and sometimes dominant tree, contributing 20% mean cover in mature stands. This ranking is fifth, following sugar maple, basswood, northern red oak, and paper birch on MHn35 sites. Northern mesic hardwood communities in general offer varying habitat for quaking aspen, favoring the MHn35, MHn44, and MHn46 communities in the north-central part of the state (see Suitability Tables). Among the better drained hardwood communities, MHn35 offers the best commercial opportunity for growing quaking aspen.

MHn35 sites provide ***good habitat*** for big-toothed aspen trees. The ***suitability rating*** of 3.7 for big-toothed aspen is based upon its 13% presence and 19% mean cover when present **(R-1)**. This ranking is seventh highest among trees common on MHn35 sites. MHn35 is by far the best northern mesic hardwood community for big-toothed aspen (see Suitability Tables).

Young Growth-stage: 0-55 years
Historically, aspen was an important tree in young MHn35 stands recovering from stand-regenerating disturbance **(PLS-1, PLS-2)**. Young aspen represented 22% of the trees at survey corners described as burned, which is second only to paper birch **(PLS-3)**. Aspen was common at windthrown survey corners as well with 11% relative abundance, following only paper birch and red oak. For a post-disturbance dominant, it was surprising to find that aspen trees were almost always mixed with other species at survey corners considered younger than 55 years. Just 6% of these corners were attended by all aspen. Typical though of a true initial-cohort tree these aspen were mostly the largest tree at young MHn35 corners. Aspen's abundance in the young growth-stage and its importance following fire and windthrow is why we consider aspen to be an ***early successional*** species on MHn35 sites. Small-diameter, aspen regeneration was abundant in the post-disturbance window, but drops to nearly nothing by age 40 **(PLS-5)**. Nearly all aspen regeneration was coming in beneath other aspen, but it was common also for them to be beneath older, initial-cohort red oak and paper birch. We interpret aspen's regenerative success in the post-disturbance years as it showing excellent ability to recruit into under-stocked areas of burned or windthrown stands.

Transition: 55-95 years
Transitioning of young MHn35 forests was driven by the steady loss of initial-cohort aspen early in the stage, followed by some loss of the longer-lived paper birch as stands approached age 95 **(PLS-1, PLS-2)**. We estimate that this decline started as early as age 30, with the greatest loss between the 30 and 50 year age-classes just prior to the transition stage. This trend slowed, but continued throughout the transition stage until there were no initial-cohort aspen left. Small-

diameter, aspen regeneration coming in among larger trees was detectable until age 60 **(PLS-5)**, but was not a significant means of establishing aspen. Smaller diameter trees, most likely established at the end of the young growth stage, were present and coming in beneath older aspen, paper birch, and sometimes red oak. It was exceedingly rare for smaller diameter aspen to be beneath shade-tolerant hardwoods like sugar maple and basswood. Our interpretation is that for aspen, the transition stage on MHn35 sites was a period where mature trees senesced and died without much regeneration or replacement.

Mature Growth-stage: 95-205 years
The mature growth-stage is really the last episode where we have adequate numbers of bearing trees to interpret the historic behavior of aspen. By the beginning of the mature growth-stage, the initial-cohort aspen were gone and its relative abundance stabilized at about 4-6% **(PLS-1, PLS-2)**. Small-diameter aspen regeneration was not detected during the mature growth-stage. At this time, aspen were more common as the larger tree at a survey corner compared to when it was the smaller tree. When aspen were the smaller trees at survey corners, they were subordinate to paper birch and sometimes white pine. We believe that the low, but steady, presence of aspen in the mature growth stage is an expression of its limited ability to persist in older MHn35 forests. Because of its association with less-tolerant trees and avoidance of shade-tolerant species, we favor the idea that maintenance disturbances were responsible for any regeneration and recruitment beyond the initial-cohort. In modern forests, quaking aspen actually has good indices of regeneration for regenerants and seedlings (3.7-3.3), but it has trouble recruiting to heights above 2m **(R-2)**. Almost certainly this is a sucker bank, and as long as there are even a few canopy aspen present, suckers can occur throughout MHn35 stands. Creeping surface fires and perhaps some pocket diseases of hardwoods could have created canopy openings large enough to release patches of these suckers and account for about 6% relative abundance of aspen in mature MHn35 forests. Big-toothed aspen is not nearly as successful as quaking aspen regenerating under a canopy **(R-2)**, and big-toothed aspen probably were not a significant component of persistent aspen in the mature growth-stage. Though the background abundance of aspen is low in mature stands, its persistence allowed it to be an important tree following major disturbances.

Second Transition and Very Old Growth-stage: 205-295 years and older
Very few bearing trees contribute to our concept of second transition and very old MHn35 forests. Both stages are the consequence of white pine having some success when MHn35 forests are left without large disturbances. Also, white pines were the only trees to attain large enough diameters to suspect that a survey corner represented a stand that had escaped disturbance for over 200 years. The relative abundance of aspen in the very old growth-stage (4%) was essentially the same as it was in the mature stage (6%, **PLS-1**). We believe that aspen persisted in the very old growth-stage the same way that it did in the mature stage, as limited regeneration in response to maintenance disturbances.

Regeneration Strategy
Quaking aspen's primary regenerative strategy on MHn35 sites is to occupy ***open habitat*** after stand-regenerating disturbance. It was most successful at this following fire, but windthrow too removed enough canopy for aspen to thrive **(PLS-3)**. In the historic PLS data this interpretation is supported by: (1) the fact that aspen was an abundant tree in young forests **(PLS-1)**, (2) aspen represented a large proportion of bearing trees at burned and windthrown corners **(PLS-3)**, and (3) aspen's peak regeneration was in the post-disturbance window **(PLS-5)** with it's absolute peak being the initial age-class. The high percent of quaking aspen and big-toothed aspen as saplings in sapling stands (situation 11) in the FIA data is also characteristic of species that regenerate effectively in the open **(FIA-1)**. The releve sampling of mostly transitional MHn35 forests shows that quaking aspen under 2m tall are fairly common **(R-2)**. These are mostly suckers, and even a few canopy aspen can maintain a fairly extensive sucker bank. These suckers are unlikely to succeed unless large canopy gaps form over them. Big-toothed aspen is not nearly so good as quaking aspen in maintaining a sucker bank and may have depended more on seeding into burned or windthrown MHn35 stands.

Historic Change in Abundance

Today, aspen is about as abundant as it ever was on MHn35 sites. Its relative abundance and distribution among the growth stages in stands sampled by FIA plots is nearly identical to our estimates based upon bearing trees **(PLS/FIA-1)**.

Red Maple

- ***excellent habitat suitability rating***
- ***mid-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at ~30 years***

Identification Problems
The PLS surveyors did not consistently distinguish between red and sugar maple. Thus, interpretations of PLS data for the less common red maple should always be done knowing that some of these trees were likely sugar maple. MHn35 releve samples show that for plots with maple present: 29% have both species present; just 6% have red maple without sugar maple; 65% have sugar maple without red maple.

Suitability
MHn35 sites provide ***excellent habitat*** for red maple trees. The ***suitability rating*** of 4.1 for red maple is influenced mostly by its presence (31%) as trees on these sites in modern forests **(R-1)**. When present, red maple can be an important co-dominant tree, contributing 12% mean cover in mature stands. The ranking is sixth behind sugar maple, basswood, northern red oak, paper birch, and quaking aspen on MHn35 sites as sampled by releves. Northern mesic hardwood communities in general offer fair-to-excellent habitat for red maple (see Suitability Tables). MHn35 along with MHn44 and MHn46 offer excellent opportunities for growing red maple.

Young Growth-stage: 0-55 years
Historically, red maple was present in just trace amounts in young MHn35 stands recovering from stand-regenerating events **(PLS/FIA-1)**. Young red maples were not recorded at all at survey corners described as burned or windthrown **(PLS-3)**. Possibly though, red maple might account for some of the surveyor's generic references to maple that were assigned to sugar maple. Small-diameter, red maple regeneration was first detected in trace amounts in the 20- to 50-year age-classes at the close of the young growth-stage **(PLS-5)**. Our interpretation is that there was very limited regeneration of red maple under the initial-cohort paper birch and aspen. Though the sample numbers are low, red maple seems to peak in abundance as a tree at about age 50, some 20 years after we detected its peak regeneration at age 30. For this reason we consider red maple to be ***mid-successional***.

Transition: 55-95 years
As stands transitioned to mature conditions red maple persisted in trace amounts until about age 80 **(PLS/FIA-1)**. After that, there were no further surveyor references to red or soft maple that we could confidently assign to red maple. Though the records are sparse, red maples seemed to show a preference for coming in to transitioning stands below paper birch and basswood.

Regeneration Strategy
Red maple's regenerative strategies on MHn35 sites is based entirely upon its performance in modern forests. It seems that it is most likely to fill ***large-gaps***. The releve sampling of MHN35 stands older than about 40 years, shows that red maple is very capable of developing a seedling bank. It has excellent success as regenerants and seedlings beneath a canopy **(R-2)**. There seems, though to be a bottleneck recruiting seedlings to heights over 2m as its sapling and tree rankings are only good. This behavior is typical of species that require larger gaps for recruitment. In the FIA data **(FIA-1)**, red maple is present most often as poles beneath trees (situation 23). This too, is a property of trees that we normally consider large-gap strategists. Though infrequent, the few red maple bearing trees appeared as regeneration well after the stand-initiating disturbance. It is likely that red maple had some success regenerating in the shade of initial cohort paper birch and aspen. This idea is confirmed by red maple having fairly high presence as seedlings in pole stands and as seedlings in tree stands (situations 12 and 13) at FIA plots **(FIA-1)**. Our general interpretation is that red maple can establish seedlings under the shade of proximal or remote

canopies, but that recruitment to tree-sized individuals doesn’t often happen until a fairly large gap forms over the advance regeneration.

Historic Change in Abundance

Today red maple is more abundant in MHn35 forests than it was historically. The FIA sampling suggests that it is substantially more abundant in young MHn35 forests at 9% relative abundance compared to just trace amounts historically **(PLS/FIA-1)**. Red maple now has 4% relative abundance in mature stands compared to trace amounts historically. The high presence of red maple as a tree in modern stands **(R-1)** and fairly high presence as regeneration **(R-2)** would also suggest that it has had significant success in modern, unmanaged MHn35 forests. The comparison of modern to historic abundance of red maple is exaggerated, because in this case it was more likely that surveyor references to “maple” were most often, but not entirely, to sugar maple on MHn35 sites. Red and sugar maples taken together, still show substantial increase from historic times. We believe that in the past, red maple was an important tree in MHn35 forests, and that both red maple and sugar maple have benefited from the lack of surface fires in modern times.

White Pine

- ***good habitat suitability rating***
- ***late-successional***
- ***open regeneration strategist***
- ***regeneration window at 0-40 years***

Suitability
MHn35 sites provide ***good habitat*** for white pine trees. The ***suitability rating*** of 3.1 for white pine is the result of rather high mean cover when present (24%, **R-1**). Presence of white pine is low (7%) probably because of historic exploitation and the general lack of seed trees on the modern landscape. The ranking is eighth among trees common on MHn35 sites, but the fact that its cover-when-present exceeds its presence would suggest that it would move up in the ranking if its seed source were restored. The role of white pine in northern mesic hardwood communities is highly variable, ranging from unsuitable to good. The poorer MHn35 and MHn44 communities offer the good habitat for white pine, and they provide the best opportunities for growing white pine as a crop tree (see Suitability Tables).

Young Growth-stage: 0-55 years
Historically, white pine was nearly absent from young MHn35 stands **(PLS-1, PLS-2)**. Young white pines represented just 1% of the trees at survey corners described as burned, which is quite surprising given its abilities in fire-dependent forests **(PLS-3)**. White pines represented just 4% of the trees the corners affected by stand-regenerating wind. Small-diameter white pine regeneration coming in among larger trees was most often observed in the post-disturbance window **(PLS-5)**. Usually, they were coming in among slightly larger quaking aspen. Our interpretation is that white pine had limited ability to compete with young quaking aspen and paper birch under open conditions on disturbed MHn35 sites.

Transition: 55-95 years
As stands transitioned to mature conditions white pine increased slightly in abundance as trees **(PLS-1)**. This is the modest beginning of a steady trend of increasing white pine abundance throughout the course of stand maturation **(PLS-2)**. Small-diameter, white pine regeneration coming in among larger trees was not detected in the transition. When white pine was the smaller tree at survey corners, it was coming in under paper birch and aspen. We interpret this as limited success at establishment and recruitment of seed-origin white pines under a partial canopy of initial-cohort trees.

Mature Growth-stage: 95-205 years
In the mature growth-stage white pine increases significantly in relative abundance **(PLS-1, PLS-2)**. This is quite surprising, given the modest amounts of regeneration in the young growth-stage and lack of obvious regeneration after age-class 50 **(PLS-5)**. Most of the white pines in the mature growth-stage were the largest tree at the survey corner, with very few instances of it being the smaller-diameter tree. This too, suggests that there was little establishment and recruitment of white pine in mature MHn35 forests. Our interpretation is that there was no significant establishment of white pine under the developing canopy and subcanopy of shade-tolerant hardwoods like sugar maple and basswood. White pine's poor-to-fair performance in the understory of modern forests is consistent with this idea **(R-2)**. Apparently, white pines in mature MHn35 forests dated to the young growth-stage and they increased in relative abundance because of their longevity and superior survival compared to other MHn35 trees.

Second Transition and Very Old Growth-stage: 205-295 years and older
Very few bearing trees contribute to our concept of second transition and very old MHn35 forests. Both stages are the consequence of white pine having some success when MHn35 forests are left without large disturbances. The relative abundance of white pine in the very old growth-stage (31%) is the highest among MHn35 trees **(PLS-1)**. We believe that this result is entirely due to the fact that white pine was the only tree capable of attaining the large diameters necessary for us to

model a survey corner as older than 205 years. The fact though, is that the relative abundance of white pine continued to rise throughout the mature growth-stage where several different species of trees were used to estimate stand age. Though the sampling is sparse in the second transition and very old growth-stage, the species' trends in abundance seem to be a continuation of the pattern established in the earlier growth stages. For that reason, we believe that there were substantially more white pine trees in older MHn35 forests than younger ones, and that white pine must be considered a ***late-successional*** species.

Regeneration Strategy

White pine's primary regenerative strategy on MHn35 sites is to occupy new growing space when MHn35 forests were disturbed by fire or windthrow. It is most successful at this in the ***open***, competing with quaking aspen and paper birch. In the historic PLS data this interpretation is supported by the fact that white pine regeneration was limited to the post-disturbance window **(PLS-5)**. That the regeneration window lasts until age 40, allows for the idea that young aspen and perhaps paper birch could have served as a cover crop for young white pines, improving the survival of seedlings established immediately following disturbance. Alternatively, young white pines may have been successful at establishing themselves beneath the emerging aspen canopy. In the FIA data, the high percentage of seedlings in pole stands (situation 12) would be consistent with either of these ideas **(FIA-1)**. White pine's poor-to-fair performance under a remote canopy of trees **(R-2)**, would indicate that establishment was more likely in open conditions.

Historic Change in Abundance

Today, white pine is essentially absent from the average MHn35 site **(PLS/FIA-1)**. Its abundance in releves, in particular its high cover when present (24%), suggests that it is recovering mostly in unmanaged situations. Though an infrequent visitor to MHn35 sites, fire might have helped establishment of white pine on these sites historically. Fire suppression then might be used to explain the lack of white pine in the average stand and FIA samples, but this idea doesn't explain the modest gains of white pine in stands sampled by releves. More likely, logging has directly eliminated some MHn35 white pine by removal, and logging has created young forests that are different from those created by fire or windthrow from the perspective of a white pine. Most obvious is the immediate presence and abundance of shade-tolerant sugar maple, red maple, basswood, and ironwood in young stands today.

(PLS-1) Historic Abundance of MHn35 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the MHn35 community by growth-stage. Growth-stages are periods of compositional stability during stand maturation. Arrows indicate periods of compositional change during which tree abundances increase or decrease substantially. Yellow, green, and purple shading groups trees with abundance peaks in the same growth-stage. Percents on the bottom row represent a snapshot of the balance of growth-stages across the landscape *ca.* 1846 and 1908 AD.

Dominant Trees	Forest Growth Stages in Years				
	0 - 55	55 - 95	95 - 205	205 - 295	> 295
	Young	T1	Mature	T2	Very Old
Paper Birch	38%	||	28%	||	12%
Quaking (Big-toothed) Aspen	20%	||	6%	|	4%
Red Oak	10%	|	5%	|	1%
Balsam Fir	5%	|	3%	|	1%
Basswood	6%	⌉	9%	|	6%
White Spruce[1]	1%	⌉⌉	13%	|	-
Sugar Maple	11%	⌉	14%	⌉⌉	29%
White Pine	1%	⌉	7%	⌉⌉	31%
Miscellaneous	14%		15%		16%
Percent of Community in Growth Stage in Presettlement Landscape	39%	51%	8%	1%	1%

1. Important historically, white spruce is no longer a significant component of MHn35 forests and is not covered in the accounts of potential crop species.

PLS-1

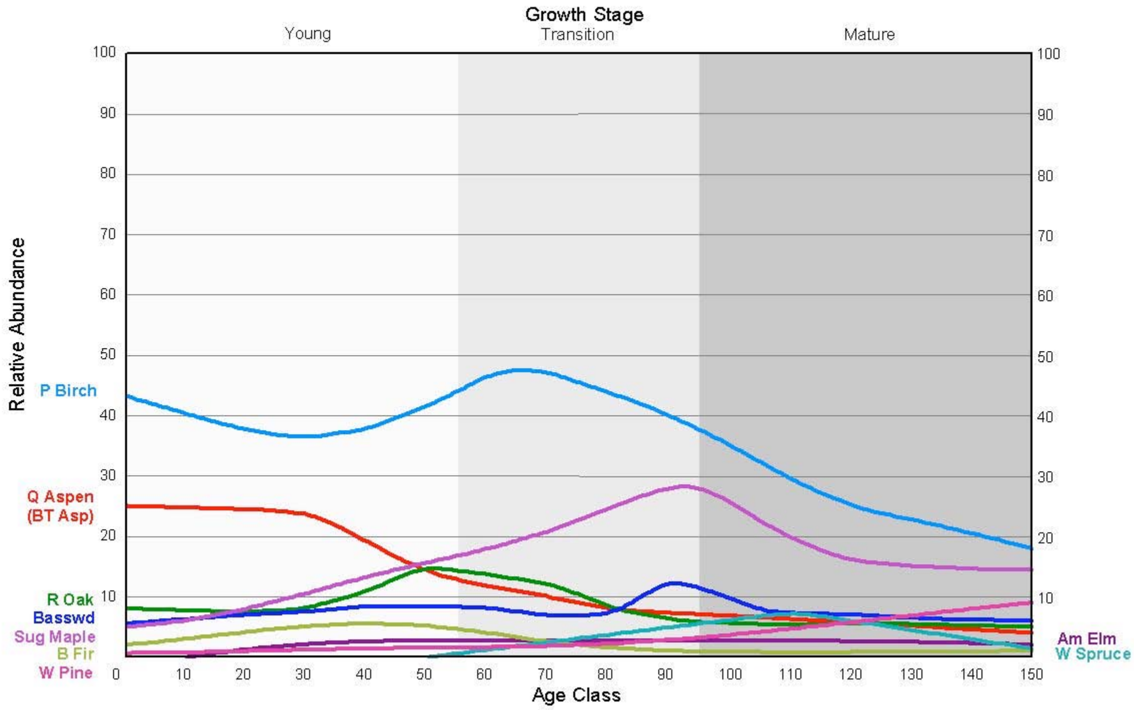
Trees included in Table PLS-1 are species with greater than 3% relative abundance in at least one growth-stage. Species that are now abundant in MHn35 forests, but were rare historically appear in Table **PLS/FIA-1**.

The PLS surveyors did not consistently distinguish the more prevalent quaking aspen from big-toothed aspen on FDn12 sites.

Public Land Survey linked text

(PLS-2) Abundance of trees throughout succession in MHn35

Caption: Graphed for the different species of MHn35 trees is their relative abundance (%) as PLS bearing trees by age class. The data were initially smoothed from adjacent classes and then by visually fitting lines to illustrate general trends.



1. Important historically, white spruce is no longer a significant component of MHn35 forests and is not covered in the accounts of potential crop species.

Documentation for Figure PLS-2

**Public Land Survey linked text

(PLS-3) Historic Abundance of MHn35 Trees Following Disturbance

Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent MHn35 forests. The columns represent our interpretation of disturbance at the survey corners. Trees in parentheses are minor species that occur in modern forests but couldn't be separated from more common trees because the surveyors did not distinguish them in their field notes. Shading associates trees that peak in the same disturbance category.

Tree	Burned		Windthrown		Maintenance		Mature	
Quaking (Big-toothed) aspen	47	22%	14	11%	55	13%	1607	13%
Ironwood	7	3%	0	0%	0	0%	158	1%
White pine	2	1%	5	4%	0	0%	392	3%
Northern red oak	38	18%	34	28%	213	50%	1040	8%
Bur oak	5	2%	3	2%	15	4%	193	2%
Paper birch	68	32%	44	36%	81	19%	5108	40%
Sugar maple	23	11%	10	8%	30	7%	2444	19%
Basswood	14	7%	8	7%	24	6%	972	8%
Balsam fir	9	4%	4	3%	4	1%	598	5%
Yellow birch	0	0%	0	0%	3	1%	179	1%
Red maple	0	0%	0	0%	1	0%	50	0%
Total (% of grand total, 13502)	213	2%	122	0.9%	426	3%	12741	94%

PLS-3

Table PLS-3 includes only trees ranked as having excellent, good, or fair suitability for MHn35 sites. Tree sums will not match the totals in the Natural Disturbance Regime text, because trees of poorer suitability were included in that analysis.

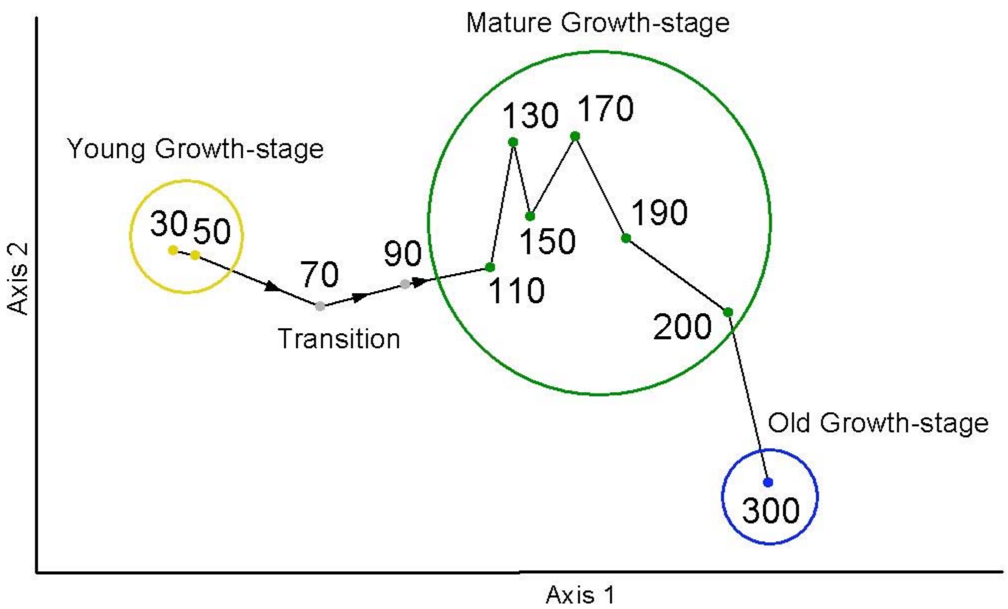
PLS survey corners were assigned to four disturbance categories:

1. The burned category is based upon explicit reference by the surveyors to burned timber or burned land.
2. The windthrown category is based upon explicit reference by the surveyors to windthrown timber.
3. The maintenance category includes corners with structural conditions requiring chronic disturbance (e.g. barrens, openings) OR forest where bearing tree distances match more closely the distances observed in the other structural categories. This category is our inference of partial canopy loss.
4. The mature category includes corners with no explicit or implicit reference to disturbance and has bearing trees at distances typical of fully stocked forest.

Public Land Survey linked text

(PLS-4) Ordination of Historic MHn35 Age-classes

The distance between age-class points reflect change in composition from one age-class to another. Long distances between age-classes indicate species mortality and replacement by other species. Short distances suggest little change in composition. Circled are growth-stages where we interpreted little change. Age-classes not in circles and with arrow connections represent episodes of significant compositional change.



PLS-4

For each PLS survey corner we estimated stand age based on the diameter of the largest tree. The corners were placed into 20-year age-classes for this analysis. We used coarse age-classes mostly because the surveyors tended to estimate diameters coarsely in even inches. For each age-class the relative abundance of each bearing tree type was calculated and used to characterize and ordinate the age-classes. Detrended Correspondence Analysis provided the smoothest ordinations, meaning that the age-classes tend to sequentially track across the ordination plot. There is always some subjectivity and uncertainty in placing the seams between growth-stages and transitions in these diagrams. When uncertain, we placed seams that match process transitions (self-thinning to density-independent mortality, ingress of shade-tolerants, etc.) described in more general models of stand dynamics in silvicultural literature.

(PLS-5) Historic Windows of Recruitment for MHn35 Trees

Windows of recruitment are stretches of contiguous age classes where Public Land Survey (PLS) trees recruit to acceptable bearing tree size (~4" dbh) in the presence of trees twice their diameter. We interpret this as their establishment in response to canopy conditions that change during the course of natural stand maturation. The table presents species' peak recruitment window and comparative success in post-disturbance, gap, and ingress windows.

Initial Cohort	Species	Peak years	P-D 0-50 years	G-1 50-110 years	I-1 110-190 years	G-2 >190 years
Minor	White Pine	0-40	Fair	--	--	--
Yes	Quaking Aspen[1]	0-30	Excellent	Poor to 60	--	--
Yes	Paper Birch	0-40	Excellent	Fair to 80	--	--
Yes	Basswood	0-40	Good	Poor to 70	--	--
Yes	Sugar Maple	0-50	Good	Fair to 90	--	--
Yes	Red Oak	0-50	Fair	Poor to 70	--	--
No	American Elm	20-40	Fair	Poor to 80	--	--
No	Red Maple	30	Poor	Poor to 70	--	--
No	Balsam Fir	30-50	Fair	--	--	--
No	Bur Oak	50	--	Poor to 70	--	--
No	Yellow Birch	60-80	--	Poor at 60-80	--	--
No	White Spruce[2]	150+	Poor after 30	Poor	Good	--

Recruitment windows from ordination PLS-4:

- **P-D:** post-disturbance filling of understocked areas, 10-50 years
- **G-1:** gap filling during decline of initial-cohort paper birch, quaking aspen, and red oak, 50-110 years
- **I-1:** ingress of seedlings under canopy of paper birch, sugar maple, and white spruce, with some basswood, white pine, quaking aspen, and red oak, 110-190 years
- **G-2:** gap filling during decline of paper birch, red oak, basswood, and white spruce, >190 years

-- : No trees were recorded as < half the diameter of the largest bearing tree. A property of PLS data is that diameter variation among bearing trees at the same corner decreases with increasing diameter. Corners estimated to be older than about 100 years only rarely have subordinate bearing trees and should not be taken to mean that small diameter trees didn't occur at all.

Shading: light yellow = trees with peak regeneration immediately after disturbance; **gold =** trees with peak regeneration later in the P-D window; **light green** = trees with peak regeneration in gaps formed during the decline of the initial cohort; **purple** = trees with peak regeneration by ingress under a mature canopy or by filling small gaps in old forests

1. Quaking aspen bearing trees couldn't be segregated from bigtooth aspen in the PLS notes for this community. The quaking aspen data probably include some bigtooth aspen, which we consider ecologically similar to quaking aspen.
2. White spruce was important historically but is no longer a significant component of MHn35 forests and is not covered in the accounts of potential crop species.

PLS-5

Recruitment windows were defined from ordinations of age-classes (PLS-4) that illustrate rates of compositional change. Windows are strings of contiguous age-classes where the rate of change is either consistently high or low.

Post-disturbance windows (P-D) are strings of contiguous age classes that start at age zero and during which we observe little compositional change.

For windows showing lots of compositional change (G-1, G-2) we assume gap-filling because canopy species are declining and being replaced by subordinate trees of another species.

Mid- and late-successional windows showing little compositional change (I-1, I-2) represent episodes of seral stability and subordinate trees are assumed to have established themselves by ingress under a canopy.

After setting post-disturbance, gap, and ingress windows from the ordinations, we calculated how often trees are were found in a subordinate condition during those episodes. A tree was considered subordinate when its diameter was less than half that of the largest tree at a PLS corner. Our assumption is that subordinate trees are younger than the larger diameter trees and that they could not have been established in response to a stand-regenerating disturbance.

Initial-cohort trees that rarely show diameter subordination are true pioneers that regenerate almost entirely in response to stand conditions after catastrophic fire, wind, or flooding.

Initial-cohort trees that show diameter subordination are presumed to have some regenerative ability under stand conditions not associated with the stand-initiating disturbance. For initial-cohort species in forest classes, such windows represent and a shift in regenerative strategy, e.g. from post-disturbance sprouting to seeding into understocked areas. For initial-cohort woodland species, such windows represent a persistent strategy in naturally long windows of recruitment where trees are replacing brush or grass.

For species not in the initial cohort, the windows define the timing of a tree's ability to ingress beneath a canopy or to fill gaps created when canopy species senesce. Ingress or gap-filling windows can end or continue indefinitely depending upon species' reaction to stand maturation processes that result in smaller gaps, deepening shade, increasingly organic seedbeds, and increased likelihood of infection by diseases or pests.

(R-1) Suitability ratings of trees on MHn35 sites

This table presents an index of suitability for trees in MHn35 forests. The index is based upon releve samples from modern forests. Trees that occur often (high percent presence) and in abundance (high mean percent cover when present) have high suitability indices. Suitability ratings indicate our interpretation of likely success of natural regeneration and growth to crop tree status with little silvicultural manipulation.

Dominant canopy trees of MHn35			
Tree	**Percent Presence as Tree**	**Mean Percent Cover When Present**	**Suitability Index***
Sugar maple (Acer saccharum)	**81**	**32**	**5.0**
Basswood (Tilia americana)	**65**	**15**	**4.8**
Northern red oak (Quercus rubra)	**49**	**20**	**4.7**
Paper birch (Betula papyrifera)	**61**	**13**	**4.6**
Quaking aspen (Populus tremuloides)	**31**	**20**	**4.4**
Red maple (Acer rubrum)	**31**	**12**	**4.1**
Big-toothed aspen (Populus grandidentata)	**13**	**19**	**3.7**
White pine (Pinus strobus)	**7**	**24**	**3.1**
Bur oak (Quercus macrocarpa)	**11**	**10**	**2.5**
Yellow birch (Betula alleghaniensis)	**10**	**9**	**2.2**
Balsam fir (Abies balsamea)	**8**	**8**	**2.0**

*Suitability ratings: **excellent**, **good**, **fair**

R-1

Suitability ratings indicate our interpretation of likely success of natural regeneration and growth to crop tree status with little silvicultural manipulation. Statewide suitability tables are available at: link to Tree Tables Field Version.pdf.

What we know of the behavior of trees and their suitability for sites is based upon a classification[1] of thousands of vegetation (releve) plots in Minnesota's native forests. The classification is purely empirical, based upon the occurrence and abundance of all vascular plants in these plots. For the purpose of land management, we have identified 52 basic forest Classes that are not only vegetationally different, but also have interpretable differences in parent material, landform, soil texture, soil moisture regime, and hydrology. The premise of this approach is that the NPC classification has captured the "realized" niche[2] of our trees and provides a field tool for recognizing the physical and competitive environment of forest sites.

The releve plots come from stands of trees older than 40 years through old-growth. The majority of sampled stands are 60 to 80 years old, and most plots were collected over the past 10 years. This means that we are most often observing tree success that reflects regeneration conditions *ca.* 1930-1960 and survival conditions since that time. We are assuming that most of the site conditions important to trees are the same now as then, or at least within their range of natural variability[3]. Thus, predictions of suitability from this table should always be considered in light of modern conditions that depart from past reference conditions.

A second consideration is that our sample plots were of natural forests. Here natural means that the vegetation is mostly composed of native plants and that enduring effects of human activity are not obvious. Most stands sampled have been logged and many grazed. We are assuming that current stand composition includes most of the plants and other trees with which a tree has coexisted in the past. The effect of these plants on the tree species under consideration may be mutualistic or competitive. Also, the effect of these plants on individual trees can change as the tree undergoes physiological changes as it matures. Altering the effects of these plants to benefit certain trees at the appropriate times during their maturation is the essence of silviculture. Because we sampled natural stands with little evidence of manipulation, high ratings imply little need for silvicultural intervention or tending. Conversely, trees with low ratings for certain NPCs will require intensive silvicultural effort.

For this analysis we created a very simple index to estimate suitability. This index is the product of percent presence and percent cover when present. For example, there are 256 sample plots of Northern Mesic Hardwood Forest (MHn35). Basswood trees over ten meters tall (~33 feet) occur in 164 of these plots, thus its percent presence as a tree is (164/256)*100= 64.1%. The mean cover of basswood trees on those 164 plots is 15.0%. Thus, its index is 64.1*15.0=962.

To communicate our estimates of suitability, we ranked the indices of plants that often occur (>5% presence) in a community and divided that ranking into 5 equal parts to create five suitability classes: excellent, good, fair, poor, and not suitable. Continuing the example above, 113 plants were ranked for MHn35 and basswood had the 8th highest ranking, placing it in the excellent class along with 22 other plants.

To estimate relative suitability, we simply expressed the rank order of a tree's index among all of the trees that occur in that community. In the above example, sugar maple was the only tree with a higher index than basswood, thus basswood's rank is 2.

1. Minnesota Department of Natural Resources (2003). Field Guide to the Native Plant Communities of Minnesota: the Laurentian Mixed forest Province. Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. MNDNR St. Paul, MN.

2. Oliver, C.D. and B. C. Larson. 1996. Forest Stand Dynamics, update edition. John Wiley & Sons, Inc.

3. Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179-1188.

4. Forest Inventory & Analysis Plots 1977, 1990, 2002. North Central Research Station, 1992 Folwell Ave, St. Paul, MN 55108

(R-2) Natural Regeneration and Recruitment of Trees in Mature MHn35 Stands

This table presents an index of regeneration for MHn35 trees in four height strata: regenerants, seedlings, saplings and trees. The index is based upon releve samples of modern, mature forests. Index ratings express our interpretation of how successful tree species are in each stratum compared to other trees that one commonly finds in MHn35 communities. Changes in the index values from one stratum to another can be used to estimate regenerative bottlenecks, whether establishment (R-index) or recruitment (SE-, SA-, or T-indices).

Natural regeneration indices for germinants, seedlings, saplings, and trees common in the canopy of Northern Mesic Hardwood Forest – MHn35					
Trees in understory	**% presence R, SE, SA**	**R-index**	**SE-index**	**SA-index**	**T-index**
Sugar maple (Acer saccharum)	96	5.0	5.0	5.0	5.0
Ironwood (Ostrya virginiana)	83	4.8	4.8	4.8	3.0
Northern red oak (Quercus rubra)	80	4.2	4.0	3.3	4.3
Basswood (Tilia americana)	80	4.5	4.3	4.5	4.5
Red maple (Acer rubrum)	64	4.3	4.2	3.8	3.8
Balsam fir (Abies balsamea)	51	3.7	3.5	2.5	2.3
Quaking aspen (Populus tremuloides)	47	3.7	3.3	2.7	4.0
Paper birch (Betula papyrifera)	39	1.7	1.3	3.2	4.5
Bur oak (Quercus macrocarpa)	17	2.2	1.7	2.3	2.8
Big-toothed aspen (Populus grandidentata)	11	1.8	1.5	1.8	3.8
White pine (Pinus strobus)	10	2.7	2.3	1.5	3.3
Yellow birch (Betula alleghaniensis)	10	1.3	1.3	2.5	3.0

Index ratings: **Excellent**, **Good**, **Fair**, **Poor**, N/A

% presence: the percent of 322 MHn35 sample plots with that species present under 10m (33 feet) tall (R, SE, SA layers)
R-index: index of representation as true seedling or under 10cm (4 inches) tall
SE-index: index of representation as seedlings over 10cm and under 2m (0.3-6.6 feet) tall
SA-index: index of representation as saplings 2-10m (6.6-33 feet) tall
T-index: index of representation as a tree >10m (33 feet) tall
All indexes: equally weight (1) presence, (2) mean cover when present, and (3) mean number of reported strata, the frequency distributions of which are segmented equally by area into 5 classes.

R-2
The releve method of sampling forest vegetation describes explicitly how trees occur at different heights. We modified raw releve samples by interpreting the occurrence of trees in four standard height strata: germinants 0-10cm tall, seedlings 10cm-2m tall, saplings 2-10m tall, and trees taller than 10m.

The releve samples all come from forests with an established canopy, so this dataset documents the presence and cover of trees in strata that have formed during the process of stand maturation, i.e. understory development.

We created an index to measure roughly the regenerative success of a tree in each stratum. The index is the product of (1) percent presence in that stratum for all releves classified as that community, (2) mean percent cover of that species when present in a stratum, and (3) the mean number of different strata reported in the releves when that species is present.

The indices for all trees were ranked, the range was then scaled to range between zero and 5. The index ratings of excellent, good, fair, poor, and not-applicable are the 5 whole number segments of the index.

(FIA-1) Structural Situations of Trees in Mature MHn35 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples MHn35 forests. The purpose of the table is to provide a general impression of how often a species is seen certain regenerative situations: canopy of a regenerating forest (situations 11, 22), in the subcanopy (situations 12, 23), or in the seedling bank below a remote canopy (situation 13). The situation of trees in older stands at tree height (33) provide no insight about regeneration. Species are ordered by the sum of their percents in 12 and 13 situations, which generally ranks them as would shade-tolerance ratings. The total number of trees counted for each species is presented to provide a sense of reliability.

Species	Tree Count	Structural Situations					
		11	22	12	23	13	33
Yellow birch	24	-	4%	-	12%	4%	79%
Paper birch	549	4%	19%	4%	36%	3%	34%
Bur oak	100	2%	12%	2%	18%	5%	61%
Northern red oak	534	3%	8%	4%	15%	4%	67%
Quaking aspen	491	21%	13%	12%	9%	8%	37%
Basswood	840	3%	6%	8%	21%	12%	50%
White pine	11	-	18%	27%	-	-	54%
Big-toothed aspen	31	19%	-	16%	3%	13%	48%
Red maple	340	8%	19%	14%	23%	17%	19%
Sugar maple	1178	2%	16%	13%	19%	28%	2%
Balsam fir	102	8%	15%	28%	30%	17%	3%

Canopy Situations
- 11 = Sapling in a young forest where saplings (dbh <4”) are the largest trees
- 22 = Poles in a young forest where poles (4”<dbh<10”) are the largest trees
- 33 = Trees in a mature stand where trees (>10”dbh) form the canopy

Subcanopy Situations
- 12 = Saplings under poles
- 23 = Poles under trees

Understory Situation (remote canopy)
- 13 = Saplings under trees

FIA linked text

(PLS/FIA-1) Abundance of MHn35 trees in Pre-settlement and Modern Times by Historic Growth-stage

Table values are relative abundance (%) of trees at Public Land Survey corners and FIA subplots modeled to represent the MHn35 community and estimated to fall within the young, mature, and old growth-stages. Arrows indicate increase or decrease between historic growth-stages only and for the more common trees. Green shading and text was used for the historic PLS data and blue was used for the FIA data. Percents on the bottom row allow comparison of the balance of growth-stages across the pre-settlement landscape (*ca.* 1846-1908 AD) and the modern landscape (*ca.* 1990 AD).

Dominant Trees	Forest Growth Stages in Years									
	0 - 55		55 - 95		95 - 205		205 - 295		> 295	
	Young		T1		Mature		T2		Old[2]	
Paper Birch	38%	9%	||		28%	7%	||		12%	0%
Quaking Aspen	20%	22%	||		6%	4%	|		4%	0%
Red Oak	10%	6%	|		5%	11%	|		1%	0%
Balsam Fir	5%	4%	|		3%	2%	|		1%	0%
Basswood	6%	9%	⌉		9%	19%	|		6%	0%
White Spruce[1]	1%	1%	⌉⌉		13%	0%	|		-	0%
Sugar Maple	11%	24%	⌉		14%	32%	⌉⌉		29%	50%?
White Pine	1%	0%	⌉		7%	1%	⌉⌉		31%	0%
American Elm	3%	2%	|		2%	3%	|		0%	0%
Red Maple	--	9%			--	4%			0%	0%
Ironwood	1%	7%			1%	7%			1%	0%
Bur Oak	1%	1%			2%	3%			0%	50%?
Miscellaneous	3%	6%			10%	7%			15%	0%
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	39%	29%	51%	52%	8%	18%	1%	1%	1%	0%

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 5,887 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 3,470 FIA subplots that were modeled to be MHn35 sites.

1. Important historically, white spruce is no longer a significant component of MHn35 forests and is not covered in the accounts of potential crop species.

2. Just 4 FIA trees contributed to the old growth-stage and the results are unreliable.

Public Land Survey linked text
FIA linked text

Silviculture Systems for MHn35: No arrow - least favorable, ⇧ Favorable, ⇧⇧ Very Favorable

	Silviculture Systems	Clearcut	Patch Cutting	Group Seedtree	Dispersed Seedtree	Uniform Shelterwood	Group Shelterwood	Irregular Shelterwood	Group Selection	Strip Selection	Single Tree Selection
	Regeneration Strategy										
Northern Red oak	Large-gap (Small-gap)		⇧	⇧	⇧	⇧⇧	⇧⇧	⇧⇧	⇧⇧	⇧	⇧
Red Maple	Large-gap (Small-gap)		⇧	⇧	⇧	⇧⇧	⇧	⇧⇧	⇧⇧	⇧	⇧
Sugar Maple	Small-gap							⇧	⇧⇧	⇧⇧	⇧⇧
Basswood	Small-gap (Large-gap)		⇧	⇧		⇧	⇧⇧	⇧⇧	⇧⇧	⇧⇧	⇧
Quaking Aspen	Open (Large-gap)	⇧⇧	⇧⇧	⇧⇧	⇧⇧		⇧				
Paper Birch	Large-gap (Open)	⇧⇧	⇧⇧	⇧⇧	⇧⇧	⇧⇧	⇧⇧	⇧			
Bur Oak	Large-gap		⇧	⇧⇧	⇧	⇧	⇧⇧	⇧			
Big-toothed Aspen	Open (Large-gap)	⇧⇧	⇧⇧	⇧⇧	⇧⇧		⇧				
White Pine	Large-gap		⇧	⇧	⇧	⇧⇧	⇧⇧	⇧⇧	⇧⇧	⇧	
Yellow Birch											
Balsam Fir											

Forest Health Considerations

Red and Sugar Maple

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Maple borer	Pole-sized and larger	Volume loss/ degrade
Stem cracks	"	Volume loss
Stem decay	"	Volume loss

WATCHOUTS!

• When thinning, discriminate against maples with maple borer galleries and/ or stems with cracks.

• When planning intermediate or final harvests, write sale specifications to penalize wounding of residual trees and supervise sale closely to prevent wounding. The major entry points for decay fungi include mechanical wounds to the bole, dead branches, and dead or broken tops.

Basswood

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Stem decay	Pole-sized and larger	Volume loss

WATCHOUTS!

• When planning intermediate or final harvests, write sale specifications to penalize wounding of residual trees and supervise sale closely to prevent wounding. The major entry points for decay fungi include mechanical wounds to the bole, dead branches, and dead or broken tops.

Northern Red Oak

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Oak wilt	"	"
Defoliators (FTC, GM, etc.)	"	Predispose to mortality
Deer/ rodent browse	Seedlings and saplings	Mortality, topkill
Two-lined chestnut borer	Pole-sized and larger	Mortality
Stem decay	"	Volume loss

WATCHOUTS!

• Protect seedlings and saplings from browse damage.

• Avoid thinning oaks during a drought and/or defoliation event. It is best to wait one growing season after the drought or defoliation is over to thin or harvest.

• Maintain optimal stocking in high-value stands to avoid mortality losses due to two-lined chestnut borers and Armillaria root disease.

• If oak wilt is known to occur within one mile of the stand, prevent overland spread of oak wilt by not allowing thinning, harvesting, trail building, pruning or other activities that wound oaks from April 1st to July 15th.

• If oak wilt is present in this stand, several precautionary steps must be made prior to thinning or harvest. Please contact your Regional Forest Health Specialist for assistance.

• When planning intermediate or final harvests, write sale specifications to penalize wounding of residual trees and supervise sale closely to prevent wounding. The major entry points for decay fungi include mechanical wounds to the bole, dead branches, and dead or broken tops.

Paper Birch

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Forest tent caterpillar	“	Defoliation
Bronze birch borer	Pole-sized and larger	Mortality
Inonotus canker & decay	“	Volume loss
Stem decay	“	Volume loss

WATCHOUTS!

• Declining birch stands should be harvested within two years to prevent loss of the sites to invading brush species.

•Avoid thinning in birch during a drought and/or defoliation event. It is best to wait one growing season after the drought or defoliation is over to thin or harvest.

• Maintain optimal stocking in high-value stands to avoid mortality losses due to bronze birch borers and Armillaria root disease.

• Attempt to maintain a closed canopy in existing stands because soil temperature increases of as little as 4E can cause root death leading to tree mortality.

• Promote dense regeneration to help shade the soil and prevent excessive temperatures.

• The presence of fruiting bodies of Inonotus canker (sterile conk of birch) indicates serious decay. The presence of two fruiting bodies on a single stem usually indicates that the stem is cull due to decay.

• When planning intermediate or final harvests, write sale specifications to penalize wounding of residual trees and supervise sale closely to prevent wounding. The major entry points for decay fungi include mechanical wounds to the bole, dead branches, and dead or broken tops.

Quaking Aspen

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Forest tent caterpillar	“	Defoliation
Hypoxylon canker	Pole-sized and larger	Topkill and mortality
Saperda borer	“	Mortality
Stem decay = white trunk rot	“	Volume loss

WATCHOUTS!

• In over-mature stands, prolonged defoliation will accelerate mortality.

• Harvest during the winter to ensure adequate regeneration.

• To estimate the basal area of a stand affected by white trunk rot, determine the basal area with conks then multiply that number by 1.9.

• Trees along stand edges, openings and trees in low-density stands are more likely to be infected with Hypoxylon canker and infested with Saperda borer.

• When planning intermediate or final harvests, write sale specifications to penalize wounding of residual trees and supervise sale closely to prevent wounding. The major entry points for decay fungi include mechanical wounds to the bole, dead branches, and dead or broken tops.

Big-toothed Aspen

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Forest tent caterpillar	“	Defoliation
Hypoxylon canker	Pole-sized and larger	Topkill and mortality
Saperda borer	“	Mortality
Stem decay = white trunk rot	“	Volume loss

WATCHOUTS!

• In over-mature stands, prolonged defoliation will accelerate mortality.

• Harvest during the winter to ensure adequate regeneration.

• Trees along stand edges, openings and trees in low-density stands are more likely to be infected with Hypoxylon canker and infested with Saperda borer. Note that bigtooth aspen is five times more resistant to Hypoxylon canker than trembling aspen.

• When planning intermediate or final harvests, write sale specifications to penalize wounding of residual trees and supervise sale closely to prevent wounding. The major entry points for decay fungi include mechanical wounds to the bole, dead branches, and dead or broken tops.

White Pine

Agent	Growth stage	Concern/ Effect
White pine blister rust	All stages	Mortality
Armillaria root disease	"	"
Deer/ rodent browse	Seedlings and saplings	Mortality, topkill
White pine weevil	"	Topkill, forking
White pine blister rust	Pole-sized and larger	Topkill, branch death
Stem decay	"	Volume loss

WATCHOUTS!

• Protect seedlings and saplings from browse damage.

• Always regenerate/ plant white pine under an overstory to avoid losses from white pine blister rust and white pine weevil.

• For cross-pollination, parent trees must be within 200 feet of each other.

• In the northern half of the state, natural and artificial regeneration are very likely to develop blister rust cankers and die if they are not pathologically pruned from the time of establishment until there is 9 feet of clear stem.

• Pole-sized and larger trees will survive for a long time with multiple blister rust infections in their crowns. Do not be too hasty in harvesting them because they are good seed sources.

• When planning intermediate or final harvests, write sale specifications to penalize wounding of residual trees and supervise sale closely to prevent wounding. The major entry points for decay fungi include mechanical wounds to the bole, dead branches, and dead or broken tops.

MHn35 - Acceptable Operating Season to Minimize Compaction and Rutting

Primary Soils | **Secondary Soils** | **Not Applicable**

Surface Texture [1]	Drainage [2]	Depth to Semipermeable Layer (inches) [3]	Landscape Position [4]	Acceptable Operating Season [5] Compaction	Acceptable Operating Season [5] Rutting
Coarse (sand & loamy sand)	Excessive & Somewhat Excessive	Not Applicable	Top, Mid-slope, Level	All	All
			Toe & Depression	Wf > Sd > Fd > W > S	All but spring break up
	Well	> 12	Any	Wf > Sd > Fd > W > S	All but spring break up
		< 12	Top, Mid-slope, Level	Wf > Sd > Fd > W > S	Wf > Sd > Fd > W > S > F
			Toe & Depression	Wf > Sd > Fd > W	Wf > Sd > Fd > W > S > F
	Moderately Well	> 12	Top, Mid-slope, Level	Wf > Sd > Fd > W > S	Wf > Sd > Fd > W > S > F
			Toe & Depression	Wf > Sd > Fd > W	Wf > Sd > Fd > W > S
		< 12	Any	Wf > W	Wf > Sd > Fd
	Somewhat Poor	Any	Any	Wf > W	Wf > Sd > Fd
	Poor	Any	Any	Wf	Wf > Sd
Medium (sandy clay, silty clay, fine sandy loam, clay loam, sandy clay loam, silty clay loam, loam, v fine sandy loam, & silt loam)	Excessive & Somewhat Excessive	Not Applicable	Top, Mid-slope, Level	Wf > Sd > Fd > W > S	Wf > Sd > Fd > W > S > F
			Toe & Depression	Wf > Sd > Fd > W	Wf > Sd > Fd > W > S > F
	Well	> 24	Any	Wf > Sd > Fd > W	Wf > Sd > Fd > W > S > F
		< 24	Top, Mid-slope, Level	Wf > Sd > Fd > W	Wf > Sd > Fd > W > S > F
			Toe & Depression	Wf > W	Wf > Sd > Fd > W > S
	Moderately Well	> 24	Top, Mid-slope, Level	Wf > W	Wf > Sd > Fd > W > S
			Toe & Depression	Wf	Wf > Sd > Fd > W
		< 24	Any	Wf	Wf > Sd > Fd > W
	Somewhat Poor	Any	Any	Wf	Wf > Sd > Fd
	Poor	Any	Any	Wf	Wf > Sd
Fine (clay & silt)	Excessive & Somewhat Excessive	Not Applicable	Top, Mid-slope, Level	Wf > Sd > Fd > W > S	Wf > Sd > Fd > W > S > F
			Toe & Depression	Wf > Sd > Fd > W	Wf > Sd > Fd > W > S > F
	Well	> 24	Top, Mid-slope, Level	Wf > Sd > Fd > W	Wf > Sd > Fd > W > S > F
			Toe & Depression	Wf > W	Wf > Sd > Fd > W > S
		< 24	Any	Wf > W	Wf > Sd > Fd > W
	Moderately Well	> 24	Top, Mid-slope, Level	Wf > W	Wf > Sd > Fd > W
			Toe & Depression	Wf	Wf > Sd > Fd
		< 24	Any	Wf	Wf > Sd > Fd
	Somewhat Poor	Any	Any	Wf	Wf > Sd > Fd
	Poor	Any	Any	Wf	Wf > Sd
Peat & Muck	Poor	Any	Any	Wf	Wf
	Very Poor	Any	Any	Wf	Wf

Plants below indicate wetter inclusions in MHn35 that are more susceptible to compaction and rutting. They are listed in descending order of presence.

Lady fern (*Athyrium filix-femina*)
Mountain maple (*Acer spicatum*)
Black ash (U) (*Fraxinus nigra*)
American elm (U) (*Ulmus americana*)
Nodding trillium (*Trillium cernuum*)
Yellow birch (C) (*Betula alleghaniensis*)
Yellow birch (U) (*Betula alleghaniensis*)
Side-flowering aster (*Aster lateriflorus*)
Common Oak fern (*Gymnocarpium dryopteris*)
Palmate sweet coltsfoot (*Petasities frigidus*)

(U) – understory **(C) - canopy** **Footnotes on back**

Foot Notes

1. Surface Texture and Landform Affinity – the dominant texture within 12 inches of the mineral soil surface, listed in ascending order of moisture holding capacity; landforms are listed when distinct associations with soil texture are evident

2. Soil Drainage
   Excessive – water moves very rapidly through the soil; saturation does not occur during the growing season except for brief periods

   Somewhat Excessive – water moves rapidly through the soil; saturation occurs greater than 60 inches below the surface but within the rooting zone periodically during the growing season

   Well – water moves readily through the soil; saturation occurs 40 inches or more below the surface during the growing season

   Moderately Well – water saturation occurs within 20 to 40 inches of the surface periodically during the growing season

   Somewhat Poor – water saturation occurs within 20 inches of the surface periodically during the growing season

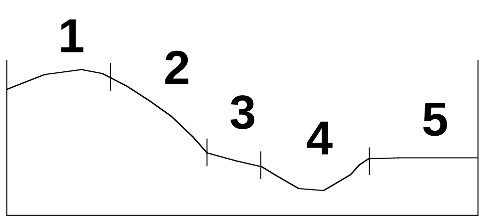
   Poor – water saturation occurs within 10 inches of the surface for most of the growing season

   Very Poor – water saturation occurs at the surface or within 10 inches of the surface for most of the growing season

3. Semipermeable Layer – any feature that retards downward water movement such as: hardpan, clay layer, bedrock, contrasting soil texture.

4. Landscape Position

   1 – Top
   2 – mid-slope
   3 – toe
   4 – depression
   5 – level



5. Acceptable Operating Season
   Listed in order of decreasing preference and increasing risk for compaction based on duration of dry conditions

   Wf Winter with frozen soil - ground is frozen enough to support heavy equipment

   Sd Dry Summer – extended periods without rain during the growing season when surface soil is dry; delay operations for brief periods after rain

   Fd Dry Fall - extended periods without rain in the fall when surface soil is dry; cease operations when significant rain occurs (1”-2” cumulative)

   W Winter – the ground is snow covered or partially frozen

   S Summer – the growing season; delay operations for a brief period after rain

   F Fall – after leaves fall until the ground is snow covered or frozen

   Sp Spring – after the frost goes out until herbaceous forest plants have reached full size (commonly two to three weeks after tree canopy leaf-out); delay operations during break-up

The presence of an intact duff layer and slash on the surface together with use of low ground pressure equipment may help reduce the risk, severity, and extent of compaction.

Public Land Survey linked text

Natural stand dynamics and disturbance were evaluated using data from the original Public Land Survey (PLS) of Minnesota. The investigation begins by selecting from all section corners in the state, the set that possibly occurred on sites of the Native Plant Community (NPC) under consideration. Selected corners had to: occur on landforms (LandType Associations, LTAs) where we have modern samples of the community, have the full set of 4 bearing trees, have bearing trees typical of the community (>30% frequency in our sample set), and NOT have trees atypical of the community (<5% frequency). It is possible for an individual corner to contribute to the analysis of more than one community but more often, corners were eliminated from all analyses because of atypical species combinations. This commonly happens in Minnesota because of the incredible amount forest acreage in riparian edge between terrestrial forest and wetlands or lakes. Also, the glaciated terrain of Minnesota results in many sharp contacts between sorted materials and till, creating System-level changes in forest communities and further elimination of survey corners from the analysis.

From this set of corners for a NPC we assigned a stand age to the corner based upon the diameter and modeled age of the largest/oldest tree present. Presumably, the age of the oldest tree at a corner is a minimum estimate of how long the stand has avoided a catastrophic disturbance. Corners were then placed into 10-year age classes with the exception of the initial 15-year class that matches the 15-year disturbance “recognition window” used to calculate the rotations of fire and windthrow. Experience shows that when applied to PLS data, a 15-year window for catastrophic disturbance and a 5-year window for maintenance disturbance results in a reasonable match with far more reliable, but local studies of disturbance using techniques of fire-scar analysis, stand origin mapping, and the analysis of charcoal in varved lake sediments. Small diameter (<4”) bearing trees were “forced” into age class 0-15 when they occurred at corners described as burned or windthrown. Otherwise, corners were assigned to age classes when the diameter of the oldest tree would lead us to believe that it was between 15-25 years old, 25-35 years old, etc. The fundamental property of an age-class in our analyses is the relative abundance of the component species.

By ordinating age-classes (PLS Figure 4) we can discover natural periods of stability known as growth-stages, as well as periods of instability known as transitions. Summarizing data by growth-stages and transitions allows us to present a general model of stand dynamics and succession for the NPC Classes. Such models can be presented in tabular (PLS Table 1) or graphic form (PLS Figure 2).

It is important to remember that ***this is a landscape composite of tree abundance by age. One should not expect a particular stand of a certain age to match exactly the composition suggested by the table or graphic.*** A universal result in habitats with several tree species is that the younger age classes are highly variable and often monotypic, presumably the result of variation in the intensity and type of regenerating disturbance. As stands age, they become more mixed, often to the point where the relative abundance of trees in the landscape age-classes match what one sees in a stand.

Modern Forest linked text

Releve Samples

Releves are large (400m2) sample plots that we used to sample ecologically intact and generally mature forests in Minnesota. This means that most of the stands sampled were regenerated from events that pre-date the Forest Inventory Analysis (FIA, below) and post-date the Public Land Survey (PLS) data (above). The releves are the basis for the Native Plant Community (NPC) classification itself. For silvicultural interpretation releve data were used to develop two important concepts.

First, releves were used as a means of determining just how well adapted the different species of trees are to living with other plants in the NPC and to important soil characteristics like drainage and water-holding capacity. Based upon how often we find certain trees in a community and how abundant it is when we do find it, we created an Index of Suitability for trees (Table R-1). The most important use of this table is understanding the variability of ecological potential that trees have among the different NPCs. This table was used to define the set of trees to be addressed in this document.

Secondly, releves were used to interpret of the ability of trees to regenerate and then recruit germinants to taller strata beneath a canopy. Indices of seedling (SE-index) and sapling (SA-index) success allows the tree species to be ranked by their success in recruiting germinants to seedling (<2m) or sapling (2-10m) status whereby one extreme is characterized by species capable of ingress and growth under a full canopy, versus species that seem to need the full sunlight and soil conditions that follow major disturbance and opening of the canopy (Table R-2).

For more information on the releve method and NPC Classification:

Link to the releve handbook.
Link to the NPC Field Guides

FIA Samples

Forest Inventory Analysis (FIA) data were used to confirm aspects of species behavior interpreted from the Public Land Survey analyses and also to provide a general feeling for just how much Minnesota's forests have changed after a century of management. Because comparison to PLS analyses was a major goal, FIA subplots were treated as point samples similar to PLS survey corners. For abundance comparisons (e.g. Table PLS/FIA-1) , FIA subplots were "reduced" to approximate PLS section corners by selecting randomly a tree > 4" dbh in each quadrant around the point. For structural comparisons (e.g. Table FIA-1) all trees at FIA subplots were used. In both cases PLS data and FIA data were pooled and analyzed by the same computer programs so that comparisons could be made.

Similar rules were used for deciding which FIA plots and subplots and PLS survey corners could belong to a dataset for each forested NPC Class. The FIA analysis began by selecting from all FIA subplots the set that possibly occurred on sites of the Native Plant Community (NPC) under consideration. Selected subplots had to: occur on landforms (LandType Associations, LTAs) where we have modern samples of the community, have trees typical of the community (>30% frequency in our sample set), and NOT have trees atypical of the community (<5% frequency). If FIA plots, with either 10 or 4 subplots, were heterogeneous with regard to subplot community assignments, only the subplots with the dominant NPC were used. If no NPC occurred on more than 3 of 10 or 2 of 4 subplots (i.e. 30% or more), then entire FIA plot was eliminated from the analysis. It is possible for an individual subplot to contribute to the analysis of more than one community but more often, subplots were eliminated from all analyses because they didn't meet plot homogeneity rules. This commonly happens in Minnesota because of the incredible amount forest acreage in riparian edge between terrestrial forest and wetlands or lakes. Also, the glaciated terrain of Minnesota results in many sharp contacts between sorted materials and till, creating System-level changes in forest communities and further elimination of FIA plots from the analysis.

From this set of subplots for a NPC we assigned a stand age to the corner based upon the diameter and modeled age of the largest/oldest tree present. Presumably, the age of the oldest tree at a subplot is a minimum estimate of how long the stand has avoided a catastrophic disturbance. Corners were then placed into the same age-classes as were the PLS survey corners: 0-15, 15-25, 25-35, etc. The fundamental property of an age-class in our analyses is the relative abundance of the component species. From this dataset it is possible to perform analyses parallel to those done for PLS bearing trees. Table PLS/FIA-1 is such a comparison of tree abundance by growth-stage.

The FIA data were too sparse to construct a table similar to PLS-5 so that we could guess at regeneration windows based upon diameter subordination. The main reason for this is that quaking aspen dominates a lot of modern forests and populations of most conifers have crashed in historic times. For example, FIA plots retrieve very little data for trees like jack pine and tamarack, even on sites that were historically dominated by these trees. By simplifying the FIA data into just three broad diameter classes, we were able to perform a similar analysis (Table FIA-1) that can confirm or cause us to re-examine our interpretations of table PLS-5.

A great advantage of FIA data is the re-sampling of plots from one inventory cycle to another. The fate of individual trees on these plots can thus be tracked and we can examine how stand conditions might have influenced their survival or mortality. By the time FIA plots were winnowed by homogeniety rules and assigned to 52 forested plant communities, the total number of tracked trees is rather low ... especially for minor species of some communities and for the conifers that have declined significantly in the past century. Because of the low sample numbers, we present no summary tables for observed mortality or survivorship. However, these are real observations that were not dismissed in writing the individual species accounts in this document. These observations are very useful in confirming or dismissing our inferences about mortality and replacement in the PLS data.

For more information on the FIA methods and inventory in Minnesota:

Link to the USFS website, north central